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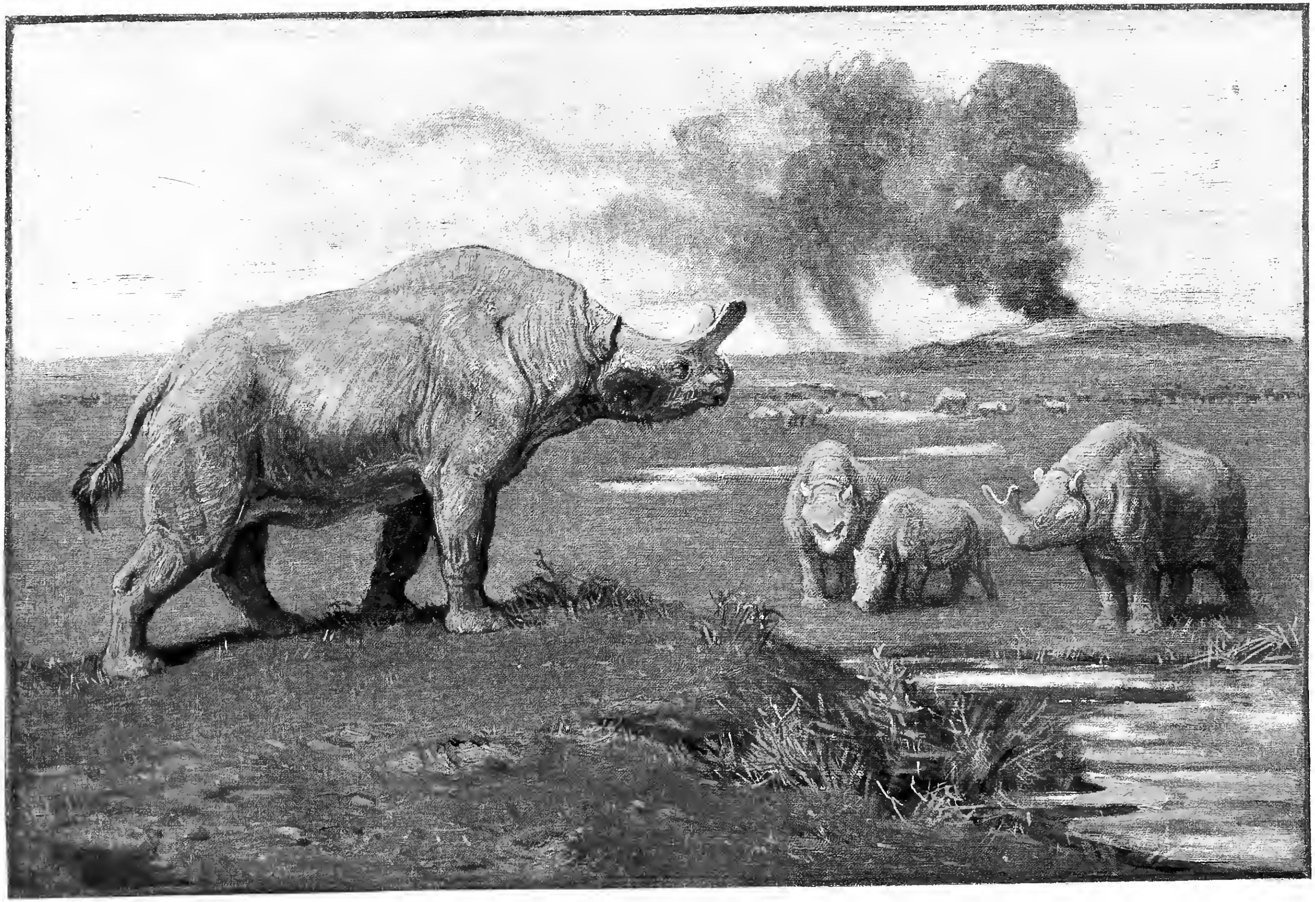

HERD OF BRONTOTHERIUM PLATYCERAS, THE FLAT-HORNED BRONTOTHERES, ON THE OLIGOCENE FLOOD PLAINS OF THE PRESENT BLACK HILLS REGION OF SOUTH DAKOTA

After restorations by Erwin Christman and Charles R. Knight,
under direction of Henry Fairfield Osborn, 1924

DEPARTMENT OF THE INTERIOR
Ray Lyman Wilbur, Secretary

U. S. GEOLOGICAL SURVEY
George Otis Smith, Director

Monograph 55

THE TITANOTHERES OF ANCIENT WYOMING, DAKOTA, AND NEBRASKA

BY

HENRY FAIRFIELD OSBORN

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CONTENTS

Page

LETTER OF TRANSMITTAL ---- XIX

PREFACE ---- XXI

  Vertebrate paleontology in the national surveys ---- XXI

  Preparation of the present monograph ---- XXI

  Work by the author, 1878–1919 ---- XXII

  Research and collaboration ---- XXII

  Cooperation of museums ---- XXIII

  Work on text and illustrations ---- XXIII

  Summary of geologic and anatomic principles ---- XXIII

CHAPTER I. Introduction to mammalian paleontology ---- 1

  Section 1. Exploration and research made in the preparation of this monograph ---- 1

  Section 2. Preliminary survey of the monograph and the conclusions presented ---- 2

    Range of the titanotheres in geologic time ---- 2

    Hayden's subdivisions of the Eocene and the Oligocene ---- 5

    Discovery of the titanotheres of the plains ---- 6

    Discovery of the mountain-basin environment of the titanotheres ---- 6

    Discovery and delimitation of periods of sedimentation and of life zones ---- 8

    Principle of local and continental adaptive radiation ---- 10

    Comparison of the four life phases of Europe and North America during Eocene and early Oligocene time ---- 12

    Old and new systems of classification ---- 13

      Old terminology retained ---- 13

      Linnaean methods of defining species, genera, and phyla of titanotheres ---- 14

      Recognition of many lines of descent; polyphyly the key to interpretation of the family ---- 14

      Relation of the phylogenetic classification to the Linnaean classification ---- 15

      Comparison between zoologic and paleontologic species ---- 18

      Proportions of the skull in bears and in titanotheres ---- 19

      Features distinguishing phyla of titanotheres ---- 19

      Mutations of Waagen ---- 19

      Zoologic and paleontologic nomenclature ---- 20

      Summary of differences between old and new systems ---- 22

    Study of the evolution of single characters ---- 22

    Phylogeny of the nine typical families of the Perissodactyla ---- 23

    Wide geographic distribution of the Perissodactyla ---- 24

    Causes of evolution ---- 27

    Adaptive evolution and overevolution of the form of skull, tooth, and foot ---- 27

    Phyletic divergence in the evolution of new proportions in horses and in titanotheres ---- 28

    Evolution of the limbs and feet of the titanotheres ---- 33

    Origin of new characters as distinguished from changes in proportion ---- 34

    Velocity in the development of characters and in phylogeny ---- 39

    Summary of the evolution of the titanotheres ---- 41

  Section 3. Bibliography of literature cited or consulted in the preparation of Chapter I ---- 42

CHAPTER II. Environment of the titanotheres and effect of adaptive radiation on their variation ---- 43

  Section 1. Geology and geography ---- 43

    Correlation of early Tertiary events in the Rocky Mountain region with those in western Europe ---- 43

    Late Cretaceous and early Tertiary climates ---- 45

    Eocene geography of western North America and its relation to faunal migrations ---- 47

      Geographic divisions and their bearing on migration ---- 47

      Character of the mountain-basin, plateau, and plains regions ---- 51

      Eocene topography in the Rocky Mountain region ---- 51

      Contrast in physiographic conditions east and west of the Rocky Mountain Front Range ---- 53

      Lateral and main river systems in the mountain-basin region ---- 54

  Section 2. Eocene and lower Oligocene formations and faunal zones ---- 56

    First faunal phase (basal Eocene) ---- 56

      Seventeen life zones ---- 56

      Basal Eocene time in Montana and New Mexico ---- 60

      Summary of faunal events of basal Eocene time ---- 60

      Basal Eocene faunal zones ---- 63

        Zones 1 and 2: *Ectoconus* and *Polymastodon* zones (Puerco fauna; part of Thanetian of Europe) ---- 63

        Zones 3 and 4: *Deltatherium* and *Pantolambda* zones (Torrejon and Fort Union faunas; part of Thanetian of Europe) ---- 64

CHAPTER II—Continued.

Section 2—Continued.

Page
Second faunal phase (lower Eocene) 64
Transitional basal Eocene faunas 64
Zone 5: *Phenacodus-Nothodectes-Coryphodon* zone (base of Wasatch formation of Big Horn Basin, first Wasatch life zone, Big Horn A; Cernaysian of Europe) 64
Early Eocene time 65
Lower Eocene faunal zones 68
Zone 6: *Eohippus-Coryphodon* zone (second Wasatch life zone, Big Horn B; lower Sparnacian of Europe) 68
Zone 7: *Systemodon-Coryphodon-Eohippus* zone (third Wasatch life zone, Big Horn C; upper Sparnacian of Europe) 69
Zone 8: *Heptodon-Coryphodon-Eohippus* zone (fourth Wasatch life zone, Big Horn D and Wind River A; lower Ypresian of Europe) 69
Zone 9: *Lambdotherium-Eotitanops-Coryphodon* zone (fifth Wasatch life zone, Big Horn E, Wind River B, and Huerfano A; upper Ypresian of Europe) 69
Transitional lower to middle Eocene deposits 74
Huerfano formation of Colorado 74
Wind River beds and their fauna 74
Third faunal phase (middle and upper Eocene) 77
Correlation of American zones with European stages 77
Typical Bridger formation 78
Zone 10: *Eometarhinus-Trogosus-Palaeosyops fontinalis* zone (Bridger A and Huerfano B; lower Lutetian of Europe) 82
Zone 11: *Palaeosyops paludosus-Orohippus* zone (Bridger B; upper Lutetian of Europe) 84
Zone 12: *Uintatherium-Manteoceras-Mesatirhinus* zone (Bridger C and D, Washakie A, and Uinta A; part of Bartonian of Europe) 84
Washakie Basin, Wyo 85
Stratigraphy of the basin 85
Zones 13 and 14: *Metarhinus* zone and *Eobasileus-Dolichorhinus* zone (Uinta B 1 and Washakie B 1; Uinta B 2) 89
Uinta Basin, Utah 91
Physiographic, climatic, and volcanic conditions in the Uinta Basin during middle (?) and later Eocene time 91
Geologic horizons in the Uinta Basin 91
Uinta B 1 (*Metarhinus* zone=zone 13) 94
Uinta B 2 (*Eobasileus-Dolichorhinus* zone=zone 14) 94
Zone 15: *Diplacodon-Protitanotherium-Epihippus* zone (Uinta C 1; Ludian of Europe) 94
Summary of faunas of Uinta B and C 97
Adaptive radiation of the titanotheres in the Uinta Basin 97
Genera and species represented 97
Adaptive radiation of phyla 98
Fauna unrepresented 99
Zone 16: Theoretic Uinta C 2 99
Composite Eocene and lower Oligocene section at Beaver Divide 99
Fourth faunal phase (lower Oligocene) 101
Lower Oligocene mammals 101
Correlation of European and American forms 101
Zone 17: *Titanotherium-Mesohippus* zone (Chadron A, B, and C; Sannoisian of Europe) 101
Oligocene flood-plain sedimentation in the western Great Plains region 103
Conditions of deposition 103
South Dakota in *Titanotherium* time 106
Rapid fluviatile sedimentation in the Cypress Hills, Saskatchewan 109
Slow sedimentation in South Dakota 109
Geographic distribution of the Chadron formation 110
Comparison of basins in western United States with the flood plain of the Nile 112
Faunal divisions in the Chadron formation 113
Three faunistic levels determined 113
Stratigraphic distribution of species of Oligocene titanotheres 113
Hatcher's collections, 1886–1888 115
Sources of error in determining stratigraphic levels 116
Mammalian life of the lower Oligocene *Titanotherium* zone 117
Notes on the habitat of the fauna of the clay and sandstone as a whole 120
Section 3. Adaptive radiation, primary and secondary, through change of environment a cause of diversification of the titanotheres 121
Habitat of the ungulates 121
Polyphyly among hoofed mammals 121
The titanotheres and other extinct forms 121
The existing African antelopes 124

CHAPTER II—Continued. Page
Section 3—Continued.
Continental adaptive radiation of the African antelopes 125
Adaptive radiation in the feeding habits of antelopes 126
Causes of variation and polyphyly among quadrupeds 127
Habits of the rhinoceroses parallel to those of the Oligocene titanotheres 128
Habits of the existing tapirs parallel to those of the Eocene titanotheres 128
Vertical geographic range of quadrupeds 129
Vertical geographic range of the titanotheres 129
Ten chief habitat zones of mammals 129
Conclusions as to habitats of the titanotheres 132
Section 4. Bibliography for Chapter II 132
CHAPTER III. Discovery of the titanotheres and original descriptions of the types 141
Section 1. History of discovery 141
The Oligocene titanotheres 141
The pioneer period: Prout, Owen, Evans, Leidy (1846–1873) 141
Taxonomic arrangement and comparison 144
Work of Marsh and Cope (1870–1887) 144
Summary of Marsh's contributions 145
Summary of Cope's contributions 146
Reinterpretation and phylogenetic study (Osborn, 1887–1919) 146
Study of certain features 146
Geologic levels and succession of types (Hatcher, 1886–1893) 147
First European notice (Toula, 1892) 148
Distinctions of sex (Osborn and Wortman, 1895) 148
Monophyletic interpretation (Osborn, 1896) 148
Polyphyletic interpretation (Osborn, 1902–1919) 148
Recent discoveries by Lull, Lambe, and others 149
The Eocene titanotheres 149
Pioneer discoveries 149
Work in the Bridger, Washakie, and Uinta Basins by Leidy, Marsh, Cope, Scott, Osborn, and others (1870–1889) 149
Discovery in Hungary 150
Princeton and Cope-Wortman expeditions 150
First systematic and evolutionary revision (Earle, 1889–1891) 150
American Museum and other explorations of the Eocene basins (1891–1895) 151
Investigations and explorations made in preparation for the present monograph (1900–1919) 152
Section 2. Original descriptions of types of Eocene titanotheres 153
Five rules for determining the names of titanotheres 153
The genera and species of Eocene titanotheres 155
Descriptions of the species 157
Section 3. Original descriptions of types of Oligocene titanotheres 201
List of genera and species 201
Prout's descriptions of a fragmentary lower jaw, the first titanothere made known to science 202
Pomel's genus *Menodus*, based on Prout's description and figure 204
Early notices by Leidy and others, 1850–1870 205
Species described by Marsh and Cope in 1873–1876 209
First notice of Canadian titanotheres by Cope, 1886 219
Species described by Scott and Osborn in 1887 219
Species described by Marsh in 1887 222
Canadian species described by Cope in 1889 225
Last five species described by Marsh, 1890–91 227
Last species described by Cope, 1891 229
First European Oligocene species, described by Toula, 1892 230
Species described by Osborn in 1896 and 1902 231
Species described by Lull in 1905 234
Species described by Osborn in 1908 235
Canadian species described by Lambe in 1908 235
Second European Oligocene species, described by Kiernik, 1913 240
Final Oligocene species described by Osborn in 1916–1919 241
CHAPTER IV. Systematic classification of the titanotheres 243
Section 1. Phyletic versus Linnaean system of classification 243
Neo-Linnaean systematic divisions (zoologic) and evolutionary phyla (paleontologic) 243
Superfamily names proposed by Osborn (1898) and Hay (1902) 243
Family names proposed or adopted by Marsh (1873), Flower (1875), Cope (1879-1889), and Osborn (1889) 243
Subfamily names and phyla proposed by Steinmann and Döderlein (1890), Earle (1892), and Riggs (1912) 245
Division of the Oligocene titanotheres into four contemporary phyla, Osborn (1902) 245
Reclassification of the Eocene and Oligocene subfamilies by Osborn (1914) 246
Species wrongly referred to the titanotheres 246
Section 2. Classification of the titanotheres adopted in this monograph 247

Page
Chapter V. Evolution of the skull and teeth of Eocene titanotheres 251
Section 1. General principles of the study of the characters of the skull and teeth 251
Proportion characters and tendencies of evolution distinguished by analysis and synthesis 251
Distinctions between proportion characters and new rectigradation characters 251
Steps in transformation of characters 252
Proportion and flexures of the skull 254
Summary as to craniometry 255
Changing proportions of the cranium and face 256
Cyptocephaly, or faciocranial flexure 256
Dolichocephaly, brachycephaly, and correlation 257
Zygomatic cephalic indices in the titanotheres and other perissodactyls 259
Relative values of indices 259
Indices of skulls of Eocene and Oligocene titanotheres 259
Differences in terminology of skull proportions in titanotheres and in man 260
Contrast in features of brachycephalic and dolichocephalic skulls and teeth 261
List of abbreviations used in illustrations of skulls 262
Terminology of the upper molar teeth 263
Section 2. Introduction to the anatomy of the skull and teeth of the Eocene titanotheres 264
Types of skull of Eocene titanotheres 264
Feeding habits of broad-headed and long-headed titanotheres 264
Origin and structure of the "horns" in titanotheres 266
Proportion and rectigradation in the grinding teeth of Eocene titanotheres 267
Mechanism of the titanothere grinding teeth 269
Molarization of the premolars 270
Correlation of dimensions of upper and lower teeth 272
Geologic succession and geographic distribution of the Eocene titanotheres 272
Section 3. The lower Eocene titanotheres 273
Ancestral titanotheres of the *Lambdotherium* zone of Wyoming at the end of lower Eocene time 273
Physiographic environment at the end of lower Eocene time 273
Contrasts and resemblances between *Lambdotherium* and *Eotitanops* 276
Explorations and discoveries 279
Systematic descriptions of the lower Eocene titanotheres 279
Section 4. The middle and upper Eocene titanotheres 297
Phyla distinguished 297
Species of Palaeosyopinae and Dolichorhininae from the upper Huerfano (*Trogosus* zone) 297
Systematic descriptions of the middle and upper Eocene titanotheres 297
The palaeosyopine group 297
The *Manteoceras-Dolichorhinus* group 357
Successors to the *Manteoceras-Dolichorhinus* group 434
Chapter VI. Evolution of the skull and dentition of Oligocene titanotheres 443
Section 1. Review of the environment, geologic succession, and geographic distribution of the lower Oligocene titanotheres 443
Section 2. Introduction to the anatomy of the skull and the dentition of the Oligocene titanotheres 444
Horns: transformation, elongation 444
Nasals: expansion, abbreviation 446
Zygomatic arches: expansion, buccal plates 446
Occipital pillars: auditory meatus 446
Sexual characters common to all phyla 448
Teeth: distinctive features and evolution 448
Development of the skull and dentition 451
Summary of the replacement of the teeth in Oligocene titanotheres 455
Stages of wear of the adult grinding teeth 456
Age and other characters common to both sexes of titanotheres of all stratigraphic levels 456
Section 3. Division of the Oligocene titanotheres into groups and subfamilies 457
Characters of the skull and teeth of the menodontine and brontotheriine groups 457
Characters and relations of the subfamilies 465
Possible Eocene ancestors of the brontotheriine group 468
Section 4. Oligocene genera accepted as valid in this monograph 469
Section 5. The menodontine group 470
Subfamily Brontopinae, including the phyla *Menteoceras*, *Protitanotherium*, *Telcodus*, *Brontops*, and *Diploclonus* 470
Stratigraphic level and distinguishing features 470
Subfamily characters of *Teleodus*, *Brontops*, and *Diploclonus* 471
Comparisons and contrasts 471
Conspectus of characters of the subfamily 477
Conspectus of characters of species 478
Measurements of the *Brontops* series 479
Systematic descriptions of genera and species in the *Brontops-Diploclonus* phylum 481

Chapter VI—Continued.

Section 5—Continued.

Page

- Subfamily Menodontinae 505
    - Systematic descriptions of genera and species in the *Allops* phylum 506
    - The *Menodus* monophylum 518
    - Systematic descriptions of genera and species in the *Menodus* phylum 522
- Section 6. The brontotheriine group 538
    - Group characters 538
    - Sexual characters 540
    - Subfamily Megaceropinae 540
        - Systematic descriptions of genera and species in the *Megacerops* phylum 541
    - Subfamily Brontotheriinae 550
        - Systematic descriptions of genera and species in the *Brontotherium* phylum 555
- Chapter VII. Evolution of the skeleton of Eocene and Oligocene titanotheres 583
    - Section 1. Methods by which the titanothere skeleton has been studied 583
        - Principles of the evolution of the limbs of hoofed animals 583
        - Size and proportions of Eocene titanotheres 584
        - Divergence and convergence in the skeleton of polyphyletic series 586
            - Diverse adaptive types of limb structure 586
            - Terms used in describing the skeleton of the titanotheres 588
    - Section 2. The postcranial skeleton of lower Eocene titanotheres 590
        - Subfamily Lambdotheriinae 590
        - Subfamily Eotitanopinae 591
    - Section 3. Middle Eocene groups and phyla 598
        - Double parallelism in the palaeosyopine and *Manteoceras-Dolichorhinus* groups 598
        - Family and subfamily characters of skeletal parts in middle Eocene titanotheres 599
        - Systematic descriptions of middle Eocene titanotheres 612
            - Subfamily Palaeosyopinae 612
            - Subfamily Manteoceratinae 631
    - Section 4. The postcranial skeleton of upper Eocene titanotheres 636
        - Subfamily Dolichorhininae 636
        - Subfamilies Telmatheriinae, Brontopinae?, and Diplacodontinae 652
    - Section 5. The postcranial skeleton of Oligocene titanotheres 662
        - Subfamily Brontopinae 664
        - Subfamily Menodontinae 678
        - Subfamily Brontotheriinae 689
    - Bibliography for Chapters III–VII 698

ILLUSTRATIONS

Plate | Page

Frontispiece. Herd of Brontotherium platyceras.

I. *A*, Eruption of the crater of Taal, Philippine Islands; *B*, Flooded area 140

II. *A*, Ojo Alamo, San Juan County, N. Mex., looking north; *B*, Base of Puerco formation resting on eroded surface of Ojo Alamo sandstone 140

III. *A*, Upper Torrejon beds, Torrejon Arroyo, Sandoval County, N. Mex.; *B*, Exposures of Puerco formation east of Ojo Alamo, N. Mex 140

IV. *A*, *Eohippus-Coryphodon* zone, Little Sand Coulee, Clark Fork Basin, Wyo.; *B*, *Phenacodus-Nothodectes-Coryphodon* zone, Clark Fork Basin, north of Ralston, Wyo 140

V. *A*, Typical "Lysite" locality, at Cottonwood Draw, north of Lost Cabin, Wyo.; *B*, Typical "Gray Bull" locality, south of Otto, Big Horn Basin, Wyo 140

VI. *A*, A typical Huerfano locality, west of Gardner, Huerfano Basin, Colo.; *B*, A typical "Lost Cabin" locality, east of Lost Cabin, Wind River Basin, Wyo 140

VII. *A*, Henrys Fork Table, looking northward across Henrys Fork, Bridger Basin, Wyo.; *B*, Grizzly Buttes, south of Mountain View, Uinta County, Wyo 140

VIII. *A*, Northwest point of Haystack Mountain, head of Bitter Creek, Sweetwater County, Wyo.; *B*, View southeastward from Laclede station, Sweetwater County, Wyo 140

IX. *A*, Columnar sandstones, Uinta A, White River Canyon, Uinta Basin, Utah; *B*, Panoramic view, White River Canyon below Wagonhound Bend, Uinta Basin, Utah 140

X. *A*, Northern boundary of Coyote Basin, Uinta Basin, Utah; *B*, Divide between White River Canyon and Coyote Basin, Uinta Basin, Utah 140

XI. *A*, North face of Beaver Divide, Wind River Basin, Wyo.; *B*, Exposures at Wagonbed Spring, Beaver Divide, Fremont County, Wyo 140

XII. *A*, Contact between *Titanotherium* zone and Pierre shale, Cedar Creek, Big Badlands, S. Dak.; *B*, Badlands south of White River, Utah, showing the *Diplacodon* zone 140

XIII. "Mauvaises Terres" or Big Badlands of South Dakota 140

XIV. Exposures at Quinn Draw, Big Badlands, S. Dak., showing summit of Chadron formation 140

XV. *A*, South end of Sheep Mountain, near head of Corral Draw, Big Badlands, S. Dak.; *B*, Cedar Creek, Big Badlands, S. Dak., showing the *Oreodon* zone overlying the *Titanotherium* zone 140

Plate | Page
XVI. The region of the horn swelling in *Palaeosyops, Manteoceras*, and *Telmatherium* 266
XVII. The region of the horn swelling in *Manteoceras, Mesatirhinus*, and *Dolichorhinus* 267
XVIII. Restorations of the heads of four genera of Oligocene titanotheres 582
XIX. Incisors and canines of *Brontotherium* and *Teleodus* 582
XX. Upper and lower canines of Oligocene titanotheres 582
XXI. Left upper premolars of Oligocene titanotheres 582
XXII. Third left lower molar in *Menodus* and *Brontotherium* 582
XXIII. Juvenile jaw referred by Marsh to *Brontops* 582
XXIV. Juvenile jaws and teeth of Oligocene titanotheres 582
XXV. Superior deciduous and permanent grinding teeth of *Menodus giganteus* 582
XXVI. Type skeleton of *Eotitanops princeps* 702
XXVII. Mounted skeleton of *Palaeosyops leidyi* 702
XXVIII. Restoration of *Palaeosyops* of the Bridger Basin, Wyo 702
XXIX. Restoration of *Manteoceras* and *Dolichorhinus* of the Uinta Basin, Utah 702
XXX. Restoration of the skeleton of *Dolichorhinus longiceps* 702
XXXI. Manus and pes of *Dolichorhinus longiceps* 702
XXXII. Skeleton of *Dolichorhinus longiceps* 702
XXXIII. Mounted skeletons of *Brontops dispar* and *Brontops robustus* (type) 702
XXXIV. Mounted skeleton of *Brontops robustus* (type), oblique front and side views 702
XXXV. Mounted skeleton referred to *Brontops robustus?* 702
XXXVI. Vertebral column of *Brontop srobustus* 702
XXXVII. Manus and hind limb of *Diploclonus tyleri* 702
XXXVIII. Mounted skeleton of *Allops marshi* 702
XXXIX. Mounted skeleton of *Brontotherium hatcheri*, left side view 702
XL. Mounted skeleton of *Brontotherium hatcheri*, right side view 702
XLI. Mounted skeleton of *Brontotherium hatcheri*, front view 702
XLII. Mounted skeleton of *Brontotherium hatcheri*, back view 702

Figure
1. "Fragment of the inferior maxillary of the left side" of Prout's "gigantic *Palaeotherium*" 1
2. Type of *Palaeotherium? proutii* 1
3. Geologic ages and orogenic periods in North America 2
4. Successive and overlapping Oligocene and early Eocene formations of the Rocky Mountains 3
5. Map showing areas throughout the world in which remains of titanotheres have been found and areas in which titanotheres were probably in migration during Eocene and Oligocene time 4
6. The Meek and Hayden Tertiary section of 1862 5
7. Panoramic section of the Big Badlands of South Dakota, looking southeastward across Cheyenne and White Rivers to Porcupine Butte 6
8. Map showing the type locality of the *Titanotherium* zone on Bear Creek, S. Dak 7
9. Map showing cluster of typical lower, middle, and upper Eocene sedimentary basins in the Rocky Mountain region 8
10. Restorations of *Eotitanops borealis* and *Brontotherium platyceras* 10
11. Amblypoda: Skeletons and restorations of an ancestral and a specialized form 11
12. Diagram showing the gradual extinction of archaic mammals and their replacement by modernized mammals 14
13. *Phenacodus* and *Coryphodon* drawn to the same scale 15
14. Contrast between the Linnaean and phylogenetic systems of classification 16
15. The family tree of the titanotheres 17
16. Theoretic descent of existing members of the dog family from a common ancestor 19
17. Successive invasion of nine families of perissodactyls in North America and western Europe 23
18. Outlines of the body form of the perissodactyls, drawn to the same scale 25
19. The family tree of the Perissodactyla 26
20. Periods of expansion and extinction of the perissodactyls and contemporary forms 27
21. Phyletic divergence in the evolution of new proportions in horses and in titanotheres 29
22. Contours of the head and of parts of the mouth in browsing and grazing perissodactyls 30
23. Heads of lower Eocene and modern perissodactyls, showing changes of proportion and of the lip structure 31
24. Restorations of the heads of some of the principal types of titanotheres 32
25. Lower jaws of the first and the last of the titanotheres 33
26. Structure of the feet in extinct and living odd-toed ungulates 34
27. Restorations of nine species of titanotheres 35
28. Evolution of the skeleton of the titanotheres 36
29. Evolution of the skull and molar teeth in the titanotheres 37
30. Adaptive radiation in the evolution of the upper molar teeth in the perissodactyls 38
31. Three types of teeth of members of nine typical families of perissodactyls 39
32. The family tree of the perissodactyls, showing adaptive radiation of the nine families and thirty-five subfamilies 40
33. Outlines of the bodies of titanotheres at different stages of evolution 44
34. Map showing the known areas and the hypothetical areas of titanothere migration and habitat 45
35. General geologic sketch map of the Rocky Mountain region, showing existing topography and drainage areas and their relation to areas of Eocene and lower Oligocene sedimentation 46
36. Map of western North America showing supposed routes of migration of animals 49
37. Map showing the orogeny of the western mountain and plateau region 50

Figure Page
38. Geologic map of the Uinta Range, showing the Tertiary sediments of the Bridger Basin, Wyo., at the north, and of the Uinta Basin, Utah, at the south 52
39. Chronologic relations of formations in the mountain-basin region 54
40. Section of deposits near Barrel Springs, Washakie Basin, Wyo 55
41. Eocene and lower Oligocene mammalian life zones in eleven typical correlated areas in New Mexico, Colorado, Utah, Wyoming, South Dakota, and Montana 59
42. Section of Upper Cretaceous and basal Eocene (Fort Union) deposits in Sweet Grass County, Mont 61
43. Section of Eocene deposits in the San Juan Basin, N. Mex 62
44. Columnar section of Cretaceous and Eocene sediments exposed along Bear River, Wyo., showing the typical Wasatch group of Hayden 66
45. Generalized section through Upper Cretaceous and basal and lower Eocene deposits near Pumpkin Buttes, Powder River Valley, Wyo 68
46. Composite section of the Eocene deposits of the Big Horn and Clark Fork Basins, Wyo 70
47. A typical "Lost Cabin" locality, Alkali Creek, Wind River Basin, Wyo 71
48. Section through the Wind River formation (lower Eocene) near Lost Cabin, Wyo 72
49. Map showing cluster of lower, middle, and upper Eocene sedimentary basins in southwestern Wyoming and northern Utah, exhibiting parts of areas of the Wasatch, Wind River, Bridger, and Uinta formations 73
50. Sketch map of the region of the Huerfano and Cuchara formations in southern Colorado 74
51. Section of the Huerfano formation in southeastern Colorado 75
52. Section of exposures from lower Eocene to lower Oligocene at Green Cove, on Beaver Divide, Wind River Basin, Wyo 76
53. Section across Wind River Basin, Wyo., from Hudson to top of Beaver Divide 77
54. Map showing the Eocene sediments encircling the Uinta Mountains of southwestern Wyoming and northern Utah 78
55. Geologic section of the Bridger formation in the Bridger Basin, Wyo 80
56. Map of the Bridger Basin, Wyo., and section of the Bridger formation 82
57. Section of the lower part of the Bridger formation in the Bridger Basin, Wyo 83
58. Section of the upper part of the Bridger formation in the Bridger Basin, Wyo 86
59. Section of deposits near Barrel Springs, Washakie Basin, southern Wyoming 87
60. Section of the Washakie Basin, Wyo., from north to south 88
61. Sketch map of the Washakie Basin region, Wyo 88
62. Columnar section of Washakie Basin, Wyo., showing life zones 90
63. Section of the Uinta formation exposed in the north wall of White River Canyon, Utah 91
64. Section of the Uinta formation from Kennedy's Basin to White River Canyon, Utah 92
65. Section of the *Eobasileus-Dolichorhinus* and *Metarhinus* zones in the Uinta Basin, Utah 93
66. Badlands near mouth of White River, Uinta Basin, Utah 95
67. Section of deposits at Green Cove, Beaver Divide, Wyo 100
68. Section across the Wind River Basin, Wyo., from Hudson to top of Beaver Divide 101
69. Map showing exposures originally described as the "White River group" by Meek and Hayden 102
70. Facsimile of the Meek and Hayden Tertiary section of 1862 103
71. Map showing tributaries of Cheyenne River, S. Dak., and the type locality of the "*Titanotherium* beds" of Hayden 104
72. Type locality of the "*Titanotherium* beds" of Hayden, on Bear Creek, S. Dak 105
73. Panoramic section of the Big Badlands of South Dakota 106
74. Section of the Big Badlands of South Dakota, showing the chief faunal zones of the Oligocene (White River group) and the Miocene 107
75. Map showing principal exposures of the Chadron formation 108
76. Section showing the results of stratigraphic leveling in the Chadron formation (*Titanotherium* zone) in the badlands of White River, S. Dak 115
77. The family tree of the Perissodactyla 116
78. Geographic cross section showing the nature of the habitats of the larger existing ungulates and of the titanotheres as illustrating adaptive radiation 122
79. Original radiation of the unguligrade Herbivora, Carnivora, and Insectivora, with adaptations to environment 123
80. Adaptations in the structure of the skull and teeth of Herbivora to diverse habits of feeding 125
81. Convergent adaptations in the structure of the limbs and feet of ungulates 125
82. Adaptive radiation in the feeding habits of antelopes 126
83. Mauvaises Terres, Nebraska 142
84. "Vertical view of the posterior tooth belonging to the lower jaw of Mr. Prout's *Palaeotherium*" 143
85. Original figures of Prout's "gigantic *Palaeotherium*" 143
86. Osborn's first restoration of *Palaeosyops paludosus* Leidy 151
87. Four stages in the origin and evolution of the horns in titanotheres 152
88. Leidy's cotypes of *Palaeosyops paludosus* 157
89. Leidy's type (holotype) of *Palaeosyops mojor* 158
90. Leidy's type of *Palaeosyops humilis* 159
91. Leidy's cotypes of *Palaeosyops junius* 159
92. Marsh's type of *Palaeosyops laticeps* 160
93. Marsh's type of *Telmatherium validus* 161
94. Marsh's type of *Limnohyus robustus* 161
95. Cope's cotypes of *Palaeosyops vallidens* 162
96. Cope's cotypes of *Limnohyops laevidens* 163
97. Cope's type (holotype) of *Limnohyus fontinalis* 164

Figure Page
98. Cope's type (holotype) of *Palaeosyops diaconus* 165
99. Marsh's type of *Diplacodon elatus* 166
100. Type (holotype) lower jaw of *Brachydiastematherium transilvanicum* 167
101. Type (holotype) of *Leurocephalus cultridens* 168
102. Type (holotype) of *Palaeosyops borealis* 168
103. Type (holotype) of *Lambdotherium popoagicum* 169
104. Cope's type of *Lambdotherium brownianum* 170
105. Type (holotype) of *Palaeosyops hyognathus* 170
106. Type (holotype) of skull of *Palaeosyops megarhinus* 171
107. Earle's cotypes of *Paloeosyops minor* 172
108. Earle's type of *Palaeosyops longirostris* 173
109. Type (holotype) of *Telmatotherium diploconum* 173
110. Type (holotype) of *Telmatotherium cornutum* 174
111. Type (holotype) of *Sphenocoelus uintensis* 175
112. Type (holotype) of *Diplacodon emarginatus* 176
113. Cotypes of *Manteoceras manteoceras* (*Telmatotherium vallidens*) 179
114. Type (holotype) of *Lambdotherium primaevum* 180
115. Type (holotype) of *Limnohyops priscus* 180
116. Type (holotype) skull of *Limnohyops matthewi* 180
117. Type (holotype) skull of *Limnohyops monoconus* 180
118. Type (holotype) skull of *Palaeosyops leidyi* 181
119. Type (holotype) of *Palaeosyops grangeri* 181
120. Type (holotype) of *Palaeosyops copei* 182
121. Type (holotype) skull of *Manteoceras washakiensis* 182
122. Type (holotype) skull of *Mesatirhinus petersoni* 183
123. Type (holotype) skull of *Metarhinus fluviatilis* 183
124. Type (holotype) skull of *Metarhinus earlei* 183
125. Type (holotype) skull of *Dolichorhinus intermedius* 184
126. Type (holotype) skull of *Telmatherium ultimum* 184
127. Type (holotype) of *Telmatherium? altidens* 185
128. Type (holotype) of *Protitanotherium superbum* 185
129. Type (holotype) skull of *Telmatherium? incisivum* 186
130. Type (holotype) of *Telmatherium? incisivum* 187
131. Type (holotype) skull of *Manteoceras uintensis* 187
132. Type (holotype) of *Manteoceras uintensis* 187
133. Type (holotype) skull of *Dolichorhinus heterodon* 188
134. Type (holotype) of *Dolichorhinus heterodon* 188
135. Type (holotype) skull of *Dolichorhinus longiceps* 188
136. Type (holotype) of *Dolichorhinus longiceps* 189
137. Type (holotype) skull of *Mesatirhinus superior* 190
138. Type (holotype) skull of *Metarhinus riparius* 191
139. Type (holotype) skull of *Metarhinus cristatus* 191
140. Type (holotype) skull of *Dolichorhinus fluminalis* 192
141. Type (holotype) skull of *Rhadinorhinus abbotti* 193
142. Type (holotype) teeth of *Eotitanops gregoryi* 193
143. Lower jaws of *Lambdotherium* and *Eotitanops* 194
144. Type (holotype) of *Eotitanops princeps* 195
145. Type (holotype) of *Eotitanops major* 195
146. Type (holotype) of *Lambdotherium priscum* 195
147. Type (holotype) of *Lambdotherium progressum* 196
148. Type of *Diploceras osborni* 196
149. Type of *Diploceras osborni* 197
150. Type (holotype) skeleton of *Heterotitanops parvus* 198
151. Type (holotype) skull of *Heterotitanops parvus* 198
152. Type (holotype) of *Heterotitanops parvus* 198
153. Cotypes of *Telmatherium? birmanicum* 198
154. Type (holotype) of *Lambdotherium magnum* 199
155. Type (holotype) of *Eotitanops minimus* 199
156. Type (holotype) skull of *Eometarhinus huerfanensis* 200
157. "Vertical view of the posterior tooth belonging to the lower jaw of Mr. Prout's *Palaeotherium*" 203
158. Original figures of Prout's "gigantic *Palaeotherium*" 203
159. Type of *Menodus giganteus* 204
160. Owen's specimens of *Palaeotherium? proutii* 205
161. Type (holotype) of *Palaeotherium maximum* 206
162. Cotypes of *Rhinoceros americanus* 206
163. Cotypes of *Palaeotherium giganteum* 207
164. Type (holotype) of *Megacerops coloradensis* 208
165. Type (lectotype) of *Brontotherium gigas* 210

Figure Page

166. Type (lectotype) jaw of *Symborodon torvus* 211
167. Type (holotype) skull of *Megaceratops acer* 212
168. Type (holotype) skull of *Megaceratops heloceras* 213
169. Type (lectotype) skull of *Symborodon bucco* 214
170. Type skulls of *Symborodon altirostris, S. bucco,* and *Megaceratops acer* 215
171. Type (holotype) skull of *Symborodon altirostris* 216
172. Type (holotype) skull of *Symborodon trigonoceras* 217
173. Type (holotype) skull of *Brontotherium ingens* 218
174. Type (lectotype) of *Symborodon hypoceras* 218
175. Type (holotype) of *Anisacodon montanus* 219
176. Cope's cotypes of *Menodus angustigenis* 220
177. Anterior part of skulls of "*Megacerops coloradensis*," *Menodus tichoceras*, and *Menodus dolichoceras* 221
178. Type (holotype) horns of *Menodus platyceras* 222
179. Type (holotype) skeleton of *Brontops robustus* 222
180. Type (holotype) lower jaw of *Brontops dispar* 223
181. Type (holotype) skull of *Menops varians* 223
182. Type (holotype) skull of *Titanops curtus* 224
183. Type (holotype) skull of *Titanops elatus* 224
184. Type (holotype) skull of *Allops serotinus* 225
185. Type of *Menodus selwynianus* 225
186. Type of *Menodus syceras* 226
187. Type skull of *Diploclonus amplus* 227
188. Type of *Teleodus avus* 228
189. Type skull of *Allops crassicornis* 229
190. Type (holotype) skull of *Brontops validus* 230
191. Type (holotype) skull of *Titanops medius* 231
192. Type (holotype) nasofrontal shield of *Menodus peltoceras* 232
193. Cotypes of *Menodus? rumelicus* 232
194. Type (holotype) skull of *Titanotherium ramosum* 232
195. Type skull of *Megacerops brachycephalus* 233
196. Type (holotype) skull and lower jaw of *Megacerops bicornutus* 234
197. Type skull of *Megacerops marshi* 234
198. Type (holotype) skull of *Brontotherium leidyi* 235
199. Upper premolars of type skull of *Brontotherium leidyi* 235
200. Type (holotype) skull of *Megacerops tyleri* 236
201. Right manus and right hind limb of the type of *Megacerops tyleri* 237
202. Type (holotype) skull of *Brontotherium hatcheri* 238
203. Type (holotype) skull of *Symborodon copei* 238
204. Type (holotype) jaw of *Megacerops primitivus* 239
205. Type (holotype) jaw of *Megacerops assiniboiensis* 239
206. Type of *Titanotherium bohemicum* 240
207. Type (holotype) skull of *Allops walcotti* 241
208. Type (holotype) jaw of *Megacerops riggsi* 242
209. Characteristic basal sections of horns of Oligocene titanotheres 245
210. Skulls showing different numerical and proportional characters in five separate phyla of titanotheres 253
211. Standard measurements of Eocene titanothere skulls 255
212. Unequal elongation of face and cranium in titanotheres and horses 256
213. Faciocranial flexure, or cyptocephaly 256
214. Faciocranial flexure in *Palaeosyops* and *Dolichorhinus* 256
215. Cranial proportions of Eocene titanotheres—*Palaeosyops, Manteoceras,* and *Dolichorhinus* 257
216. Cranial proportions in man and in the titanotheres 258
217. Natural and artificial brachycephaly and dolichocephaly 258
218. Contrasting forms of upper teeth in Eocene titanotheres 264
219. Skulls of Eocene titanotheres of the principal genera 265
220. Heads of Eocene titanotheres of four phyla 266
221. Upper and lower molars of bunoselenodont pattern 268
222. Upper and lower molar patterns of *Hyracotherium* 268
223. Bunoselenodont patterns of upper and lower molars in Tertiary perissodactyls 268
224. Relations of upper and lower molars in *Telmatherium cultridens* 269
225. Dental mechanism of titanotheres 269
226. Grinding teeth of a titanothere and an insectivore 270
227. Contrast of brachyodont and semihypsodont molars in titanotheres 270
228. Cross sections through second upper and lower molars of *Lambdotherium* and *Menodus* 270
229. Upper premolar-molar teeth of the earliest and latest known titanotheres 271
230. Reconstructed skeletons and restorations of *Lambdotherium popoagicum* and *Eotitanops borealis* 277
231. Lower jaws of *Lambdotherium, Eotitanops,* and *Tapirus* 278
232. Restored contours of skulls of *Lambdotherium* and *Eotitanops* 278
233. Skull of *Lambdotherium popoagicum*, reconstructed 281

Figure Page
234. Lower premolars of three "species" or mutations of *Lambdotherium* 282
235. Upper and lower grinding teeth of *Lambdotherium* 283
236. Lower jaws and teeth of *Lambdotherium popoagicum* 284
237. Lower jaws and teeth of *Lambdotherium popoagicum*, side view 285
238. Front part of type lower jaw of *Lambdotherium priscum* 286
239. Incomplete lower jaw of *Lambdotherium priscum* 286
240. Jaws and teeth of *Lambdotherium priscum* and *L. magnum* 287
241. Lower jaw and teeth of *Lambdotherium progressum* 288
242. Upper teeth of *Lambdotherium progressum* 288
243. Restoration of *Eotitanops borealis* 289
244. Skulls of the oldest known titanotheres, *Lambdotherium popoagicum* and *Eotitanops borealis* 290
245. Model of skull of *Eotitanops gregoryi* 291
246. Lower premolars and molars of *Eotitanops* 291
247. Lower jaws of *Eotitanops gregoryi* and *E. brownianus* 292
248. Lower jaw of *Eotitanops borealis* 293
249. Lower teeth of *Eotitanops borealis* 294
250. Skull of *Eotitanops borealis*, palatal and side views 294
251. Skull of *Eotitanops borealis*, top and occipital views 294
252. Lower jaw of *Eotitanops princeps* 295
253. Lower grinding teeth of three species of *Eotitanops* from the upper Huerfano formation 296
254. Skull sections of brachycephalic and dolichocephalic Eocene titanotheres 299
255. Cross sections of the skull in middle Eocene titanotheres 300
256. Three skulls typical of the palaeosyopine group 301
257. Distribution of *Palaeosyops* and associated fauna in the Bridger formation 301
258. Anterior part of skull of *Limnohyops laevidens* 305
259. Skull of *Limnohyops priscus* 307
260. Back part of skull of *Limnohyops priscus* 308
261. Skulls of three species of *Limnohyops* 309
262. Skull of *Limnohyops matthewi* 309
263. Skull of *Limnohyops monoconus* 310
264. Skull of *Limnohyops laticeps* 311
265. Third right upper molar of *Limnohyops laticeps* 311
266. Lower jaws of *Limnohyops* and *Palaeosyops* 314
267. Lower jaws of *Palaeosyops* 314
268. Lower jaws of three species of *Palaeosyops* 315
269. Young skull of *Palaeosyops fontinalis* 317
270. Upper molars of *Palaeosyops fontinalis* 318
271. Teeth of *Palaeosyops fontinalis* 318
272. Skull of *Palaeosyops major* 319
273. Skull and head of *Palaeosyops leidyi* 324
274. Incisors and canines of *Limnohyops* and *Palaeosyops* 325
275. Skull of *Palaeosyops leidyi* 326
276. Type skull of *Palaeosyops leidyi* 327
277. Type skull of *Palaeosyops leidyi*, top view 328
278. Type skull of *Palaeosyops leidyi*, palatal view 328
279. Skulls of *Palaeosyops major* and *P. leidyi* 329
280. Lower jaws of *Palaeosyops leidyi* 330
281. Skulls of *Palaeosyops leidyi* and *P. copei?* (aff. *P. robustus*) 331
282. Jaws and deciduous teeth of *Palaeosyops leidyi?* 332
283. Deciduous cheek teeth of *Palaeosyops leidyi?* 332
284. Fragments of jaws of *Palaeosyops* 333
285. Skull of *Palaeosyops robustus* 333
286. Hyperbrachycephalic old male skull of *Palaeosyops robustus* 334
287. Basicranial region of *Palaeosyops robustus* 334
288. Nasals of *Palaeosyops robustus* 335
289. Progressive hypsodonty of the molars in *Telmatherium* 341
290. Upper jaw of *Telmatherium cultridens* 342
291. Upper and lower teeth of *Telmatherium cultridens* 343
292. Upper and lower teeth of *Telmatherium cultridens*, interlocked 343
293. Lower jaw of *Telmatherium cultridens* 344
294. Type skull and lower jaw of *Telmatherium ultimum* 346
295. Type skull of *Telmatherium ultimum*, side, front, and occipital views 347
296. Type skull of *Telmatherium ultimum*, palatal and top views 348
297. Paratype skull of *Telmatherium ultimum* 349
298. Lower jaw of *Telmatherium ultimum* 350
299. Hypothetical reconstruction of the skull of *Telmatherium altidens* 352
300. Lower jaws of *Telmatherium ultimum* and *T. altidens* 353
301. Type skull of *Sthenodectes incisivus* 356

Figure Page
302. Skulls of titanotheres of the *Manteoceras-Dolichorhinus* group 359
303. Skulls of *Manteoceras manteoceras* 363
304. Type skull of *Manteoceras manteoceras* 366
305. Skulls of *Manteoceras manteoceras* and *Palaeosyops leidyi* 367
306. Skulls of *Manteoceras manteoceras* and *M. washakiensis* 367
307. Skull of *Manteoceras manteoceras*, side view 368
308. Skull of *Manteoceras manteoceras*, anterior half 368
309. Incisors and canines of *Manteoceras manteoceras* 369
310. Lower jaw of *Manteoceras* 370
311. Skulls of *Manteoceras manteoceras* and *M. washakiensis* 371
312. Type skull of *Manteoceras uintensis* 373
313. Upper canines and incisors of *Manteoceras uintensis* 374
314. Restoration of *Protitanotherium emarginatum* 374
315. Lower jaws of *Protitanotherium* and *Brachydiastematherium* 375
316. Type skull of *Protitanotherium emarginatum;* reconstruction, side view 376
317. Type skull of *Protitanotherium emarginatum*, front and side views 376
318. Nasal region in three specimens of *Protitanotherium* 377
319. Sections of the nasals and horns of *Protitanothcrium emarginatum* 377
320. Lower jaw of *Protitanotherium emarginatum* 378
321. Lower jaw of *Protitanotherium superbum* 381
322. Phylogenetic relations of the species of *Metarhinus, Mesatirhinus, Dolichorhinus,* and *Rhadinorhinus* 383
323. Top view of the skull in the *Manteoceras-Dolichorhinus* group 385
324. Palatal view of the skull in the *Manteoceras-Dolichorhinus* group 385
325. Leidy's cotypes of *Palaeosyops junius* 386
326. Type skull of *Mesatirhinus megarhinus* 389
327. Type skull of *Mesatirhinus petersoni* 390
328. Skull of *Mesatirhinus petersoni*, side, top, and palatal views 391
329. Skulls of *Mesatirhinus petersoni*, front and occipital views 392
330. Incisors, canines, and premaxillae of *Mesatirhinus* 392
331. Lower jaws of *Mesatirhinus* 394
332. Lower jaw of *Mesatirhinus* sp. with deciduous dentition 395
333. Imperfect cranium of *Mesatirhinus petersoni?* 396
334. Geologic section of the Bridger formation in the Washakie Basin 397
335. Restoration of *Dolichorhinus longiceps* 398
336. Skull and lower jaw of *Dolichorhinus hyognathus* 398
337. Skulls of *Dolichorhinus hyognathus* and modern horse 399
338. Geologic section of the *Eobasileus-Dolichorhinus* and *Metarhinus* zones in the Uinta Basin 400
339. Skulls showing progressive dolichocephaly in the *Mesatirhinus-Dolichorhinus* phylum, side view 401
340. Skulls showing progressive dolichocephaly in the *Mesatirhinus-Dolichorhinus* phylum, top and palatal views 402
341. Upper premolars of *Mesatirhinus, Dolichorhinus,* and *Metarhinus* 403
342. Skull of *Dolichorhinus intermedius* 406
343. Skulls of *Dolichorhinus intermedius, D. heterodon,* and *D. longiceps* 408
344. Skull referred to *Dolichorhinus longiceps?* 409
345. Hyoid apparatus of *Dolichorhinus longiceps?* compared with that of a modern tapir 410
346. Skulls of *Dolichorhinus* 411
347. Skull of *Dolichorhinus hyognathus*, palatal view 412
348. Skulls of *Dolichorhinus hyognathus*, front and occipital views 413
349. Skull of *Dolichorhinus hyognathus*, side view 413
350. Upper incisors and canines of *Dolichorhinus hyognathus* 414
351. Lower incisors and canines of *Dolichorhinus hyognathus* 414
352. Left upper canine of *Dolichorhinus hyognathus* 414
353. Lower jaws of *Dolichorhinus* 415
354. Skull of *Sphenocoelus uintensis* 418
355. Type skull of *Eometarhinus huerfanensis* 419
356. Skull of *Metarhinus fluviatilis* 423
357. Right lower premolars of *Metarhinus fluviatilis* 424
358. Lower jaws of *Metarhinus* 425
359. Lower jaw of *Metarhinus?* (*Rhadinorhinus?*) sp 426
360. Skull and deciduous teeth of type of *Heterotitanops parvus* 426
361. Type skull of *Metarhinus earlei* 427
362. Type skull of *Rhadinorhinus diploconus*, side and top views 432
363. Type skull of *Rhadinorhinus diploconus*, top and palatal views 433
364. Type skull of *Rhadinorhinus diploconus*, side, front, and occipital views 434
365. Skulls of *Eotitanotherium osborni* 436
366. Nasals and horn swellings of *Eotitanotherium osborni* 437
367. Two upper molars of *Eotitanotherium* ("*Diploceras*") *osborni* 438
368. Type skull of *Diplacodon elatus*, partial reconstruction, palatal view 439
369. Type skull of *Diplacodon elatus*, upper jaw and zygoma 440

Figure Page
370. Third and fourth upper premolars of *Diplacodon elatus* 440
371. Upper molars of *Diplacodon* and *Protitanotherium* compared 441
372. Facial region of *Eotitanotherium osborni* and *Brontotherium leidyi* 441
373. Map showing areas in which remains of titanotheres have been found 443
374. Comparison of upper Eocene and lower Oligocene titanotheres 444
375. Sections at base of horn in the six chief generic types of Oligocene titanotheres 445
376. Position of the standard sections and contours of Oligocene titanotheres skulls 445
377. Male and female skulls of *Brontotherium gigas* 446
378. Occipital view of skulls in different phyla of Oligocene titanotheres 447
379. Influence of progressive brachycephaly on the auditory region of perissodactyls 447
380. Inferior aspect of chin in *Manteoceras* 449
381. Upper molars of *Menodus giganteus* and *Allops marshi* 450
382. Extreme dolichocephalic and brachycephalic types of upper premolar-molar series in Oligocene titanotheres 450
383. Third left lower molar of *Brontotherium leidyi* 451
384. Development of jaws and teeth, stage 4 452
385. Development of jaws and teeth, stage 6 453
386. Occiput of young skull of *Brontops? brachycephalus* 454
387. Stages of wear in the adult upper grinding teeth of Oligocene titanotheres 455
388. Skull contours showing extreme divergence between *Menodus giganteus* and *Brontotherium platyceras* 456
389. Skulls of the menodontine group, side view 459
390. Skulls of the bronototheriine group, side view 460
391. Skulls of the menodontine group, top view 461
392. Skulls of the brontotheriine group, top view 462
393. Skulls of the menodontine and brontotheriine groups, palatal view 463
394. Skulls of the menodontine and brontotheriine groups, front view 464
395. Lower jaws of the *Brontotherium* phylum 465
396. Lower jaws of the *Brontops* and *Menodus* phyla 466
397. Lower jaws of the *Diploclonus* and *Allops* phyla 466
398. Heads of Oligocene titanotheres 466
399. Sections at base of horn in five principal lower Oligocene phyla of titanotheres 468
400. Restorations of lower Oligocene titanotheres of the four principal genera 469
401. Skulls of *Rhadinorhinus* and *Brontotherium*, palatal view 470
402. Skulls of *Rhadinorhinus* and *Brontotherium*, side view 471
403. Skulls of *Rhadinorhinus* and *Brontotherium*, top view 472
404. Lower jaws of *Metarhinus fluviatilis* and *Brontotherium hatcheri* 473
405. Progressive evolution of the upper premolars in *Brontotherium* and its predecessors 474
406. Progressive evolution of the upper premolars in *Menodus* and *Brontops* and their predecessors 474
407. Progressive evolution of the lower premolars in *Brontotherium* and its predecessors 475
408. Progressive evolution of the lower premolars in *Brontops* and its predecessors 475
409. Phyla of the Brontopinae and Menodontinae 477
410. Evolution of the horns in the *Brontops* phylum 477
411. Basal section of the horns in the *Brontops* phylum 477
412. Progressive broadening of the nasals in the *Brontops* phylum 478
413. Lower jaws of *Teleodus primitivus*, *Brontops brachycephalus*, and *Allops walcotti?* 478
414. Sections and contours of skulls of *Brontops brachycephalus* 483
415. Upper canines and incisors of *Brontops brachycephalus* 484
416. Reconstruction of crushed skull of *Brontops brachycephalus* 485
417. Left upper grinding teeth of *Brontops brachycephalus* 485
418. Skull and horn region of *Brontops brachycephalus?* 486
419. Sections and contours of skulls of *Brontops brachycephalus* and *B. dispar* 487
420. Restoration of *Brontops robustus* 492
421. Sections and contours of skull of *Brontops robustus* 493
422. Skull of *Brontops robustus* 495
423. Lower jaws of *Brontops dispar* and *B. robustus* 496
424. Sections and contours of skull of *Brontops* sp 497
425. Hyoid bones of *Brontops* compared with those of the tapir, black rhinoceros, and horse 497
426. Sections and contours of skulls of *Diploclonus bicornutus* and *D. tyleri* 498
427. Sections and contours of skull of *Diploclonus amplus* 499
428. Lower jaws of *Diploclonus bicornutus* and *D. tyleri* 503
429. Sections and contours of skulls of *Allops walcotti* and *A. marshi* 510
430. Upper teeth of *Allops walcotti* 511
431. Skull of *Allops marshi* 513
432. Lower jaws of *Allops marshi* and *Allops?* sp 514
433. Sections and contours of skulls of *Allops serotinus* and *A. crassicornis* 516
434. Coossified nasals and proximal part of horns of *Allops? serotinus?* 517
435. Sections and contours of skulls of *Menodus heloceras* and *M. trigonoceras* 519
436. Skull of *Menodus heloceras* 526
437. Lower jaws of *Menodus (Symborodon) torvus* and *M. trigonoceras* 527

Figure Page
438. Upper teeth of *Menodus proutii* 528
439. Skull of *Menodus trigonoceras* 529
440. Skull of *Menodus trigonoceras* belonging with the mounted skeleton in the Colorado Museum, Denver 530
441. Restoration of *Menodus giganteus* 531
442. Skull of *Menodus giganteus*, front view 532
443. Skull of *Menodus giganteus*, palatal view 532
444. Sections and contours of skulls of *Menodus giganteus* and *M. varians* 534
445. Sections and contours of skull of *Menodus giganteus* 535
446. Lower jaws of *Menodus giganteus* 536
447. Teeth and nasals of *Menodus montanus* 538
448. Sections and contours of nasals and horns of *Megacerops coloradensis* 544
449. Sections and contours of skull of *Megacerops bucco* 545
450. Sections and contours of skulls of *Megacerops copei* and *M. acer* 546
451. Upper part of occiput of *Megacerops acer* 547
452. Skull of *Megacerops acer*, side and top views 548
453. Skull of *Megacerops acer*, palatal view 549
454. Restoration of *Megacerops copei* 549
455. Lower jaws of *Megacerops assiniboiensis* and *M. riggsi* 550
456. Sections and contours of skull of *Megacerops? syceras* 550
457. Composite sections showing the evolution of the horns and reduction of the free nasals in the *Brontotherium* phylum 551
458. Basal sections of the horns in the *Brontotherium* phylum 552
459. Skulls of male and female brontotheres 552
460. Contrast in contour of horns and nasals between male and female brontotheres 552
461. Sections and contours of skulls of *Brontotherium leidyi* and *B. hypoceras* 558
462. Lower jaws of *Brontotherium leidyi* 559
463. Two lower molars and symphyseal region of *Brontotherium? rumelicum* 560
464. Lower jaws of *Brontotherium rumelicum?* and *B. leidyi* 561
465. Sections and contours of skull of *Brontotherium? hatcheri* 563
466. Skull of *Brontotherium hatcheri*, side view 564
467. Skull of *Brontotherium hatcheri*, front view 564
468. Lower jaws of *Brontotherium hatcheri* and *B. gigas* 566
469. Sections and contours of skull of *Brontotherium? tichoceras* 567
470. Sections and contours of skulls of *Brontotherium hatcheri* and *B. gigas* 568
471. Lower jaws of *Brontotherium gigas* and *B. medium* 569
472. Sections and contours of skull of *Brontotherium gigas?* 572
473. Sections and contours of skull of *Brontotherium dolichoceras* 572
474. Skull of *Brontotherium dolichoceras* 572
475. Sections and contours of skulls of *Brontotherium medium* and *B. curtum* 574
476. Horns of *Brontotherium curtum* 576
477. Sections and contours of skull of *Brontotherium curtum* 576
478. Left horn and nasals of *Brontotherium curtum?* 577
479. Sections and contours of skull of *Brontotherium ramosum* 578
480. Restoration of *Brontotherium platyceras* 579
481. Sections and contours of skull of *Brontotherium platyceras* 580
482. Evolution of the skeleton in titanotheres 584
483. Estimated height at shoulder of Eocene and Oligocene titanotheres and tapir 585
484. The phyla of Eocene titanotheres, as represented by the manus 587
485. Progressive broadening of the magnum in Eocene titanotheres 587
486. Reconstructed skeleton and restoration of *Lambdotherium popoagicum* 591
487. Atlas and scapula of *Lambdotherium popoagicum* 591
488. Fore limb of *Lambdotherium popoagicum* 592
489. Forearm and manus of *Lambdotherium popoagicum* 592
490. Left manus of *Lambdotherium* and *Eotitanops* 592
491. Astragalus of *Lambdotherium popoagicum* 593
492. Restorations of *Lambdotherium popoagicum*, *Eotitanops princeps*, and *E. gregoryi* 593
493. Metatarsals of *Eotitanops* 593
494. Reconstructed skeleton and restoration of *Eotitanops borealis* 594
495. Atlas of *Eotitanops borealis* 595
496. Vertebrae of *Eotitanops princeps* 595
497. Radius of *Eotitanops borealis* 595
498. Lunars of *Eotitanops* 595
499. Manus of *Eotitanops princeps* 595
500. Humerus and femur of *Eotitanops princeps* 596
501. Pelvis of *Eotitanops borealis* 596
502. Left pes of cursorial and subcursorial Eocene Perissodactyla 597
503. Astragalus and calcaneum of cursorial and submediportal Eocene Perissodactyla 598
504. Astragalocalcaneal facets in lower Eocene Perissodactyla 598
505. Left astragalus and calcaneum of *Eotitanops* sp 599

Figure Page
506. Metatarsal and tibia of *Eotitanops major* 599
507. Restoration of *Eotitanops borealis* 600
508. Atlas of Eocene titanotheres 601
509. Types of scapula in middle Eocene titanotheres 602
510. Types of fore limb in Eocene and Oligocene titanotheres 603
511. Characteristic details of radius and ulna in middle and upper Eocene titanotheres 604
512. Manus of lower and middle Eocene titanotheres 605
513. Comparison of the right scaphoid in middle Eocene titanotheres 605
514. Terminal phalanges of the manus in middle Eocene titanotheres and amynodonts 605
515. Progressive graviportal adaptation in the pelvis of Eocene and Oligocene titanotheres 606
516. Femora and tibiae of middle Eocene titanotheres 609
517. Distal end of the femur in *Manteoceras* and *Amynodon* 610
518. Angulation of the knee joint: relation of patellar facet to long axis of femur 611
519. Inner side view of left fibula of *Palaeosyops*, *Limnohyops*, and *Brontotherium* 611
520. Comparison of pes in four species of middle Eocene titanotheres 613
521. Astragali of Eocene titanotheres 614
522. Calcanea of Eocene titanotheres 615
523. Left ectocuneiform tarsi of lower and middle Eocene titanotheres 615
524. Principal measurements of the carpus and tarsus 615
525. Humerus, radius, and ulna of *Limnohyops monoconus?* 615
526. Left manus, radius, and ulna of *Mesatirhinus petersoni* 616
527. Manus, radius, and ulna of *Limnohyops monoconus* 616
528. Right scaphoid of *Palaeosyops* sp. and *Limnohyops monoconus* 617
529. Left hind limb of *Limnohyops monoconus* 618
530. Right pes of *Limnohyops monoconus?* 618
531. Ventral surface of sacrum of *Limnohyops laticeps* 618
532. Right os innominatum of *Limnohyops laticeps* 619
533. Pelvis of *Palaeosyops major* 619
534. Right femur and tibia of *Palaeosyops major* 620
535. Astragalus and calcaneum of *Palaeosyops major* 620
536. Composite mounted skeleton of *Palaeosyops leidyi* 621
537. Manus of *Palaeosyops leidyi* 622
538. Pelvis of *Limnohyops* 624
539. Pelvis of *Palaeosyops* cf. *P. leidyi* 624
540. Left pes of *Palaeosyops leidyi* 625
541. Relations of facets of the astragalus and calcaneum in *Palaeosyops* 626
542. Atlas of *Palaeosyops robustus* 627
543. Atlas and axis of *Palaeosyops leidyi?* 627
544. Cervicals and dorsals of *Palaeosyops robustus* 627
545. Left scapula of *Palaeosyops robustus* 627
546. Bones of forearm of *Palaeosyops* 628
547. Left astragalus of *Palaeosyops copei?* 629
548. Fore limb of *Palaeosyops copei?* 629
549. Left manus of *Palaeosyops copei?* 629
550. Right hind limbs of *Palaeosyops major* and *P. copei?* 630
551. Atlas of *Manteoceras manteoceras* 632
552. Seventh cervical vertebra of *Manteoceras manteoceras* compared with that of *Palaeosyops leidyi* 633
553. Left humerus of *Manteoceras manteoceras* 633
554. Right manus of *Manteoceras manteoceras* 633
555. Pelvis of *Manteoceras?* 634
556. Femora and tibiae of *Manteoceras manteoceras* 635
557. Left astragalus of *Manteoceras manteoceras* 635
558. Restoration of the skeleton of *Mesatirhinus petersoni* 637
559. Restorations of *Mesatirhinus petersoni* and *Palaeosyops leidyi* 637
560. Atlas of *Mesatirhinus megarhinus* 638
561. Humerus of *Mesatirhinus megarhinus* 638
562. Radius and ulna of *Mesatirhinus petersoni* 638
563. Left forearm and manus of *Mesatirhinus petersoni?* 639
564. Right manus and fragments of radius and ulna of *Mesatirhinus petersoni* 639
565. Left manus, radius, and ulna of *Mesatirhinus petersoni?* 639
566. Right scaphoid of *Mesatirhinus* and *Manteoceras* 639
567. Right manus of *Mesatirhinus petersoni?* 641
568. Left femur and tibia of *Mesatirhinus petersoni?* 642
569. Left pes of *Mesatirhinus petersoni?* 642
570. Left astragali of *Mesatirhinus petersoni?* 642
571. Left entocuneiform tarsi of *Palaeosyops* and *Mesatirhinus* 642
572. Pes referred to *Mesatirhinus* 644
573 Pes of *Metarhinus* cf. *M. earlei* 644

Figure		Page
574.	Astragalus, calcaneum, and navicular of *Metarhinus* cf. *M. earlei*	644
575.	Astragalus of *Metarhinus* cf. *M. earlei*	644
576.	Left scapula of *Metarhinus?* sp	645
577.	Left radius and ulna of *Metarhinus earlei?*	645
578.	Skeleton of a newly born animal, provisionally identified as *Metarhinus* sp	646
579.	Provisional restoration of the skeleton of *Dolichorhinus hyognathus*	646
580.	Vertebral column of *Dolichorhinus hyognathus*	647
581.	Atlas referred to *Dolichorhinus* sp	647
582.	Left scapula of *Dolichorhinus? hyognathus*	649
583.	Humerus of *Dolichorhinus hyognathus*	649
584.	Radius and ulna of *Dolichorhinus hyognathus*	649
585.	Metatarsals of *Dolichorhinus hyognothus*	649
586.	Manus of *Amynodon* and *Mesatirhinus* compared	650
587.	Left fore limb of the amphibious rhinoceros *Amynodon intermedius?*	650
588.	Left astragali of *Dolichorhinus* and allied types	651
589.	Cervical vertebrae of *Dolichorhinus longiceps?*	651
590.	Right fore limb of *Dolichorhinus longiceps?*	652
591.	Manus of *Dolichorhinus longiceps?*	652
592.	Hind limb referred to *Telmatherium ultimum*	653
593.	Pes of *Telmatherium? ultimum?*	653
594.	Vertebrae and fore limb of *Diplacodon* or *Protitanotherium*	654
595.	Astragalus and calcaneum of *Diplacodon* or *Protitanotherium*	655
596.	Left astragalus of *Protitanotherium superbum*	655
597.	Incomplete ilium and ischium of *Diplacodon elatus*	656
598.	Atlas and axis of *Eotitanotherium osborni*	656
599.	Vertebrae of *Eotitanotherium osborni*	657
600.	Scapula of *Eotitanotherium osborni*	657
601.	Humerus, radius, and ulna of *Eotitanotherium osborni*	657
602.	Manus of *Eotitanotherium osborni*	658
603.	Femur, tibia, and pelvis of *Eotitanotherium osborni*	658
604.	Pes of *Eotitanotherium osborni*	658
605.	Restoration of skeleton of *Eotitanotherium osborni*	659
606.	Mounted skeleton of *Brontops*	670
607.	Three views of mounted skeleton of *Brontops*	671
608.	Scapulae of Oligocene titanotheres	673
609.	Manus of *Brontops?* sp. and *B. dispar?*	674
610.	Mounted skeleton of *Brontops brachycephalus?*	676
611.	Mounted skeleton of *Brontops brachycephalus?*, oblique front view	677
612.	Parts of skeleton of *Allops crassicornis?*	680
613.	Pes of *Menodus trigonoceras*, referred, and *M. heloceras*	681
614.	Manus of *Menodus trigonoceras?*	682
615.	Restorations of *Menodus trigonoceras* and *Allops marshi*	683
616.	Mounted skeletons of *Brontops dispar?* and *Menodus trigonoceras*	684
617.	Left astragalus of *Menodus giganteus*	685
618.	Cervical and first four dorsal vertebrae of *Brontops robustus* and *Menodus giganteus*	686
619.	Manus referred to *Menodus giganteus*	687
620.	Restorations of *Brontotherium leidyi* and *B. platyceras*	688
621.	Atlas and axis of *Brontotherium leidyi*	689
622.	Vertebrae of *Brontops robustus* and *Brontotherium gigas*	689
623.	Scapulae of Oligocene titanotheres	690
624.	Humeri of *Brontops robustus* and *Brontotherium leidyi*	691
625.	Humeri of *Megacerops? acer?* and *Brontotherium gigas?*	691
626.	Radii of *Brontops robustus*, *Brontotherium leidyi*, and *Brontotherium gigas*	691
627.	Radius and ulna of *Brontotherium*	692
628.	Ulnae of *Brontops robustus*, *Brontotherium leidyi*, and *Brontotherium gigas*	692
629.	Olecrana of *Brontotherium* and *Megacerops?*	692
630.	Manus of Oligocene titanotheres	693
631.	Manus and pes referred to *Brontotherium gigas hatcheri*	694
632.	Manus and pes referred to *Brontotherium hatcheri?*	695
633.	Manus referred to *Brontotherium gigas*, as restored	695
634.	Pelvis of *Brontotherium gigas hatcheri*	696
635.	Femora of *Brontops robustus* and *Brontotherium leidyi*	696
636.	Tibiae of *Brontops robustus* and *Brontotherium leidyi*	696
637.	Tibia and fibula of *Brontotherium leidyi*	696
638.	Femora of *Megacerops?* and *Brontotherium?*	696
639.	Pes of Oligocene titanotheres	697

LETTER OF TRANSMITTAL

Dr. George Otis Smith,
Director United States Geological Survey,
Washington, D. C.

Dear Sir: I have the honor to transmit herewith a monograph on the evolution of a peculiarly American family of quadrupeds known as the titanotheres. This designation was given to them in 1852 by Joseph Leidy while he was employed as vertebrate paleontologist in David Dale Owen's survey of a part of the ancient territory of Nebraska. This family is one of a group of vertebrate animals whose fossil remains, found in the western United States, were long studied by Othniel Charles Marsh, my distinguished predecessor in this work in the United States Geological Survey. Early in the eighties Professor Marsh projected a monograph on the Brontotheridae (here called the titanotheres), and subsequently he made the largest and most valuable contributions to our knowledge of this family and of its evolution. He planned the monumental field work of John Bell Hatcher, by which the great collection for the United States National Museum was made, and he supervised the preparation of sixty lithographic plates, which are here reproduced. Unfortunately he died before he had even begun to prepare the manuscript. The duty of continuing his work was intrusted to me June 30, 1900, by your predecessor, Charles D. Walcott. During this period of nearly 20 years I have supervised the preparation of the monograph on the Ceratopsia by Hatcher and Lull and have half completed the monograph on the Sauropoda. The monograph on the Stegosauria has not yet been prepared.

The task of preparing the present monograph has been long and difficult. First, it proved necessary to reexplore the entire Eocene and lower Oligocene series of rocks in Wyoming, Colorado, and South Dakota, where the fossilized remains of titanotheres are found, both to determine precisely their geologic succession and to close up gaps in the stages of evolution; second, it proved necessary to examine and compare the titanotheres of these geologic epochs in all the museums of this country and in several museums abroad; third, it proved necessary, in order thoroughly to understand the titanotheres, to discover and to follow many side lines of investigation that have not hitherto been followed in vertebrate paleontology.

This work has been done with the aid of many specialists, foremost among whom is my junior colleague Prof. William K. Gregory, without whose intelligent and unremitting cooperation the monograph could never have been completed.

It is perhaps not too much to say that this work has transformed our knowledge of the early Tertiary geology of the Rocky Mountain basin region. First, the six life periods recognized by Marsh and his no less distinguished contemporary Edward Drinker Cope may now be replaced by sixteen life periods, which may be clearly defined and separated and certain of which may be more or less precisely correlated with life periods established for western Europe. Second, a much clearer notion has been gained of the changing geographic, physiographic, climatic, and volcanic conditions in Wyoming and Dakota and of their influence on the migration and succession of forms of life. Third, the whole method of attack on problems of vertebrate paleontology has been developed; we seek to know the entire living animal, its musculature, its mode of locomotion, and its feeding habits, in order to insure the complete restoration of the body. Fourth, the study of the many branches of this group has given the most convincing demonstration that evolution, even in any one geographic region, seldom moves along a single line of descent; more frequently it moves along many lines—it is polyphyletic; in other words, it radiates, following the principles of local adaptive radiation. Finally, the history of the titanothere family in its evolution from very small and relatively weak forms into titanic quadrupeds, second in size only to the elephants, has afforded us a unique opportunity to enlarge our previous knowledge of the actual modes of evolution as well as to revise our theories as to the causes of evolution and of extinction.

I desire to express my appreciation of the support given by the Geological Survey under your direction in the completion and publication of this work.

With the aid of many coworkers I have endeavored to set a new standard of broad, thorough, and exhaustive research in vertebrate paleontology which shall be worthy of the great geologic traditions of our national Geological Survey. I trust that this monograph, like Leidy's classic memoir of 1869, may exercise a permanent influence upon future studies of the geologic history of the great West.

Henry Fairfield Osborn,
Vertebrate Paleontologist.

American Museum of Natural History,
December 19, 1919.

PREFACE

VERTEBRATE PALEONTOLOGY IN THE NATIONAL SURVEYS

Joseph Leidy, Edward Drinker Cope, and Othniel Charles Marsh, who successively served as members of United States Government surveys of the West, were the founders of American vertebrate paleontology. Leidy's memoir of 1869, entitled "The extinct mammalian fauna of Dakota and Nebraska, including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America," marked the end of the first period of exploration. Cope's great memoir of 1885, entitled "The Vertebrata of the Tertiary formations of the West," marked the end of the second period of exploration.

Meanwhile the subject had become too broad to be comprehended in a single work. Accordingly Marsh, as vertebrate paleontologist, planned a series of exhaustive monographs on special groups of extinct birds, reptiles, and mammals, which should treat in great detail the anatomical structure and form the basis of a systematic classification. For these monographs he carried out the most intensive field explorations known to science and published a large number of preliminary papers, which fairly revolutionized our knowledge of these and many other groups. In 1880 the Fortieth Parallel Survey published his monograph on the Odontornithes, an extinct group of birds of North America. In 1883 the United States Geological Survey published his paper entitled "Birds with teeth," and in 1886 his monograph on the Dinocerata, an extinct order of gigantic mammals. This was the first of the series of five monographs projected for publication by the United States Geological Survey on the Dinocerata, the Stegosauria, the Sauropoda, the Ceratopsia, the Brontotheridae. The monograph last indicated has developed into the present monograph on the titanotheres, which covers a much broader field than that contemplated by Marsh for the monograph on the Bronototheridae.

For the monographs on the Ceratopsia and on the Brontotheridae exploration on an unprecedented scale was begun by the United States Geological Survey under the direction of Marsh. For the four monographs on the Stegosauria, Sauropoda, Ceratopsia, and Brontotheridae 204 superb lithographic plates were completed under Marsh's direction. Altogether he had been engaged on this work nearly 17 years when death interrupted his monumental labors on March 18, 1899.

PREPARATION OF THE PRESENT MONOGRAPH

The first important step taken by Marsh in his series of contributions to our knowledge of this extinct family was the publication of his paper on "The structure and affinities of the Brontotheridae," published in 1874, based on the collections at Yale University. The second was his paper entitled "Principal characters of the Brontotheridae," published in 1876. In the meantime he had made a geologic excursion to White River in South Dakota, in the vicinity of the Red Cloud Agency. This visit marks an interesting epoch in the history of paleontologic exploration for the titanotheres.

Late in the autumn of 1875 Marsh, accompanied by an escort from Fort Laramie to the Red Cloud Agency, went to the Badlands of Nebraska and Dakota. The consent of the Indians was deemed necessary to permit safe search for fossil bones in their country. This consent was obtained with difficulty, and after it had been obtained the Indians withheld their assistance. An account of Marsh's visit is given in a manuscript entitled "Sketches of the life of Red Cloud," by Capt. James H. Cook, of Agate, Nebr., at that time serving as a scout for the United States Army. Captain Cook writes:

> It was in the autumn of 1875 that I visited the Red Cloud Agency, which was at that time located on the White River, in the northwestern part of Nebraska, the agency buildings standing about 2 miles up the river from the place where the city of Crawford is now situated. The chief of the Sioux, Red Cloud, made me welcome to his lodge.
>
> It was on this visit that I first learned of the petrified bones of strange creatures that had once occupied the lands to the eastward of the agency. Two of Red Cloud's subchiefs, American Horse and Little Wound, took me to the lodge of Afraid of Horses, where I was shown a piece of bone, perfectly petrified, containing a molar tooth 3 inches or more in diameter. American Horse explained that the tooth had belonged to a "Thunder Horse" that had lived "away back" and that then this creature would sometimes come down to earth in thunderstorms and chase and kill buffalo.
>
> His old people told stories of how on one occasion many, many years back, this big Thunder Horse had driven a herd of buffalo right into a camp of Lacota people during a bad thunderstorm, when these people were about to starve, and that they had killed many of these buffalo with their lances and arrows. The "Great Spirit" had sent the Thunder Horse to help them get food when it was needed most badly. This story was handed down from the time when the Indians had no horses.
>
> While I was the guest of Red Cloud on this occasion, Prof. O. C. Marsh, of the Smithsonian Institution and Yale University, came over from Fort Laramie to Camp Robinson and the Red Cloud Agency to get permission to collect fossils in

the Sioux country. The Sioux, however, did not take kindly to this proposition, thinking it was yellow lead (gold) that the white chief wanted, not stone bones.

I met Professor Marsh at that time and talked with him. I showed him the tooth the Indians had shown me. When I returned to Red Cloud's lodge I told Red Cloud that Professor Marsh was a friend of the "Great Father" (the President) at Washington, and that I thought if he were allowed to hunt for stone bones in the Sioux country he would be a good friend to the Sioux people. Red Cloud said that if Professor Marsh was a good man he would help the Sioux people to get rid of the agent that was then in charge of the agency, whom they disliked very much. This being brought to the attention of Professor Marsh, he took the matter in hand, and an investigation of affairs took place at the Red Cloud Agency, the result of which was at least pleasing to the Indians concerned, as the agent was removed.

Professor Marsh was allowed to collect with his field parties unmolested from that time on. He was named by Red Cloud "Wicasa Pahi Hohu" (pronounced wē-chă-shă pă-hē hō-hü), Man-that-Picks-Up-Bones. The professor and Red Cloud became friends to the extent that Red Cloud was entertained at the home of the professor in New Haven, Conn., and the two were photographed there with clasped hands and the "peace pipe" between them.

The first collections made for this monograph were those brought together from Colorado and South Dakota, part of them under the direction of Marsh, for the Peabody Museum of Yale University. By far the greatest collection was that brought together by John Bell Hatcher for the Geological Survey, now preserved in the United States National Museum. Between 1870 and 1891 Marsh published 14 papers on these collections. These papers relate more or less directly to the Brontotheridae; the last appeared in 1891 and contained descriptions of three new types from South Dakota—*Allops crassicornis*, *Brontops dispar*, and *Brontotherium medium*.

WORK BY THE AUTHOR, 1878–1919

In the meantime the present author made his first contribution to the history of this family in 1878 in a paper on the results of the Princeton collections of 1877 and 1878 in the Bridger Basin. His second contribution was made in 1887 in a paper entitled "Preliminary report on the vertebrate fossils of the Uinta formation collected by the Princeton expedition of 1886." His third and fourth contributions were made in 1890, in the two papers entitled, respectively, "Preliminary account of the fossil mammals from the White River and Loup Fork formations," which related to a collection made in South Dakota by Dr. S. Garman for the Harvard University Museum, and "The Mammalia of the Uinta formation," Parts III and IV, on the Perissodactyla. These have been followed by 38 papers by the author, based chiefly on his paleontologic and geologic expeditions in the field for the American Museum of Natural History, planned by the author and ably directed by Dr. J. L. Wortman, Mr. O. A. Peterson, and Mr. Walter Granger. To these indefatigable field explorers science is indebted for the wonderful series of Eocene titanotheres which have enabled us to trace the ancestry of the Oligocene titanotheres and to establish all the early phases in the history of this family. To Peterson, Earl Douglass, and Elmer S. Riggs in the Uinta, and especially to Granger in the entire series from the basal Eocene to the base of the Uinta, is due the remarkable precision of the geologic records by which the faunal life zones of the Eocene have been determined.

The stratigraphic succession of the Eocene and of the lower Oligocene mammal life has been determined chiefly by the field observations and collections of Granger in the Eocene and of John Bell Hatcher in the lower Oligocene and by the systematic examinations of species by Dr. William Diller Matthew and by the author.

RESEARCH AND COLLABORATION

Prof. William K. Gregory has been in the closest cooperation with the author in all the details of the preparation of the monograph since the beginning of the work in the year 1900. Words are inadequate to express the author's sense of indebtedness to his former student and present colleague in the American Museum and in Columbia University.

The author desires also to acknowledge his special indebtedness to Mr. Granger for his valuable notes and his cooperation in the preparation of the text and the geologic sections, as presented in Chapter II, on the Eocene and Oligocene formations of the Rocky Mountains, as well as to Prof. William J. Sinclair for his work on the volcanic nature of the middle Eocene deposits and to Mr. Albert Johannsen of the Geological Survey for his analyses of the material of these deposits. It is hoped that that chapter will furnish a key to future exploration of this mountain-basin region as well as to the Oligocene sections of the Great Plains. Matthew, by means of the rich collections in the American Museum, has furnished critical determinations for the discrimination of mammalian species in the sixteen life zones and has cooperated with the author in the preparation of "Cenozoic mammal horizons of western North America," published by the Geological Survey in 1909 as its Bulletin 361, which forms the foundation of the more detailed life-zone work whose results are presented in Chapter II.

Details of the history of the collections at home and abroad are presented in Chapter III under the heading "History of explorations and discoveries and original descriptions of the Eocene and Oligocene titanotheres." Every known significant specimen is referred to, its species and its sex are determined, and its principal characters are described. This monograph will furnish a much desired key to the present and future collections and surveys in Wyoming, Nebraska, Colorado, the Dakotas, and Assiniboia.

COOPERATION OF MUSEUMS

To the museums of the United States, Great Britain, and Bavaria, where titanothere remains are preserved, the author is indebted for cordial cooperation in furnishing materials for study and in affording every possible facility for measurements and illustrations. The author would mention especially Prof. Charles Schuchert and Prof. Richard S. Lull, of the Yale University Museum, present custodians of the great Marsh collections, as well as their assistant, Mr. Thomas A. Bostwick, who is in charge of all the field records of Marsh. In connection with the superb Hatcher collection in the United States National Museum, which far surpasses any other in existence, Dr. Charles W. Gilmore and Dr. James W. Gidley have rendered every possible assistance. The author is especially indebted to the director of the Carnegie Museum at Pittsburgh, Dr. W. J. Holland, and to Mr. O. A. Peterson of that museum for the liberal use of collections of the Uinta titanotheres; also to Mr. Earl Douglass of the same institution for his invaluable field notes and observations on the Uinta section. The systematic location of species in the great Uinta section is due to the precise field work of Mr. Elmer S. Riggs of the Field Museum of Natural History, Chicago, an institution that is especially rich in remains from the horizon known as Uinta B. To his former colleague Prof. William B. Scott of Princeton University, as well as to his colleague Prof. William J. Sinclair, the author is indebted for the liberal use of valuable collections, including many types from several levels of the Bridger and from the uppermost Eocene horizon, known as Uinta C.

From 1846, when the earliest remains of titanotheres were found, until 1918 almost every year has added one or more stages or types to the history of this great family. The stages still to be discovered are in the unknown interval between the uppermost Eocene horizon, known as Uinta C, and the lowermost Oligocene horizon, known as Chadron A.

WORK ON TEXT AND ILLUSTRATIONS

The great task of preparing the bulk of the manuscript—a task performed between 1902 and 1918—fell upon Miss H. Ernestine Ripley, the work being done chiefly from the dictation and notes of the author. The preparation of the bibliography and the first revision of the entire manuscript were also undertaken by Miss Ripley with interest and performed with precision. The author warmly appreciates this invaluable service to paleontology. The final arrangement of the illustrations together with the preparation of the accompanying legends, was undertaken, under the author's general direction, by Doctor Gregory with the cooperation of Miss Christine D. Matthew, Mr. Erwin S. Christman, and Mrs. Lindsey Morris Sterling. The preliminary editorial work has been performed with celerity and skill by Miss Mabel Rice Percy, of the American Museum. The final arrangement and verification of illustrations and captions were the work of Miss Christine D. Matthew.

The final editorial work and preparation of the text for the printers were accomplished by Messrs. George M. Wood and Bernard H. Lane, Mr. Wood continuing the work as a member of the American Museum staff after his retirement from the Geological Survey.

The illustrations, which are taken from many sources, date back to the early lithographic figures of Leidy. They include the unpublished lithographic plates prepared under the direction of Cope, and especially the superb lithographic drawings made for the United States Geological Survey by Mr. F. Berger under Marsh's direction. These lithographic plates are supplemented by numerous plates based upon photographs taken chiefly by Mr. A. E. Anderson of the American Museum staff.

The text and plates are adorned with reproductions of the fine series of drawings from the pen and brush of Mr. Christman and from the numerous pen drawings of Mrs. Sterling. The geologic sections in Chapter II are the work of Mr. William E. Belanske. To Mrs. Sterling, Mr. Christman, and Mr. C. A. Weckerly of the Geological Survey were assigned the final preparation for the photoengraver of all the illustrations for the monograph, which, including those in the Appendix, consist of 797 figures and 236 plates.

This review affords a partial explanation of the great length of the period of time occupied by the author in the preparation of this monograph. The work has involved repeated explorations in the West in search of the remains of all the ancestors of the family and in establishing the full chronology. It has necessitated repeated journeys to all the museums of the country and long and painstaking research. The greatest effort, however, has been expended on the solution of the series of related problems in stratigraphy, in adaptation, in the origin of new characters, in the mechanics of locomotion, in the modes of evolution, and in the causes of evolution and of extinction that presented themselves as essential to the exposition of the life history of a long extinct family. To restore the living and the lifeless environment of the Rocky Mountain region and to present the titanotheres as living forms has been the persistent purpose of this monograph.

SUMMARY OF GEOLOGIC AND ANATOMIC PRINCIPLES

The following is a brief statement of the principles developed and discriminated in this monograph:

1. The principle of the division and correlation of geologic formations in Eocene and lower Oligocene time by mammalian life zones and by the subdivision of these zones.

2. The principle of the correlation of local physiographic diversity with the adaptive radiation, local and continental, of titanotheres and other ungulates.

3. The principle of adaptive radiation as expressed in adaptations to aquatic, forest, savanna, and plains life at different altitudes.

4. The principle of multiple lines of descent in the same regions, of polyphyly and of polyphyletic evolution as more common among ungulates than monophyletic evolution.

5. The principle of distinguishing phyla by contrasting proportions of the head (dolichocephaly and brachycephaly), of the limbs (dolichomely and brachymely), of the feet (dolichopody and brachypody), and of the teeth (hypsodonty and brachyodonty).

6. The principles of the lengthening and shortening of the limb segments in harmony, respectively, with adaptation to speed and to weight.

7. The principles of evolution by rectigradation (origination of new characters) and by allometry (changes of proportion) as effecting the chief changes in the hard parts.

8. The principles of continuity and of orthogenesis—the direct continuation of animal form established in adaptation to environment and of the evolution of new types irrespective of external influences.

The theoretic causes underlying these principles of evolution are briefly stated in Chapter I, and the conclusions reached are summarized in Chapter XI.

THE TITANOTHERES OF ANCIENT WYOMING, DAKOTA, AND NEBRASKA

By Henry Fairfield Osborn

CHAPTER I

INTRODUCTION TO MAMMALIAN PALEONTOLOGY

SECTION 1. EXPLORATION AND RESEARCH MADE IN THE PREPARATION OF THIS MONOGRAPH

The preparation of this monograph was actually begun in 1846, when a part of a jawbone of a titanothere was found in the region now known as South Dakota and sent first to Dr. Hiram A. Prout of St. Louis and then to Dr. Joseph Leidy of Philadelphia for description. This bit of bone gave the first hint to science of the wonderful deposits of vertebrate fossils in the Rocky Mountain region that have revolutionized vertebrate paleontology. The details of this epoch-making discovery are given in Chapter III. The original fragment bears the generic name *Menodus*, which was assigned to it by the keen systematic paleontologist of France, Nicolas Auguste Pomel, who gave it the specific name *giganteus*. *Menodus giganteus* is thus the first titanothere known to science, and it is a representative of the most imposing family of mammals that was evolved in ancient North America.

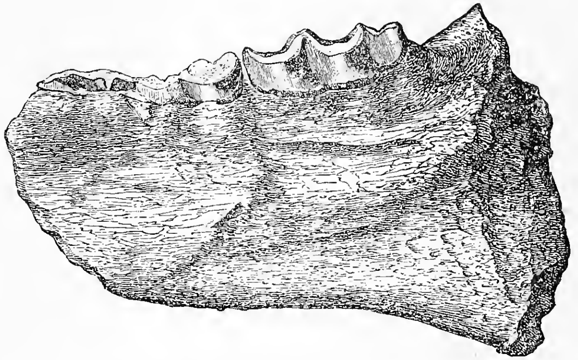

Figure 1.—"Fragment of the inferior maxillary of the left side" of Prout's "gigantic *Palaeotherium*," the first titanothere discovered

After Prout (1847). One-fourth natural size.

Figure 2.—Type of *Palaeotherium? proutii*

Owen's specimen, Nat. Mus. 113. After Leidy (1852). One-third natural size. This was one of the specimens referred to by Leidy (1852.1)[1] in proposing the name *Titanotherium*.

This family, from its earliest known beginnings in the Wind River Mountains of the present State of Wyoming to the height of its development on the plains of the ancient Dakota-Nebraska-Colorado region, attracted the attention of the leading vertebrate paleontologists of America—Joseph Leidy, Edward Drinker Cope, Othniel Charles Marsh, John Bell Hatcher—up to the time when the whole long and difficult study of family history, of geologic succession, and of environment was intrusted to the present author.

From the first it seemed desirable that this study should encompass more than a dry, systematic description—that these animals and their environment should, so far as possible through paleontology, be made to live again as the dominant animals of a long and very interesting epoch in the history of North America—the first third of the Tertiary period. The field explorations made in the prosecution of this research should, moreover, sustain the guiding principles of the union of paleontology and geology established by the pioneers of our national surveys, as seen especially in the combined work of the geologist, Frederick V. Hayden, and the paleontologists, Charles A. White and Joseph Leidy,[2] whose reports are still fundamental standards of Tertiary geologic and paleontologic history. Subsequent works have surpassed these in specialization and in number and variety of animal forms, and the geologic areas and life zones have been greatly increased by subsequent discovery, but none have surpassed them

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[1] The figures in parentheses refer to entries in the bibliography at the end of this chapter.

[2] See reports of Hayden and White (1867-73.1, 1868.1), based on surveys beginning in 1862, and Leidy's great memoir (1869.1).

in scientific method—in the constant union of paleontologic with geologic evidence in the reconstruction of the slow succession of events in the wonderful history of this western region.

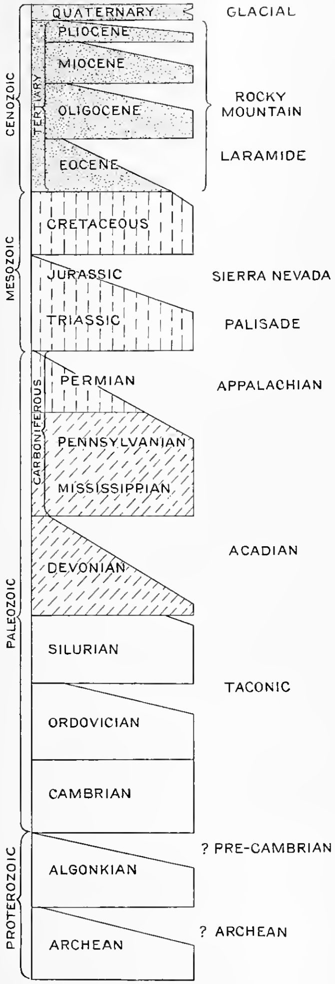

FIGURE 3.—Geologic ages and orogenic periods in North America

Age of mammals, stipple; age of reptiles, vertical lines; age of amphibians and fishes, oblique lines. The periods of the birth and elevation of the chief American mountain systems, notably the Rocky Mountains (including the Laramide revolution), are indicated approximately by incisions on the right. Modified from diagram by Henry Shaler Williams.

The present monograph is made up of this introductory chapter and of ten other chapters, covering the following six main lines of exploration and research that have been followed in order to restore, at least in part, the life and times of the titanotheres:

1. Geologic, physiographic, climatic, and faunal environmental conditions of the titanothere epoch—the Eocene and lower Oligocene divisions of the Tertiary. Principles of adaptive radiation in animals as explaining the variation of the titanotheres. (Chap. II.)
2. History of the discoveries of the remains of titanotheres, the original published descriptions, and the previous and present classification of genera and species. (Chaps. III and IV.)
3. Systematic study of the titanotheres: Eocene and lower Oligocene subfamilies, genera, and species. Characters of the skull, dentition, and postcranial skeleton. (Chaps. V, VI, and VII.)
4. Muscular anatomy of the titanotheres: Principles of locomotion and evolution of limb structure in the hoofed mammals (Ungulata) in relation to habits. (Chaps. VIII and IX.)
5. Origin, ancestry, and adaptive radiations of the titanotheres and other odd-toed ungulates. (Chap. X.)
6. Evolution and extinction of the titanotheres: Evidence regarding modes and causes of evolutionary development and decline in mammals. (Chap. XI.)

SECTION 2. PRELIMINARY SURVEY OF THE MONOGRAPH AND OF THE CONCLUSIONS PRESENTED

RANGE OF THE TITANOTHERES IN GEOLOGIC TIME

Geographic distribution.—The earliest known titanotheres lived near the end of early Eocene time, after the appearance in the Rocky Mountain region of three kinds of quadrupeds—the horses, the related forest-living tapirs, and the more remotely related rhinoceroses, which still exist elsewhere.

The successive immigrations of related odd-toed ungulates are recorded in the Eocene deposits of the region now included in the State of Wyoming, which during Eocene time was a fertile land inhabited by an abundant fauna. The Eocene titanothere epoch in northern Utah, south of the great Uinta Mountain range, which, according to Powell, rose to majestic heights, ended in late Eocene time.

In lower Oligocene time the titanotheres had seemingly become the largest mammals in North America. They were second in size to the existing elephants only, but recent paleontologic evidence indicates the existence in Oligocene time in India of mammals that exceeded in size both the titanotheres and the elephants. In 1913 Mr. C. Forster-Cooper (1913. 1) described a new genus of perissodactyls from the upper Oligocene deposits of the Bugti Hills of Baluchistan, *Baluchitherium* (*Thaumastotherium*) *osborni*, an animal of proportions so gigantic that it dwarfs the largest known titanothere.

Sedimentary divisions and faunal life zones.—The lower Eocene to lower Oligocene sediments in which titanothere remains have been found occur here and there in several of the ancient river drainage basins of Wyoming. While the remains of the animals and plants of the period were accumulating in these sediments the titanotheres and other herbivorous quadrupeds and the carnivores that preyed upon them, as well as the other mammals and invertebrates of the land, of the water, and of the air, were constantly evolving, appearing and disappearing through migration and extinction. Thus where the sediments are very rich in fossils of all kinds—mammals, reptiles, fishes, and rarely birds—we are able to restore the life that was distinctive of certain more or less continuous phases of geologic sedimentation. These time divisions are designated life zones, as distinguished from the sedimentary divisions of groups and formations.

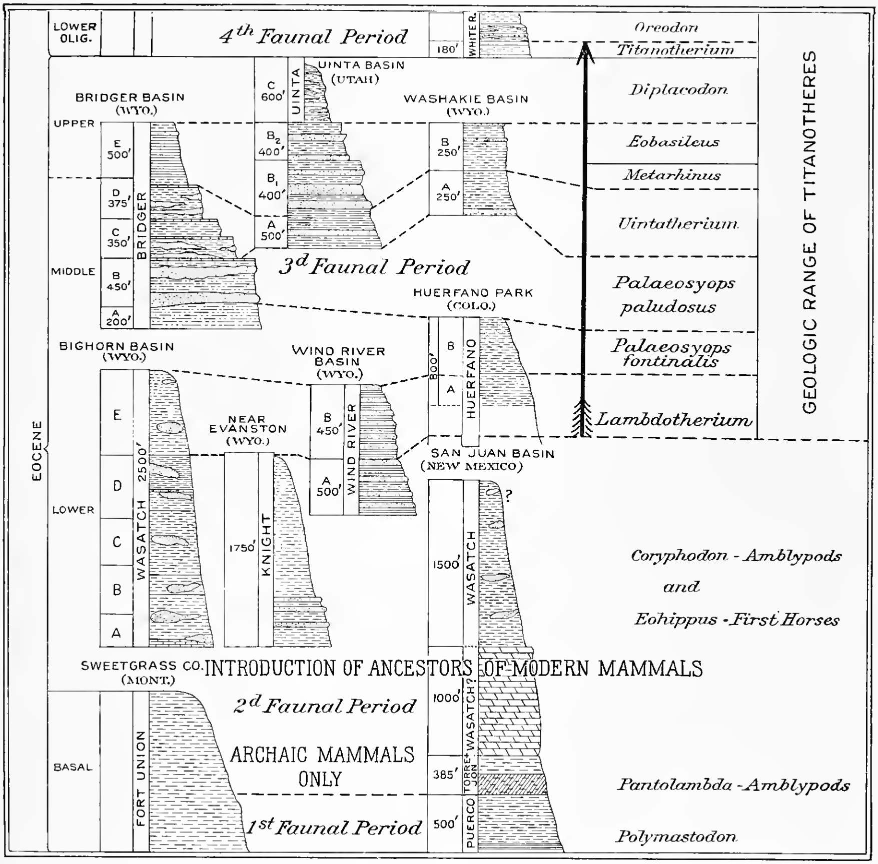

FIGURE 4.—Successive and overlapping Oligocene and early Eocene formations of the Rocky Mountains

The duration of the titanothere epoch is indicated by the arrow.

After an exploration of the *Titanotherium* zone that covered a period of over 70 years, from the discovery of Prout's "gigantic *Palaeotherium*" (*Menodus giganteus*) in 1846 to the present time, it has been found that the lower division of this zone is distinguished by the presence of 85 species of vertebrates. The names of the dominant form or forms of each zone are used to designate the several life zones. For the designation of the *Titanotherium* zone the name of this single genus *Titanotherium* (*Menodus*) is used, for it is the most distinctive form in that zone.

Many genera persist through several successive life zones. Two genera, the large-hoofed *Coryphodon* and the small primitive horse *Eohippus*, persist through four lower Eocene geologic phases or life zones, during which a succession of other species, as well as migrations, extinctions, etc., may be clearly observed. It may therefore be necessary to select more than one genus, perhaps as many as three genera, in order to define clearly a certain life zone. For example, the amblypod *Coryphodon*, the horse *Eohippus*, the tapir *Systemodon* unite to define the *Systemodon-Coryphodon-Eohippus* life zone of the lower Eocene.

It is through these zonal resemblances in the mammalian life, and more rarely in the plant life, that relatively sure estimates are made of the time during which the sediments containing certain fossils were deposited, irrespective of such geologic data as whether the sediments are thick or thin, whether they are products of erosion or of volcanic eruption, whether they were deposited in still water or in rapidly moving water, or whether they are composed of clay, sand, gravel, conglomerate, or tuff. The life zone, when adequately defined, is an absolutely reliable means of time correlation as distinguished from other means—physiographic, geologic, or lithologic.

Similar sediments.—It is true that in the Rocky Mountain region there prevailed at times over wide areas similar physiographic, climatic, and eruptive volcanic conditions, as, for example, during what we designate Fort Union time, Wasatch time, upper Bridger time. During such periods of uniform conditions the geologic evidence is concordant or harmonious with the paleontologic evidence afforded by life zones, and doubtless any paleobotanic evidence that may be found must also be concordant. In basal Eocene (Fort Union) time, for instance, the forests, the mammals, the reptiles, the climate, the physiography of the chief areas of sedimentation of the whole Rocky Mountain region were all more or less similar, and in this particular epoch these several means of time correlation afford more or less harmonious evidence.

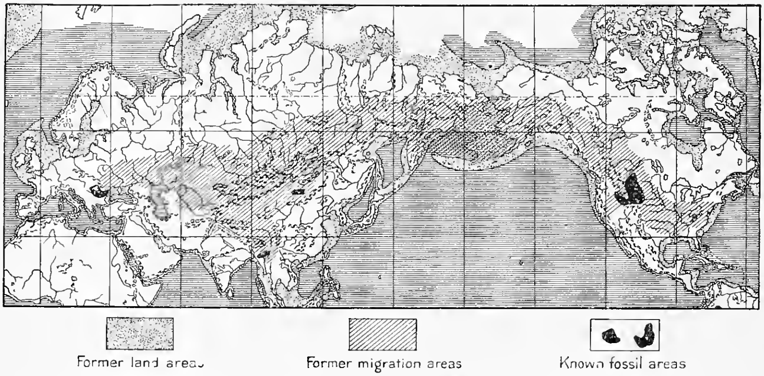

FIGURE 5.—Map showing areas throughout the world in which remains of titanotheres have been found (solid black) and areas in which titanotheres were probably in migration during Eocene and Oligocene time (oblique lines)

Titanotheres have been found in the northwestern United States, the Gobi Desert (Mongolia), Burma, and southeastern Europe.

Unlike sediments.—Such similar sediments, however, become increasingly rare in the continental deposits of Eocene and Oligocene time. A single life zone, such as the *Titanotherium* zone, may be contemporaneous with violent fluviatile action and heavy sedimentation in one region (for example, the Cypress Hills, Saskatchewan) and with excessively slow sedimentation on river flood plains in another region (Cheyenne and White Rivers, S. Dak.), or with a fall of volcanic ash in still another region (Beaver Divide, Wyo.).

Evolution of mammals a stable process.—By comparing all the events in the history of the American continent for which the records afforded by geology and paleontology harmonize with others afforded by paleontology alone we reach the conclusion that one of the most uniform, the most stable geographically, and the most widespread is the evolution of mammalian life. This evolution proceeds more or less uniformly in Europe, in Asia, and in North and South America. The apparently sensitive protoplasm (body substance) and germ plasm (hereditary substance) are far more stable and far more uniform in their progressive evolution than the surface of the earth. For this reason they form superior data for time correlation. This is one of the chief generalizations that have grown out of the long series of observations and studies of the correlation of Tertiary geologic events in America and Europe that were specially made in the preparation of this monograph.

Life zones of the titanothere epoch.—By the method of determining geologic time by discriminating life zones the whole epoch of the evolution of the titanotheres has been subdivided into titanothere zones, distinguished not only by successive genera and species of titanotheres but by corresponding changes in all the environmental forms of life. Each of these life zones probably represents a very long period of time, for in each there was a very considerable evolution of the titanotheres as well as of other forms. These zones (17–9; see table, p. 9), named in descending order, are as follows:

17. *Titanotherium-Mesohippus* zone (*Brontops robustus* zone, fauna; Chadron C fauna; *Brontops dispar* zone, Chadron B and *Brontops brachycephalus* zone, Chadron A fauna).
16. Theoretic zone (Uinta C 2).
15. *Diplacodon-Protitanotherium-Epihippus* zone (Uinta C 1 fauna).
14. *Eobasileus-Dolichorhinus* zone (Uinta B 2 and Washakie B 2 faunas).
13. *Metarhinus* zone (Uinta B 1 and Washakie B 1 faunas).
12. *Uintatherium-Manteoceras-Mesatirhinus* zone (Bridger C and D and Washakie A faunas).
11. *Paleosyops paludosus-Orohippus* zone (Bridger B fauna).
10. *Eometarhinus-Trogosus-Palaeosyops fontinalis* zone (Bridger A and Huerfano B faunas).
9. *Lambdotherium-Eotitanops-Coryphodon* zone (Wind River B and Huerfano A faunas).

Estimated duration of the titanothere epoch.—The duration of the titanothere epoch, from the time of the earliest known member of the family (*Lambdotherium*) to that of the last product of titanothere evolution (*Brontotherium*) is estimated as 600,000 years. This estimate is based on the calculation of Walcott, made from measurements of the rate of geologic sedimentation, that the entire Tertiary period covered not more than 3,000,000 years. If estimates made by Barrell (1917.1, p. 892), based on radioactivity, can be verified the duration of Tertiary time should be extended to 54,000,000 years. If this estimate is accepted the duration of the titanothere epoch alone would extend to 11,000,000 years. Though the geologic estimate of 600,000 years for titanothere evolution seems to be too small, the physical estimate seems to be too great, and for the present we may regard the estimate based on geologic data as ranging between 600,000 and 1,000,000 years.

HAYDEN'S SUBDIVISIONS OF THE EOCENE AND THE OLIGOCENE

The geologic formations in which titanothere remains occur and the life zones into which these formations are subdivided have been discovered and described during the last 56 years, the first report on them being that of Meek and Hayden (1862.1), in which the entire Tertiary geologic column is represented in a "General section of the Tertiary rocks of Nebraska," reproduced here in facsimile.

General Section of the Tertiary rocks of Nebraska.

Names.	SUBDIVISIONS.	Thickness.	LOCALITIES.	Foreign Equivalents.
Loup River beds.	Fine loose sand, with some layers of limestone,—contains bones of *Canis*, *Felis*, *Castor*, *Equus*, *Mastodon*, *Testudo*, &c., some of which are scarcely distinguishable from living species. Also *Helix*, *Physa succinea*, probably of recent species. All fresh water and land types.	300 to 400 feet.	On Loup fork of Platte River; extending north to Niobrara River, and south to an unknown distance beyond the Platte.	Pliocene.
White River Group.	White and light drab clays, with some beds sandstone, and local layers limestone. Fossils, *Oreodon*, *Titanotherium*, *Chœropotamus*, *Rhinoceras*, *Anchitherium*, *Hyœnonodon*, *Machairodus*, *Trionyx*, *Testudo*, *Helix*, *Planorbis*, *Limnœa*, Petrified wood, &c. &c. All extinct. No brackish water or marine remains.	1000 feet or more.	Bad Lands of White River; under the Loup River beds, on Niobrara, and across the country to the Platte.	Miocene.
Wind River Deposits.	Light gray and ash colored sandstones, with more or less argillaceous layers. Fossils,—fragments of *Trionyx*, *Testudo*, with large *Helix*, *Vivipara*, Petrified wood, &c. No marine or brackish water types.	1500 to 2000 feet.	Wind River valley. Also west of Wind River Mountains.	?
Fort Union or Great Lignite Group.	Beds of clay and sand, with round ferruginous concretions, and numerous beds, seams and local deposits of Lignite; great numbers of dicotyledonous leaves, stems, &c. of the genera *Platanus*, *Acer*, *Ulmus*, *Populus*, &c., with very large leaves of true fan *Palms*. Also, *Helix*, *Melania*, *Vivipara*, *Corbicula*, *Unio*, *Ostrea*, *Potamomya*, and scales *Lepidotus*, with bones of *Trionyx*, *Emys*, *Compsemys*, *Crocodilus*, &c.	2000 feet or more.	Occupies the whole country around Fort Union, — extending north into the British possessions, to unknown distances; also southward to Fort Clark. Seen under the White River Group on North Platte River above Fort Laramie. Also on west side Wind River Mountains.	Eocene?

FIGURE 6.—The Meek and Hayden Tertiary section of 1862

The deposits named are now known to include the following:
"Loup River beds." The lower Pleistocene fauna listed is found in an area that includes deposits of the Pliocene and upper Miocene (Ogalalla formation of Darton).
"White River group," including lower Miocene (Arikaree formation of Darton) and Oligocene (Brule and Chadron formations of Darton). The "*Choeropotamus*" is *Ancodus americanus*, the ancodont of the Chadron formation (*Titanotherium* zone).
"Wind River deposits" (summit of the lower Eocene).
"Fort Union or Great Lignite group" (basal Eocene).

There is little doubt that when Hayden described the White River group as "1,000 feet or more" in thickness, as including the "Bad Lands of White River; under the Loup River beds, on the Niobrara, and across the country to the Platte," and as composed of "white and light-drab clays, with some beds sandstone, and local layers limestone," he had in mind the area extending from Cheyenne River of South Dakota to the region south of North Platte River, displayed in the accompanying map and panoramic section. This section includes at its base the *Titanotherium* and *Oreodon* zones (Chadron and Brule formations), from which Hayden listed certain characteristic forms of animal life, such as *Titanotherium* (=*Menodus*), *Choeropotamus* (=*Ancodus*, *Hyopotamus*), "*Rhinoceros*" (=*Caenopus*), *Anchitherium* (=*Mesohippus*), *Hyaenonodon* (=*Hyaenodon*), *Machairodus* (=*Dinictis*).

These *Titanotherium* and *Oreodon* zones are now regarded as lower and middle Oligocene, respectively, and above them have been discovered the *Protoceras* and *Leptauchenia* zones, which embrace the highest sediments assigned to the Oligocene. The combined thickness of the Oligocene at this point is 600 to 650 feet. Above it, to the east, are "light-drab clays," having a total thickness of 500 feet, and these, when combined (1,150 feet), correspond to the "1,000 feet or more" of Hayden's section. It therefore appears that Hayden's description of the White River group conforms with the accompanying panoramic section of the Oligocene and lower Miocene exposed on the south side of White River, South Dakota, shown in Figure 7, as sketched under the direction of Osborn for the United States Geological Survey in 1909. (Osborn and Matthew, 1909.321.) Hayden did not, however, specifically define the upper limit of his group, and all the fossils listed by him as characteristic of his White River group apparently came from beds now classified as Oligocene. The name White River group has therefore for years been restricted to the beds of Oligocene age (Brule and Chadron formations).

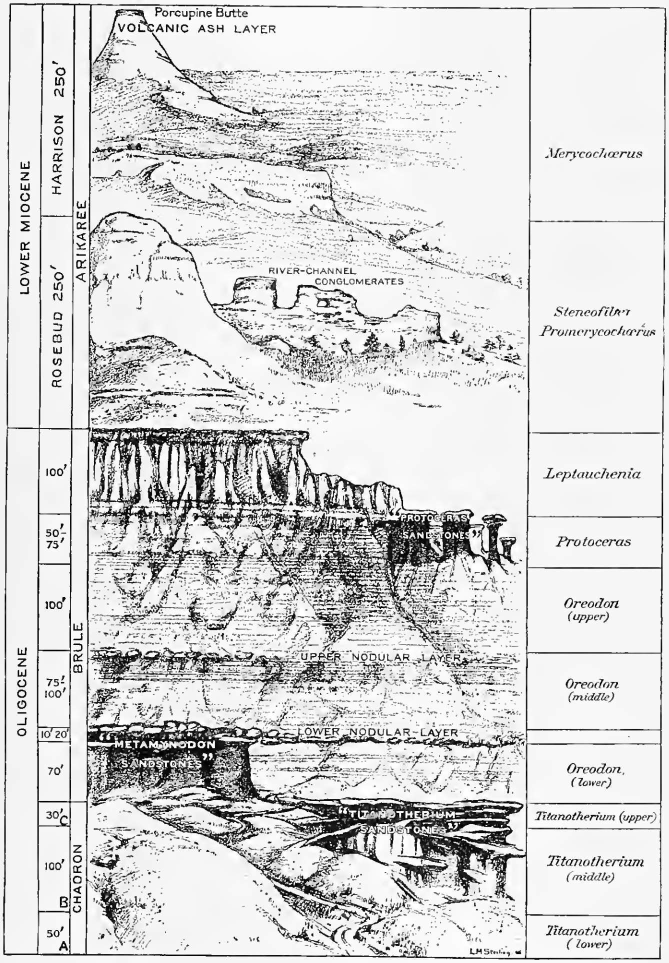

FIGURE 7.—Panoramic section of the Big Badlands of South Dakota, looking southeastward across Cheyenne and White Rivers to Porcupine Butte

This section of the ancient flood-plain sediments now exposed cuts through five great life zones—the *Titanotherium*, *Oreodon*, *Leptauchenia*, *Promerycochoerus*, and *Merycochoerus* zones. It includes also four ancient river-channel sandstones and conglomerates—the "*Titanotherium* sandstones," "*Metomynodon* sandstones," "*Protoceros* sandstones," and "*Promerycochoerus* sandstones"—each of which includes a more or less distinct river-border and forest fauna. (See map, fig. 69, vicinity of section B.)

DISCOVERY OF THE TITANOTHERES OF THE PLAINS

At the base of this great section lies the *Titanotherium* zone, or "*Titanotherium* beds" of the Hayden-Leidy memoirs, fully described in Chapter II, composed in part of clays, in part of river-channel sandstones, in which titanothere remains are extraordinarily abundant.

The northern borders of this wonderful region appear to have been first explored around Bear Creek, a dry tributary on the south side of Cheyenne River, from which Thaddeus A. Culbertson brought back the first collection of fossils in 1850. From these exposures of the *Titanotherium* and *Oreodon* life zones were obtained the greater part of Leidy's types, which are described in Chapter III. The Brule and Arikaree formations, which overlie the Chadron, belong to a period succeeding the titanothere epoch, with which this monograph closes.

The physiography of this ancient flood-plain region—its broad level stretches, its meandering rivers, its fringing river-border forests, its distant mountains and active volcanic peaks—as restored from our present knowledge of its fauna and flora, is described in Chapter II. It forms a wide contrast to the mountain-basin region, in the heart of which lie the Wind River deposits, described by Hayden in 1862.

DISCOVERY OF THE MOUNTAIN-BASIN ENVIRONMENT OF THE TITANOTHERES

As the entire lower Oligocene history of the titanotheres is recorded chiefly in the Great Plains region east of the Front Range of the Rocky Mountains, so their entire Eocene history is recorded almost exclusively in the mountain-basin region west of the Front Range, in western Wyoming, northwestern Colorado, and northeastern Utah. The interpretation of these remnants of the great Eocene sediments (given in Chapter II) involves far more difficult problems and has required more prolonged and in-

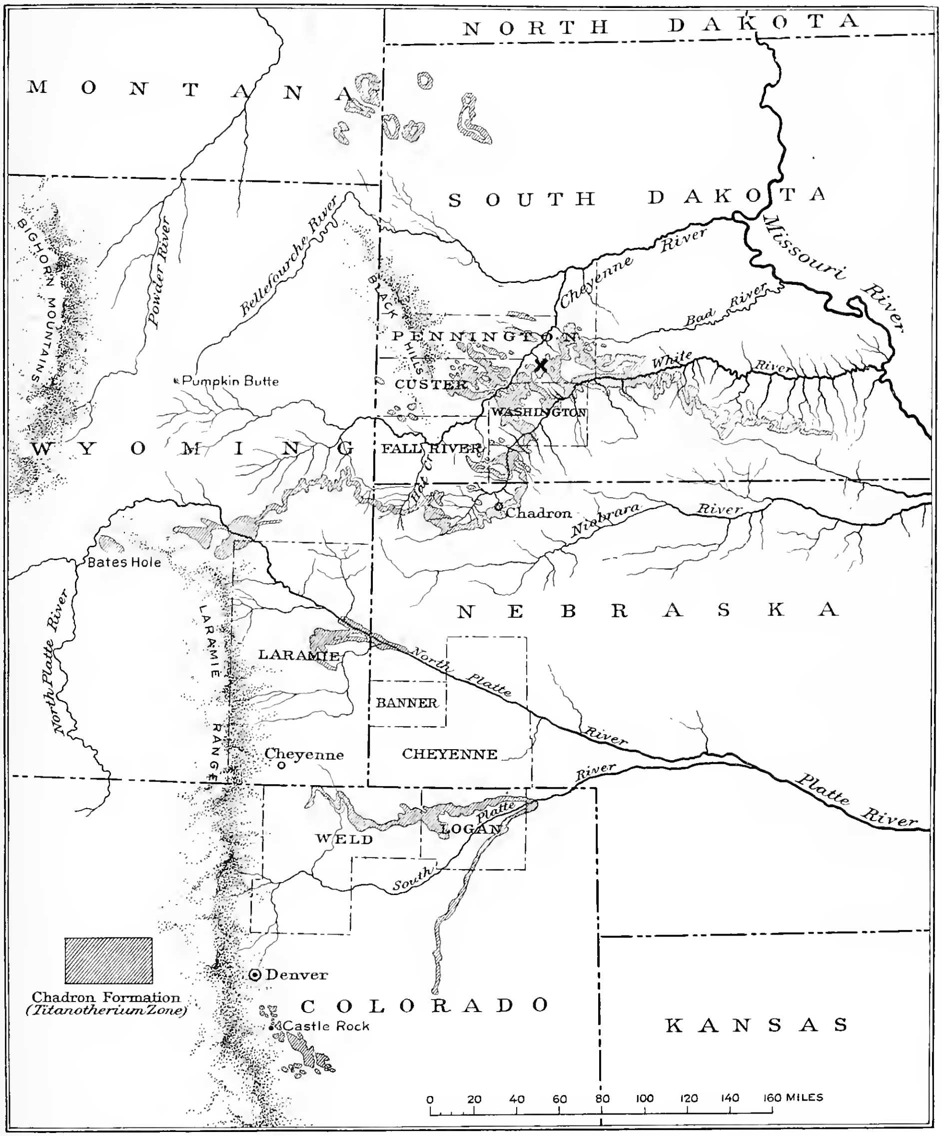

FIGURE 8.—Map showing the type geologic locality (×) of the *Titanotherium* zone on Bear Creek, branch of Cheyenne River, S. Dak.

The map shows the present exposures of the Chadron formation in South Dakota, Nebraska, Montana, eastern Wyoming, and Colorado. These exposures of the *Titanotherium* zone form the northern and western fringes of the overlying sediments, composing the Brule and Arikaree formations (the great "White River group" of Hayden). Map after Darton, U. S. Geological Survey, 1905, modified from observations of Matthew and Thomson, 1906, 1907.

tensive geologic research than the interpretation of the Oligocene sediments. The program for this exploration was proposed by the author to the Director of the United States Geological Survey in 1900.

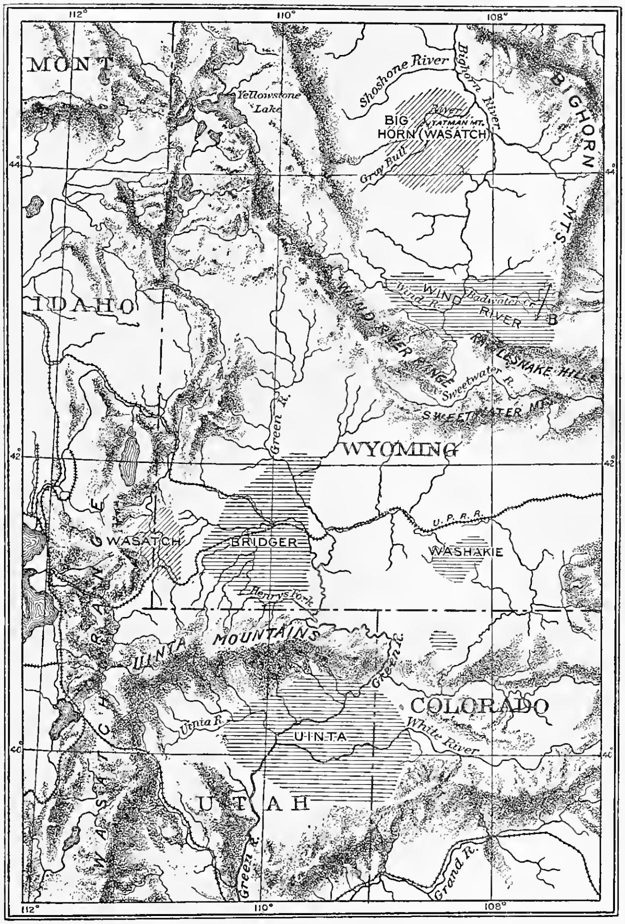

FIGURE 9.—Map showing cluster of typical lower, middle, and upper Eocene sedimentary basins in the heart of the Rocky Mountain region

Mapped chiefly after the explorations of Hayden, King, and Powell of successive Government surveys. The arrows indicate the lines along which were taken the chief geologic sections described and illustrated in Chapter II. Modified from Osborn and Matthew, 1909.321.

Each of the typical lower, middle, and upper Eocene basins shown in the accompanying map has had its antecedent historic and its recent analytic treatment, beginning with the Wind River deposits of Hayden (Meek and Hayden, 1862.1, p. 433), who described these deposits as "light-gray and ash-colored sandstones, with more or less argillaceous layers. Fossils—fragments of *Trionyx*, *Testudo*, with large *Helix*, *Vivipara*, petrified wood, etc. No marine or brackish-water types * * * 1,500 to 2,000 feet * * * Wind River Valley. Also west of Wind River Mountains." It is possible that Hayden here refers to the Wasatch or the Bridger formation, which lie southwest of the Wind River Range.

Subsequent exploration by Hayden revealed the typical Bridger, Wasatch, and "Washakie"[3] formations, each affording portions of separate chapters in the history of the ancient mammalian life of the mountain-basin region, which has proved to be no less remarkable than that of the Great Plains. Hayden was aided by the early paleontologic observations of Leidy on the Bridger fauna.

The survey along the fortieth parallel by Clarence King was supplemented by the paleontologic observations of Marsh, who described the life areas south of the Uinta Mountains and defined the *Diplacodon* zone of the Uinta. Cope hastened to describe the life of the Wind River, of the Wasatch, and of the "Washakie" formations and made known a very rich fauna contemporaneous with the Wasatch of the Big Horn Basin, to the north, and of the San Juan Basin of northern New Mexico, to the south, where he also discovered the basal Eocene fauna (Puerco). Five of these six geologic formations were long regarded also as faunistic units and were described as single life zones, namely, the "*Diplacodon* beds" (Uinta formation), the "*Dinoceras* beds" (Bridger and "Washakie" formations), the "*Lambdotherium* beds" (Wind River formation), the "*Coryphodon* beds" (Wasatch formation), and the Puerco formation.

The intensive observation of these six formations and the analysis of their fauna has enabled us to divide them into sixteen known life zones, which in turn afford the key to the time of origin and of cessation of sedimentation in each basin.

DISCOVERY AND DELIMITATION OF PERIODS OF SEDIMENTATION AND OF LIFE ZONES

The fact that these sediments accumulated very slowly, during long periods of geologic time and in the course of profound changes in climatic and physiographic environment, with consequent variations in the fauna and flora, has gradually become recognized, and the explorations and researches that have led to this recognition have

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[3] The Washakie was contemporaneous with the upper two-thirds of the Bridger formation, and the name Washakie is now abandoned by the United States Geological Survey for the name Bridger.

formed a considerable part of the work done for this monograph. At first the periods of sedimentation were regarded as broadly equivalent to a similar number of life zones. For example, up to the year 1900 the two chief formations, the Wasatch and the Bridger, were treated as containing one fauna each. It was not known that the Wasatch represents five distinct life zones, that the Bridger represents four and perhaps five life zones, and that the partly contemporaneous Washakie represents three distinct life zones. The correlation of different areas of sedimentation by means of fossils was similarly loose and inexact. The evidence discovered since 1900 by parties sent out from the American Museum of Natural History proves that there was considerable change of environment as well as a great faunal change during Bridger time. The careful recording of the precise geologic level at which every specimen, especially every type specimen, was collected, together with close analysis of lithologic evidence that the rocks afford as to modes of deposition, has worked a complete revolution in our knowledge of the history of these mountain basins in Eocene time and of the flood plains in early Oligocene time and has afforded the relatively precise and far more interesting sequence of events that is described in Chapter II.

Our geologic studies show that from basal Eocene to early Oligocene time there were six great physiographic and climatic epochs of sedimentation, shown in the accompanying table.

Epochs of sedimentation and life zones from basal Eocene to early Oligocene time in basins in the Rocky Mountain region

Physiographic epochs	Life zones
6. Lower Oligocene, represented by Chadron formation. Flood plains east of the Rocky Mountains. Sedimentation extremely slow. Moderate rainfall. Warm temperate climate.	17. Titanotherium-Mesohippus. 16. Theoretic zone. No fauna discovered.
5. Latest upper Eocene, represented by Uinta formation (Uinta C). Flood-plain basins south of the Uinta Mountains. Sedimentation relatively rapid; fine material. Heavy rainfall, diminishing.	15. Diplacodon-Protitanotherium-Epihippus.
4. Upper Eocene, represented by contemporaneous deposits in Washakie and Uinta Basins (horizons Washakie B and Uinta B) and probably by uppermost part of Bridger formation, or Bridger E. Violent river and stream action from the north and south sides of the Uinta Mountains. Eruptions of volcanic dust; coarse material. Heavy rainfall.	14. Eobasileus-Dolichorhinus. 13. Metarhinus.
3. Middle Eocene, represented by Bridger formation (horizons Bridger A, B, C, and D). More quiescent flood-plain conditions in the Bridger Basin; eruptions of volcanic dust; intervals of evaporation. Sediments composed in part of eroded material, generally laid down on lacustrine deposits.	12. Uintatherium-Manteoceras-Mesatirhinus. 11. Palaeosyops paludosus-Orohippus. 10. Eometarhinus-Trogosus-Palaeosyops fontinalis.
2. Lower Eocene, represented by Wasatch, Wind River, and Green River formations. Warm temperate climate of the Green River lake period, and evidently arid conditions in the contemporaneous Wind River sediments. Alternation of arid and fluviatile conditions characteristic of Wind River and Wasatch time. Evidence of open country, favorable to cursorial mammals.	9. Lambdotherium-Eotitanops-Coryphodon. 8. Heptodon-Coryphodon-Eohippus. 7. Systemodon-Coryphodon-Eohippus. 6. Eohippus-Coryphodon.
1. Basal Eocene, represented by the Puerco, Torrejon, and Fort Union formations. Forests, base-leveled areas, flood plains, and swamps widespread. Evidence of somewhat cooler climate.	5. Phenacodus-Nothodectes-Coryphodon. 4. Pantolambda. 3. Deltatherium. 2. Polymastodon. 1. Ectoconus.

The evidence of the existence of these successive climatic, physiographic, and biologic conditions is derived from studies by Berry of the flora; by Hay of the reptiles; by Osborn, Scott, Wortman, Granger, Matthew, Peterson, Douglass, and Riggs of the mammals; and by Sinclair and Johannsen of the lithology. These studies, the results of which are in part set forth in Chapter II, show a great advance upon the pioneer studies by Leidy, Marsh, and Cope, which were based chiefly on characters of the skeleton and teeth.

Our paleontologic division of the strata of the Eocene and lower Oligocene epochs into sixteen known life zones and one theoretic life zone enables us to fix the date of the immigrations of animals into this region, as well as the emigrations and extinctions, with much greater precision than formerly. Remains of titanotheres have been found in the upper eight of the known life zones.

Extremely important is the realization that the zonal fossil fauna reflects local conditions of sedimentation, which have a significant bearing on the kinds of animals preserved. For example, violent fluviatile action may preserve for us chiefly the river-border and aquatic fauna; but remains of the animals of the surrounding plains and of the distant forests may not have entered the river-channel sandstones. Forest-living animals, like the chalicotheres (*Moropus*), are relatively rare; and arboreal animals, like the lemurs (*Notharctus*), are seldom preserved in channel sandstones. Certain mammals apparently arriving as new immigrants, like the giant uintatheres, which suddenly appear in Bridger C, doubtless came from the surrounding plains or mountain regions, where the conditions were unfavorable for their entombment and fossilization.

The threefold division of the Wasatch and Bridger mammals by Matthew (1909.1) and Loomis (1907.1) according to their habitats, into meadow, forest, and river living groups, not only has important bearing on the gaps in the fossil record and on the interpretation of the evidence relating to immigration and emigration but is in accord with the principle of local adaptive radiation developed by Osborn, as fully set forth at the end of Chapter II.

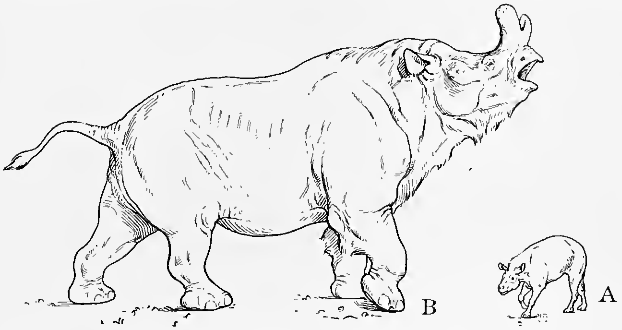

FIGURE 10.—Restorations of *Eotitanops borealis* (A) and *Brontotherium platyceras* (B), drawn to the same scale

One of the earliest members of the titanothere family (*E. borealis* of the Wind River formation, lower Eocene) and one of the latest and most formidable (*B. platyceras* of the White River group, lower Oligocene). From models in the American Museum of Natural History made by Erwin S. Christman under the direction of the author and of William K. Gregory.

PRINCIPLE OF LOCAL AND CONTINENTAL ADAPTIVE RADIATION

The changes in the climatic and physiographic conditions during the Eocene epoch, which favored not only the evolution but the fossilization of this or that type of animal, supply the key to the divergence in anatomical structure and to the presence in the diversified Rocky Mountain region and adjacent plains of a great variety of titanotheres, in a measure comparable to the great variety of ruminants found to-day in the plain and plateau regions of the continent of Africa.

Twenty branches of titanotheres.—In the eight life zones through which the observed evolution of the titanotheres has extended we invariably find more than one of the branches of the titanotheres, as in Wind River and early Bridger time, and in some areas as many as five or six contemporaneous branches. Altogether twenty branches of the great titanothere family tree have thus far been discovered in Eocene and lower Oligocene strata. This multiple branching, known as polyphyletic evolution, has made the study of the titanotheres more difficult and at the same time more fascinating than if these mammals presented only a single line of descent, as in monophyletic evolution. Some of the phyla of the titanotheres can be traced through a long series of successive evolutionary stages, such as *Palaeosyops*, *Manteoceras*, and *Dolichorhinus* in the Eocene, *Brontops*, *Menodus*, and *Brontotherium* in the Oligocene. Other phyla, such as the supposed river-dwelling *Eometarhinus* and *Metarhinus*, appear in two life zones only, in the middle Eocene, Huerfano B, and the upper Eocene, Uinta B 1, under fluviatile conditions of sedimentation favorable to fossilization.

Extremes of evolution.—Members of these twenty branches wandered in and out of the regions favorable to fossilization, and consequently no single branch (phylum) can be traced over the whole period of time. Even if this period covered 600,000 years (minimum estimate), or 11,000,000 years (maximum estimate), the descent of a gigantic horned quadruped, such as *Brontotherium platyceras*, from a small and defenseless animal akin to *Eotitanops borealis* would appear almost incredible were it not that unremitting exploration during the last half century has unearthed many phyla of species that are more or less intermediate between these two extremes. Although the whole period of life of the titanotheres was relatively brief as compared with that of the surviving horses, tapirs, and rhinoceroses, yet within this period the titanotheres became much more specialized than the modern tapirs; in fact, although in lower Eocene time they resembled superficially the existing tapir (*Tapirus terrestris*), by middle Eocene time they had reached and passed the tapir-like stage of evolution. As compared also with the contemporary horses they were more rapidly progressive; the difference between the lower Oligocene *Brontotherium* and the lower Eocene *Eotitanops* is vastly greater than that between the lower Oligocene horse *Mesohippus* and the lower Eocene *Eohippus*. The titanotheres evolved rapidly, partly because the environment was peculiarly favorable to their rapid evolution; partly because their internal germinal hereditary conditions favored their rapid evolution and differentiation.

Competition of the titanotheres with other ungulates.—In the course of their evolution the titanotheres came into competition as herbivorous quadrupeds with members of four orders of hoofed mammals. They competed with members of two archaic orders, the Amblypoda, typified by *Coryphodon*, and the Condylarthra, typified by *Phenacodus*. The titanotheres survived both these archaic orders. They came into competition with members of several other families of the Perissodactyla and rapidly outstripped them in evolution. The period of the extinction of the titanotheres, at the end of lower Oligocene time, marked also the decline of several other of the great families of perissodactyls, especially the aquatic rhinoceroses (amynodonts), the cursorial rhinoceroses (hyracodonts), and the fleet lophiodonts (*Colodon*), all of which became extinct soon after the titanotheres disappeared. The aberrant perissodactyl chalicotheres, which are in many respects similar to the titanotheres, survived, perhaps because they retreated, like the okapi of the Congo region of Africa, into the recesses of the forests. The tapirs, horses, and true rhinoceroses are the only odd-toed ungulates that outlived the titanotheres and survived to the present time. The fourth order of quadrupeds that competed with the titanotheres were the Artiodactyla, the diminutive ancestors of the even-toed ungulates, including the ruminants, which entered a great era of expansion soon after the titanotheres became extinct.

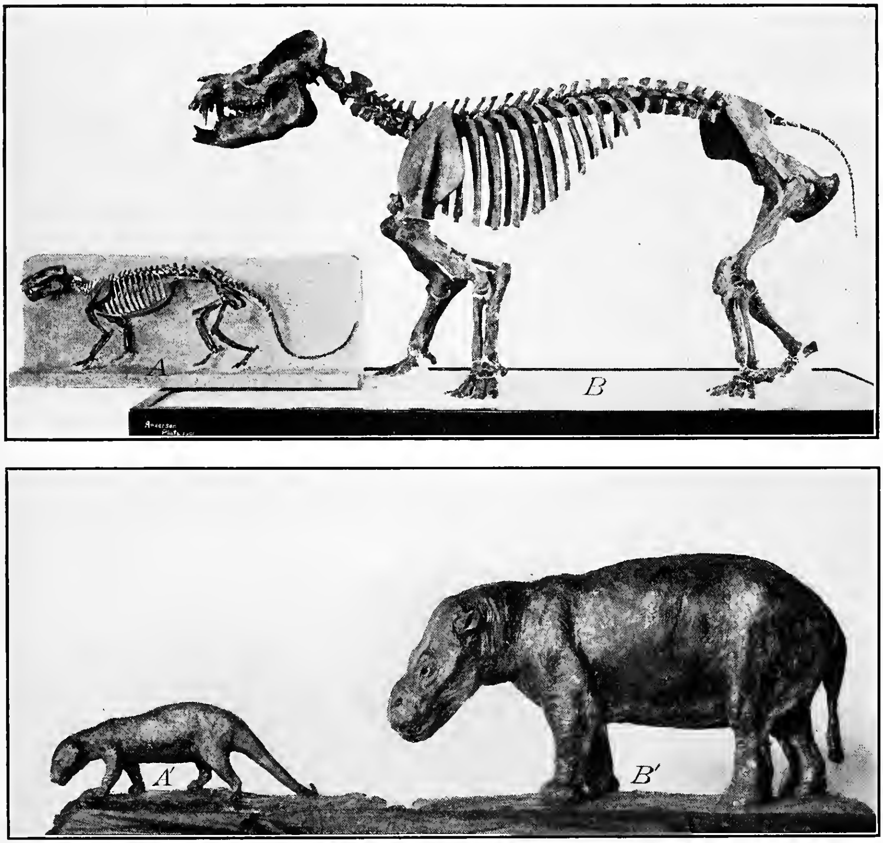

FIGURE 11.—Amblypoda: Skeletons and restorations of an ancestral form (*A*) and a specialized form (*B*)

A, *Pantolambda* of the basal Eocene Torrejon formation; *B*, *Coryphodon* of the Wasatch formation, persisting throughout five life zones of lower Eocene time, contemporaneous in its later stages of development with *Eotitanops* and *Lambdotherium*, ancestral titanotheres.

The earliest known types of titanothere evolution, *Lambdotherium* and *Eotitanops*, which were contemporaneous, appear in the fourth *Coryphodon* life zone. *Coryphodon* is a clumsy but powerful mammal of very archaic type, heavily armed with great canine tusks. It is descended from *Pantolambda* of the basal Eocene.

As *Coryphodon* appears in the far distant region of the Sparnacian of France as the companion of a giant bird (*Gastornis*) and of a primitive horse (*Hyracotherium*) similar to the American *Eohippus*, France and western America are brought close together in their mammalian life during lower Eocene time, so that we shall probably discover a similar *Coryphodon* fauna in the intermediate regions of eastern Europe, northern Asia, and British Columbia.

COMPARISON OF THE FOUR LIFE PHASES IN EUROPE AND IN NORTH AMERICA DURING EOCENE AND EARLY OLIGOCENE TIME

Length of Eocene time.—It is the comparison of the ancient life of the Old and the New World, especially by means of the results of the successive studies of Cope, Filhol, Depéret, Osborn, and Matthew, that has led to the demonstration by Osborn of four great continental faunal phases in Eocene and lower Oligocene time—phases that probably extended over the entire Northern Hemisphere and that were separated by the rise and fall of the archaic forms of life, by the union or separation of western Europe and western America into one single or two distinct centers of mammalian life, and by the severance of all connection between North and South America. Together these three series of events form a sequence that affords evidence of the great length of Eocene time. In other words, the biologic evidences of very marked evolution in single families like the titanotheres, of the zoogeographic events of migration, and of the succession and extinction of faunas together indicate that the Eocene epoch alone may have been longer than the 600,000 to 1,000,000 years allotted to the titanothere epoch in accordance with Walcott's estimates of Tertiary time based upon purely geologic data.

The archaic succeeded by the modernized mammals.—The long duration of Eocene time is further indicated by the subdivision of the Wasatch (*Coryphodon*) epoch (the "*Coryphodon* beds" of Marsh and Cope) into five lesser time divisions. Thus the term *Coryphodon* alone no longer serves as the designation of a life zone, because *Coryphodon* is now known to have survived through at least five life zones, Nos. 5–9 in the zonal series (p. 57), as follows:

"Coryphodon beds" of Marsh and Cope

9. *Lambdotherium-Eotitanops-Coryphodon* zone of Osborn	First appearance of the titanotheres in America. "Wind River" fauna of Cope.
8. *Heptodon-Coryphodon-Eohippus* zone	First appearance of lophiodonts in America. "Lysite" fauna of Granger.
7. *Systemodon-Coryphodon-Eohippus* zone	First appearance of tapirs in America. "Gray Bull" fauna of Granger.
6. *Eohippus-Coryphodon* zone	First appearance of horses in America. "Sand Coulee" fauna of Granger.
5. *Phenacodus-Nothodectes-Coryphodon* zone	*Phenacodus* extremely abundant. "Clark Fork" and "Tiffany" fauna of Granger. The closing phase of the reign of the archaic mammals of North America, *Pantolambda, Coryphodon, Phenacodus.*

The modernized mammals in the series tabulated above are the titanotheres, lophiodonts, tapirs, horses; the archaic mammals are the condylarths (*Phenacodus*) and amblypods (*Coryphodon*).

As remarked above, no single biologic phenomenon affords stronger evidence of the long duration of Eocene time than the complete replacement of the archaic fauna of North America, which exclusively held the stage during basal Eocene time, in itself a very long epoch, by the ancestors of modern mammals, as shown in the accompanying diagram (fig. 12) and indicated precisely in the transition between the *Phenacodus* and *Eohippus* zones. The modernized mammals came in not suddenly or en masse, as we formerly supposed, but gradually, family by family, the first apparently being the swiftest and most vitative family—the horses (*Eohippus*).

We infer that western Europe witnessed a similar replacement, for, although sparsely known, the basal Eocene life of western Europe was broadly similar to that of western North America.

The archaic life of American basal Eocene time, first made known by Cope, then studied by Osborn and Earle, and finally given very full and precise geologic and zoologic determinations by Matthew, Granger, and Gidley, affords the basis of our present knowledge of the wonderfully rich and varied fauna embraced within the four basal Eocene life zones.

The precision with which we are now able to note the extinction or disappearance of the archaic mammals and their replacement, one by one, by members of modernized families is due especially to the explorations of the American Museum of Natural History, led by Granger with the assistance of Sinclair, and to the analyses of the fauna by Matthew and Granger in a series of researches which are classic not only for their precision but for the revelation of new and hitherto unsuspected affinities of the mammals of North America with those of South America and with the existing mammals of the oriental region of the Old World.

Relation of the titanotheres to other quadrupeds.—In their broadest relations the titanotheres were mammals of the cohort Ungulata, which possess hoofs as distinguished from claws. We know that eleven great orders of ungulates (see accompanying table) were distributed through different parts of the earth during ancient and modern time. Of these eleven orders, which were the sources of the herbivorous quadrupeds of the world, only five have survived to the present time.

The eleven orders of Tertiary ungulates

I. Archaic ungulates:	
1. Amblypoda (amblypods)	America and Eurasia. Originating in Cretaceous time and contemporaneous in Eocene time (*Coryphodon*) with the titanotheres, becoming extinct in late Eocene time (*Uintatherium* and *Eobasileus*).
2. Condylarthra (condylarths)	America, Eurasia, and possibly South America. For a short period contemporaneous with the titanotheres, becoming extinct in the lower Eocene (Phenacodontidae).
II. Modernized ungulates:	
A. Primarily North American and north Eurasian:	
3. Artiodactyla (ruminants, etc.)	America, Eurasia, and subsequently South America. First appearing in early Eocene time. The Perissodactyla gradually gave way to the Artiodactyla. The chalicotheres were in part contemporaneous with the titanotheres near the end of their life period.
4. Perissodactyla (horses, titanotheres, tapirs, rhinoceroses).	
B. Originally African-Asiatic ungulates:	
5. Hyracoidea (hyraces)	First appearing on the African continent; subsequently, in part, entering southern Eurasia and North America. None of these orders is known to have been contemporaneous (in Europe) with the titanotheres or to have entered into competition with them.
6. Proboscidea (elephants and mastodons).	
7. Sirenia (sirenians)	Aquatic mammals, first known in Africa, possibly related to the same ancestors as the Proboscidea; believed to have sprung from ungulate ancestors.
8. Embrithopoda (arsinoitheres)	Known solely on the African continent; Oligocene.
C. Distinctively South American ungulates:	
9. Pyrotheria (extinct)	Exclusively South American in history and evolution.[4] None of these orders entered into competition with the titanotheres. Part of them (Litopterna) imitated the other orders of ungulates, and part (Toxodontia) evolved into unique forms.
10. Toxodontia (extinct)	
11. Litopterna (extinct)	

Only three of the eleven ungulate orders shown in the table were living in the Rocky Mountain region when the titanotheres arrived—(1) the archaic Amblypoda, represented, as we have seen, by *Coryphodon,* extremely small-brained, of very clumsy build, heavy-footed, in general proportions somewhat like the African rhinoceroses, *Rhinoceros* (*Ceratotherium*) *simus* and *R.* (*Opsiceros*) *bicornis;* (2) the Condylarthra, represented by a diminutive *Phenacodus,* also extremely small-brained, contrasting with *Coryphodon* in its small size and cursorial build, formerly but no longer believed to be ancestral to the higher ungulates; (3) the modernized Perissodactyla, including the ancestors of the horses (*Eohippus*), tapirs (*Systemodon*), and lophiodonts (*Heptodon*).

The newly arriving perissodactyl titanotheres equaled in size and resembled in their general cursorial limb structure the condylarths as well as the horses, tapirs, and lophiodonts. They were greatly surpassed in size by members of the *Coryphodon* family, some species of which were quadruple the size of the earliest known titanotheres. However, certain of the titanotheres of this stage (*Eotitanops*) exceeded the condylarths (*Phenacodus*) in size.

It is noteworthy that the archaic Condylarthra (*Phenacodus*) were numerically preponderant in the *Phenacodus* zone, just prior to the arrival of the earliest perissodactyl horses. There was doubtless an incessant competition between all these modernized, alert, large-brained perissodactyl ungulates and the archaic, small-brained ungulates (*Coryphodon* and *Phenacodus*), which were especially inferior in the mechanics of their foot structure. When, in the upper Eocene, the clumsily built Amblypoda reached the final phase of their evolution in the gigantic *Uintatherium* and *Eobasileus*, they apparently became suddenly extinct, and at the same time the titanotheres suddenly began to develop into more formidable animals. At no time in the Tertiary period was the earth populated in the same region with more than one type of very large quadruped. In the Northern Hemisphere the dominance of the amblypods (in the *Eobasileus-Coryphodon* epoch) was succeeded by the dominance of the titanotheres (in the closing titanothere epoch), and the titanotheres in turn, when they had reached their largest development, suddenly became extinct with no trace of a preliminary stage of decline.

OLD AND NEW SYSTEMS OF CLASSIFICATION

OLD TERMINOLOGY RETAINED

The studies for this monograph were begun by Professor Marsh under the old ideas of classification in mammalogy, derived from Linnaeus and his successors. These studies were continued by Osborn on the same old lines, as shown in his first paper on the titanotheres. (Osborn, 1896.107.) The discovery of adaptive radiation and of polyphyletic evolution, which was one result of the researches made for this monograph, has developed a new phyletic system of classification. Yet even in this new system it is necessary to adhere to the old Linnaean terminology, for the reason that Linnaean methods have been used during the long period of systematic description in

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[4] A single jaw attributed to one of the aberrant South American ungulates has been found in the *Eohippus-Coryphodon* life zone, "Sand Coulee beds" of Clark Fork Basin, Wyo.

which the greater number of genera and species of titanotheres have been described; and the Linnaean generic and specific names can not be replaced unless two systematic names have been given to the same animal. Rather than introduce a new terminology we attempt to place each Linnaean species in its proper phyletic position—that is, in its true phylum—and to connect it with other species by intermediate or transition stages, which are termed mutations, the "ascending mutations" of Waagen as distinguished from the contemporaneous "mutations" of De Vries.

LINNAEAN METHODS OF DEFINING SPECIES, GENERA, AND PHYLA OF TITANOTHERES

Between 1847 and 1902 as many as 29 genera and 67 species of Eocene and Oligocene titanotheres were defined, but of all the definitions given hardly a single one has proved to be distinctive and valid. The main characters utilized in the old classifications by the chief contributors to the history of the Oligocene titanotheres—that is, by Leidy, Marsh, Cope, Scott, and Osborn—were the following:

1. The presence or the absence and the number of incisor teeth (Cope and Marsh, in generic definition).
2. The number of premolar teeth (Marsh, in generic definition).
3. The development of the cingulum on the premolar teeth (Cope and Marsh, in generic definition).
4. The presence of a second cone on the last superior molar (Marsh, in generic definition).
5. The length and shape of the nasal bones (Cope, Marsh, Scott, and Osborn, in generic definition).
6. The length and shape of the fronto-nasal horns (Cope and Marsh, in generic definition).
7. The presence or absence of a trapezium in the carpus (Hatcher, in phyletic definition).

Proceeding along these lines Marsh and Cope defined a number of genera of titanotheres, certain of which have since proved to be closely successive members of the same phylum and consequently members of the same genus. Osborn went to the opposite extreme in attempting to reduce all the titanotheres to a single genus. In his paper of 1896, entitled "The cranial evolution of *Titanotherium*" (Osborn, 1896.110), he reached the wholly erroneous conclusion that there had been only a single distinct and definable genus of titanotheres—the original *Titanotherium* of Leidy—and that all the variations among the titanotheres were of the rank of species, representing different stages of development. This has proved to be a greater error than that of Marsh, because it was based on the hypothesis that the titanotheres belonged to a single—monophyletic—line of descent.

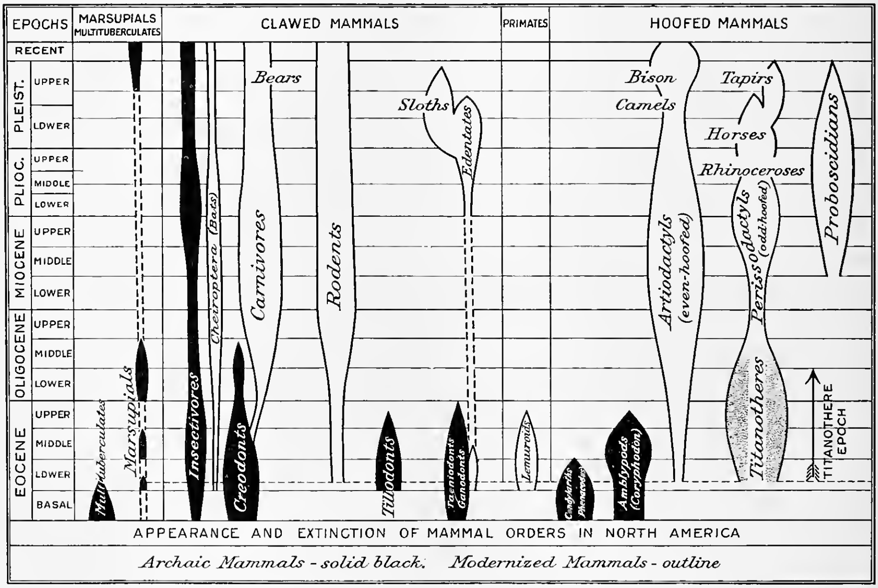

FIGURE 12.—Diagram showing the gradual extinction of orders of archaic mammals (solid black) of earliest Eocene time and their gradual replacement during later Eocene time by the ancestors of modernized orders of mammals (outline), including related forms that are now extinct

RECOGNITION OF MANY LINES OF DESCENT; POLYPHYLY THE KEY TO INTERPRETATION OF THE FAMILY

In January, 1901, a few months after the studies for this monograph were begun, all the data, observations, skull sections, and measurements were assembled, and by July of the same year it was demonstrated by Osborn that at least four lines of separate descent are to be found among the lower Oligocene titanotheres, and this number has since been increased to five or eight.

In 1902 Osborn established the fact that throughout lower Oligocene time, when the *Titanotherium*-bearing beds were being deposited, as many as eight more or less different phyla, or series, were independently evolving in the same region. Certain of these phyla embrace one or more of the genera originally proposed by Pomel, Leidy, Cope, and Marsh. Other phyla correspond with certain genera—for example, *Menodus* Pomel (syn. *Titanotherium* Leidy), *Brontops* Marsh, *Allops* Marsh, *Megacerops* Leidy, *Brontotherium* Marsh. These five generic names correspond to members of five phyla that persisted throughout a very long period of geologic time. The remaining phyla of titanotheres are branches that persisted only for a short time, so far as we know at present—for example, *Diploclonus*.

As shown in the accompanying diagram (fig. 15) these generic phyla are branches of the family tree of the titanotheres. When two of these branches run close together they may for convenience be united into a single subfamily. Thus, for purposes of description the graphic presentation of the titanothere family tree in the accompanying diagrams may be supplemented by the systematic subdivision of these animals into 12 subfamilies and 24 genera, as shown on a subsequent page.

The free use of subfamily divisions to distinguish the branches of Eocene and Oligocene generic phyla from one another is similar to that which the author has adopted in expressing the relationships and descent of the rhinoceroses, animals whose evolution presents in many respects analogies to the evolution of the titanotheres, especially in the modes of the evolution of horns, in the loss or retention of cutting teeth (incisors), and in the adaptations of limb structure to swift and slow movement.

RELATION OF THE PHYLOGENETIC CLASSIFICATION TO THE LINNAEAN CLASSIFICATION

Linnaeus described one or more species of mammals geographically distributed in space (see table on p. 16), whereas the phylogenetic classification of the titanotheres covers species extending over both space and time. The geographic range of the existing red deer (*Cervus*) and of the extinct titanotheres lies within the same zoogeographic region—Holarctica, which includes Europe, Asia, and North America. The comparison is therefore significant. (See table on p. 18.)

The classification presented in this monograph is more than phylogenetic: it is polyphyletic. Linnaeus (1758.1), when he wrote the several editions

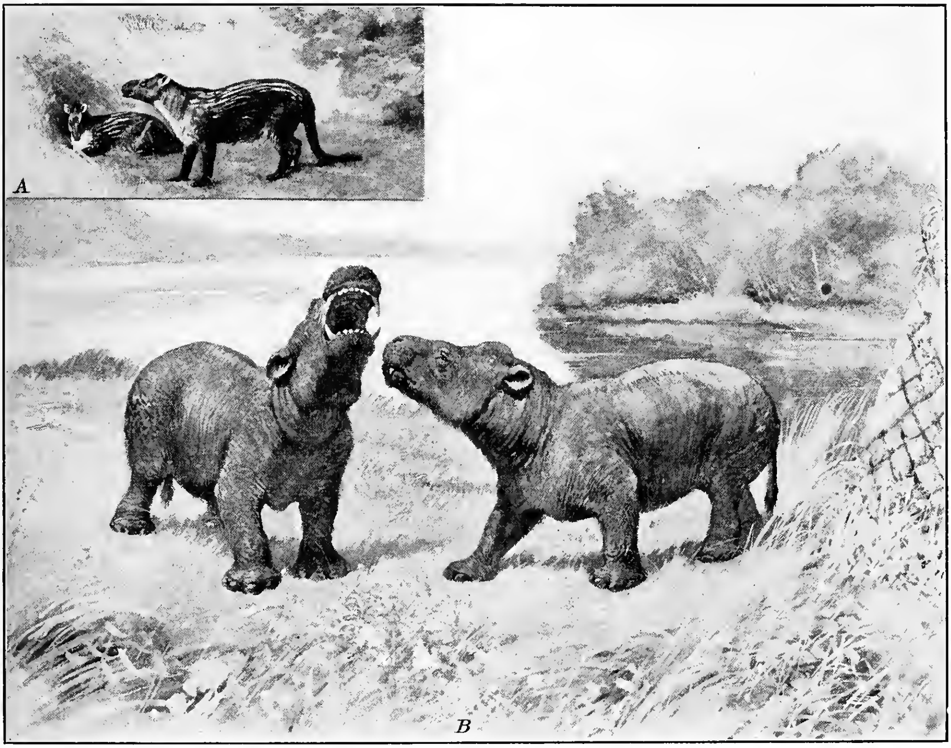

FIGURE 13.—*Phenacodus* (*A*) and *Coryphodon* (*B*) drawn to the same scale

Restorations made by Charles R. Knight under the author's direction.

of his "Systema naturae" (1735–1768), did not dream of the succession of species of mammals in time; he did not know of a single phylum, much less of polyphyla. Darwin's theory of descent and divergence implied the existence of phyla, but when he published "The origin of species" (1859.2) he also did not know of a single phylum or a single direct line of descent. Waagen (1869.1) was the first to discover a continuous phylum (namely, of ammonites)—that is, successive hereditary stages, which he named "mutations." Many direct phyla of invertebrate animals have since been made known.

In this monograph we first learn the full meaning of a mammalian phylum—namely, a phylum is a continuous geologic line of descent diverging from other phyla (1) in the gradual transformation of every character in size and proportion and (2) in the relatively rapid gain or loss of certain characters. This definition relates to the hard parts, which are preserved in fossilization; the principle applies equally to characters of all kinds.

In contemporaneous Linnaean genera and species we observe differences of many kinds, such as differences in color and proportion, and, more rarely, we may note the presence or absence of simple characters of teeth, vertebrae, or claws. The "species" of Linnaeus are now known to be actually superspecies and to include one or more modern species, subspecies, and geographic races and varieties, distinguished by differences in coloring, habit, proportion, or otherwise. These differences are due in part to environment and in part to habit. They represent the different bodily effects produced on animals of similar ancestral stock under different environments, in which somatic changes

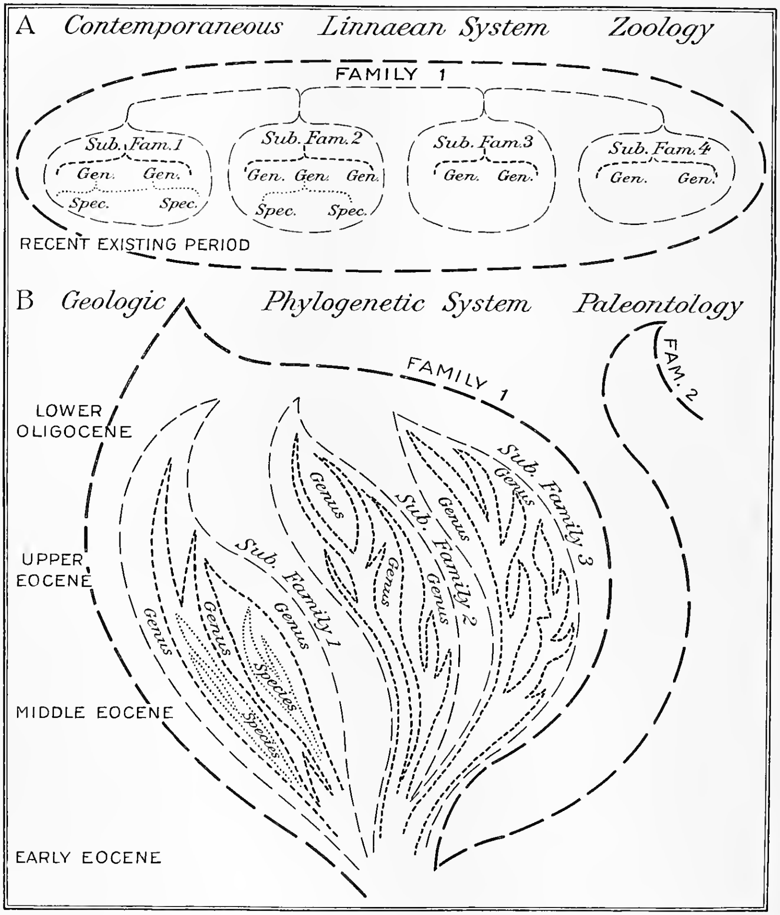

Figure 14.—Contrast between the Linnaean and phylogenetic systems of classification of subfamilies, genera, and species

are rapid and conspicuous. They are in part hereditary (germinal) differences, which pass down for generations unmodified by habit or environment.

For example, the American genus *Peromyscus* (the white-footed mouse), as studied by Osgood (1909.1), presents a continuous series of transition changes in color and form in species having a geographic range from Tehuantepec to Alaska. In the northern regions *Peromyscus* is larger and has relatively longer teeth and a skull that may be somewhat elongate (dolichocephalic). *Peromyscus* may have been widely distributed from some common center during the last 40,000 years, and during this long period there may have been both geographic or space evolution and geologic or time evolution, the evolution in time being comparable to that which we observe in the geologic phyla of the titanotheres.

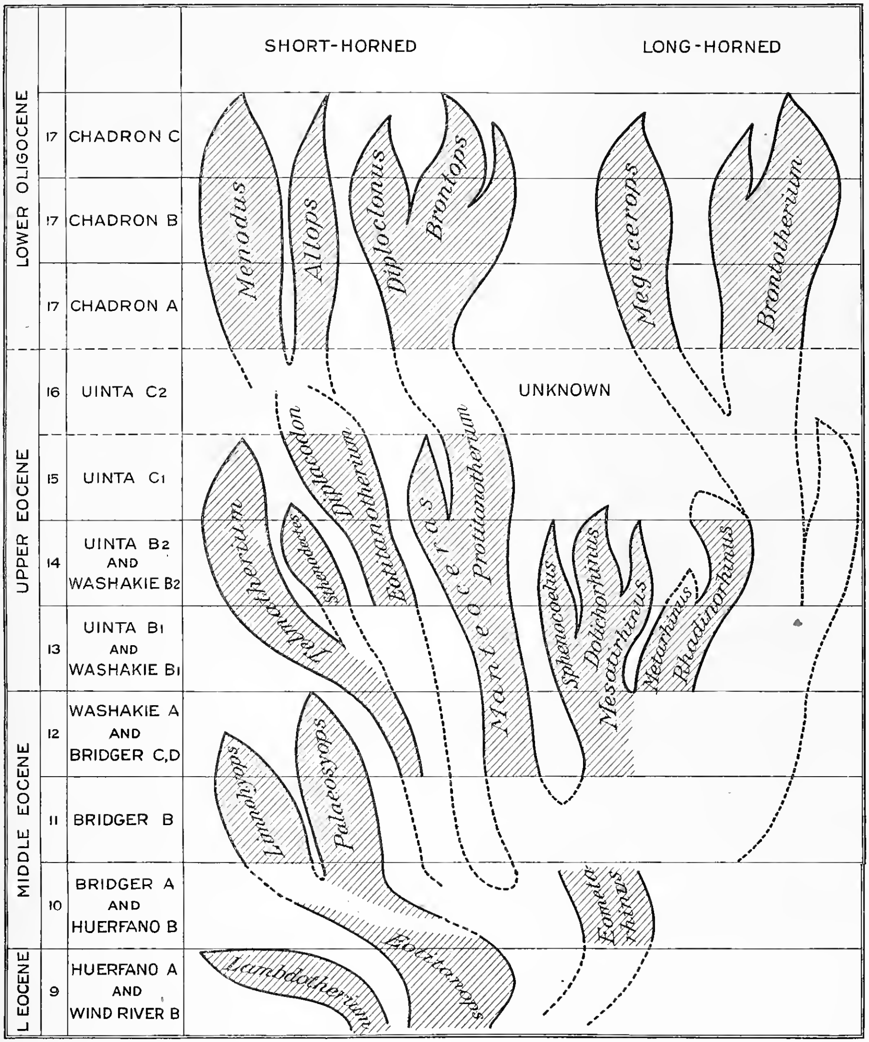

Figure 15.—The family tree of the titanotheres, showing the relation between the branches (phyla), subfamilies, and genera, as known to science in 1919

The shaded areas show connections that are well established; the dotted lines show gaps that remain to be filled by future discovery, especially in the Uinta formation of Utah.

The existing genus *Cervus* affords another example, significant because its geographic range is similar to that of certain Oligocene titanotheres.

Species and subspecies of the genus Cervus

[Table prepared by Gerrit S. Miller, 1918]

Name	Habitat	Nature of habitat	Climate
Cervus canadensis (American elk = wapiti).	New York and New Jersey southward to the Carolinas; central western States; Nebraska, the Dakotas, and the country farther west, across the Rockies.	Open plains, badlands, sand hills; forests and meadows.	Humid to extremely arid.
C. c. merriami (Merriam's elk)	New Mexico and Arizona	Mountains and plateaus; forests and meadows.	Generally arid; forests wet.
C. nannodes (dwarf elk)	San Joaquin Valley, Calif., and adjoining foothills.	Plains and tule swamps	Generally arid.
C. occidentalis (Olympic elk)	Washington, Oregon, California; formerly south to San Francisco Bay. Vancouver Island?	Chiefly forested regions; some meadows.	Humid.
C. xanthopygus (Bedford's deer; Manchurian stag).	Manchuria and adjoining parts of Siberia	Forests	Do.
C. sibiricus (Altai maral)	Baikal, Saiansk, and Altai Mountains; southern Siberia and northern Mongolia.	Formerly forests and open timberless country; even open high desert mountains. Now restricted to forests and meadows.	Extremely humid to extremely arid.
C. songaricus (Tien-Shan stag)	Tien-Shan Mountains	Forests and alps	Mostly arid(?)
C. yarkandensis (Yarkand stag)	Eastern Turkestan		Do.
C. macneilli (Kansu stag)	Kansu and Szechwan border of Tibet		
C. albirostris	Tibet		
C. wallachi	do		
C. wardi (Ward's stag)	do		
C. hanglu (Kashmir deer; hangul, hanglu).	Vale of Kashmir and adjacent mountains	Chiefly forest; some open parks.	Humid.
C. bactrianus	Russian Turkestan		Chiefly arid.
C. maral (maral)	Persia, Crimea, Caucasus	Chiefly forest	
C. elaphus (red deer)	Sweden		Humid.
C. e. atlanticus (Norwegian red deer).	West coast of Norway		Do.
C. e. germanica (red deer).	Middle Europe		Do.
C. e. bolivari (red deer of central Spain).	Central Spain		
C. e. hispanicus (red deer of southern Spain).	Southern Spain		Humid and semiarid.
C. scoticus (red deer)	Great Britain and Ireland		Humid.
C. corsicanus (Corsican stag)	Corsica and Sardinia		Semiarid.
C. barbarus (Barbary deer)	Morocco, Algiers, palearctic north Africa		Chiefly arid.

COMPARISON BETWEEN ZOOLOGIC AND PALEONTOLOGIC SPECIES

The difference between zoologic and paleontologic species is represented in the accompanying diagram (fig. 16), showing the descent and relationship of certain members of the dog family (Canidae). A theoretic stem or central form is shown from which geographic races have been given off horizontally, as it were, and the ascending mutations and species of the evolutionary line of development from the ancestral form have arisen geologically.

It follows that in making an anatomic comparison between the existing geographic species and subspecies of such genera as *Peromyscus* or *Cervus* and a geologic phylum of species such as that of *Menodus* or *Brontotherium* the same comparative anatomical methods of measurement and observation should be employed. Direct measurements of the length and breadth of the skull should be recorded, by which indices (proportions of single structures like the skull) and ratios (proportions between different parts like the upper and lower segments of the limbs) should be established.

The proportional changes technically known as dolichocephaly (elongation of the head), brachycephaly (broadening of the head), dolichopy (elongation of the face), brachyopy (abbreviation of the face), dolichopody (elongation of the feet), brachypody (abbreviation of the feet), dolichomely (elongation of the limbs), brachymely (abbreviation of the limbs) occur in geographic species and subspecies in their corresponding stages exactly as they occur in geologic phyletic time series. The chief difference is that in the geologic time phyla these differences of proportion may be followed through long periods of time from their incipient to their final stages, in which various climaxes of change of proportion are reached, such as extreme length or breadth of head or extreme length or shortening of the feet.

PROPORTIONS OF THE SKULL IN BEARS AND IN TITANOTHERES

In comparing the Eocene and Oligocene titanotheres with the modern bears (*Ursus*), for example, as studied by C. Hart Merriam (1918.1), we may note certain parallelisms. The members of each of the eleven subfamilies of titanotheres are distinguished by certain proportions of the skull—that is, they are broad-headed, round-headed, or long-headed—by the shape of the horns and the acceleration or retardation in their development, by the presence or absence of cutting (incisor) teeth, by certain proportions of limb, according as they are swift-footed (cursorial), slow-footed (mediportal), or heavy-footed (graviportal), and by other minor features. The methods applied to the study of the existing bears may be applied to the study of the skull or other hard parts of the titanotheres. In the titanotheres, however, we may observe all these changes of proportion actually in progress from stage to stage as revealed by paleontology, whereas in the bears we can observe only certain structural forms, which, so far as our observation goes, appear to be fixed or completed, although they undoubtedly represent stages in a state of actual progression.

FEATURES DISTINGUISHING PHYLA OF TITANOTHERES

The first application of changes of proportion to the arrangement of the subfamilies of titanotheres is the following synopsis, prepared in 1914:

Proportions of skull and limbs; presence and absence of characters distinguishing the subfamilies (main phyla) of titanotheres

[Osborn, 1914.409]

B. Bridger and succeeding titanotheres; cranium longer than face:
   11. Brontotheriinae; mesaticephalic to brachycephalic; horns long, transversely flattened, and divergent (*Brontotherium*).
   10. Megaceropinae; mesaticephalic to extreme brachycephalic; horns long, vertically placed; no incisor teeth (*Megacerops* (=*Symborodon*)).
   9. Brontopinae; brachycephalic; horns short, rounded, or oval; incisors persistent (*Brontops* (=*Megaceratops*), *Diploclonus*).
   8. Menodontinae; mesaticephalic to dolichocephalic; short triangular horns; incisor teeth reduced or wanting; feet and limbs long (*Menodus* (=*Titanotherium*), *Allops*).
   7. Dolichorhininae; mesaticephalic to dolichocephalic; limbs, so far as known, short (*Dolichorhinus, Mesatirhinus, Sphenocoelus, Metarhinus, Rhadinorhinus*).

B. Bridger and succeeding titanotheres—Continued.
   6. Manteoceratinae; mesaticephalic to brachycephalic; accelerated development of the horns; mediportal (*Manteoceras, Protitanotherium*).
   5. Diplacodontinae; dolichocephalic; accelerated molarization of the premolars; imperfectly known (*Diplacodon*).
   4. Telmatheriinae; mesaticephalic to dolichocephalic (*Telmatherium, Sthenodectes*).
   3. Palaeosyopinae; brachycephalic; short-limbed (*Palaeosyops, Limnohyops*).

A. Wind River titanotheres; face longer than cranium:
   2. Eotitanopinae; medium-limbed, mediportal (*Eotitanops*).
   1. Lambdotheriinae; light-limbed, cursorial (*Lambdotherium*).

The above scheme presents the eleven subfamilies of titanotheres as they were distinguished in 1914.

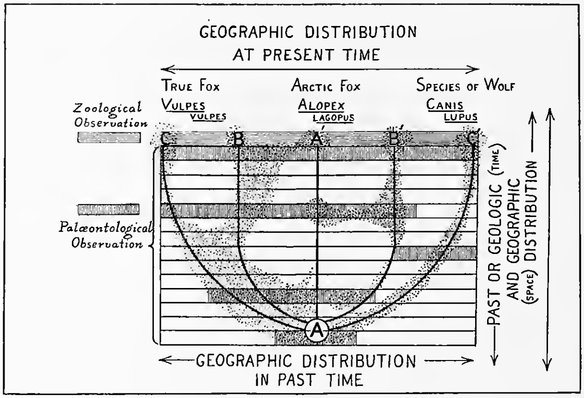

FIGURE 16.—Theoretic descent of existing members of the dog family (Canidae) from a common ancestor

A represents the ancestral type. Dots represent intergradations indicated by paleontologic observations (vertical lines) covering five periods of geologic time. A', B, B', C, and C' represent existing forms, and dots represent a few existing intergradations demonstrated by zoologic observations (horizontal lines). Heavy lines and the adjacent dots represent the phyla; also the past and present distribution of geographic (ontogenetic and environmental) subspecies, races, and intergrades.

Since that time certain phyla have been condensed by the discovery of titanotheres that link together some of these subfamilies, and others have been expanded by the discovery of new subfamilies, such as the Rhadinorhininae.

MUTATIONS OF WAAGEN

Where the fossil material is abundant the genera and species are found to be connected by a series of intergradations. These intergradations, though continuous, are measurable, and therefore a species is subdivisible into a series of intergrading forms. The monophyletic, systematic, or taxonomic unit division of these species is the mutation of Waagen, which is a subspecific stage in the development of one or more characters. Such an actual sequence of mutations of Waagen may be illustrated in the genus *Brontotherium*, as indicated on the following page.

Oligocene stages of titanotheres of the Brontotherium phylum in the Titanotherium zone

Division of zone	Stage	Species	Theoretic ascending mutations
Upper.	Ultimate flat-horned stage	Brontotherium platyceras	Species.
	Penultimate branching horn	Brontotherium ramosum	Subspecies. Mutation. Do.
	Short nasal stage	Brontotherium curtum	Species. Subspecies. Mutation. Do.
	Intermediate nasal stage	Brontotherium medium [a]	Species. Subspecies. Mutation. Do.
	Long-horned stage	Brontotherium dolichoceras	Species. Subspecies. Mutation. Do.
	Do	Brontotherium gigas [b]	Species. Subspecies. Mutation. Do.
Middle.	Medium-horned stage	Brontotherium hatcheri	Species. Subspecies. Mutation. Do.
	Thick-horned stage	Brontotherium tichoceras	Species. Subspecies. Mutation. Do.
Lower.	Low-horned stage	Brontotherium hypoceras	Species. Subspecies. Mutation. Do.
	Primitive low-horned stage	Brontotherium leidyi	Species. Subspecies. Mutation. Do.

[a] Genus *Titanops* Marsh.

[b] Type of genus *Brontotherium* (Marsh).

ZOOLOGIC AND PALEONTOLOGIC NOMENCLATURE

Significance of the table.—The sequence shown in the accompanying table, which presents what is believed to be a generic, monophyletic, or nearly single phyletic series of changes of form, evolving in a single geographic region of South Dakota, illustrates the manner in which the Linnaean binomial system and the mutation substages of Waagen may be adapted to express a phyletic sequence. The newer trinomial names of modern mammalogy and the subspecific names may be employed to connect the intergrading mutations.

The most primitive species, *Brontotherium leidyi*, is so notably distinct in size and skull structure from the most advanced species, *Brontotherium platyceras*, that, if named by zoological standards, it might well be placed in a separate genus—in fact, several generic names have been suggested for members of this phylum, namely, *Brontotherium*, *Titanops*, *Brontotheridion* (MS.)—but the subdivision of such a phylum into a number of genera would obscure the all-important monophyletic unity, for such a phyletic genus is defined by its peculiar and distinct evolutionary tendencies. For example, the genus *Brontotherium* tends toward the evolution of flattened horns, a characteristic which begins in a very slight flattening of the posterior side of the horn, as observed in *B. leidyi*, and develops into the extraordinarily broad, flattened horns of *B. platyceras*.

New phyletic meaning of species.—The species represented by large collections of mammals like those of some of the phyla of the titanotheres, especially the

Brontops phylum, are so closely intergraded and connected by "ascending mutations" that the dividing lines between them can be drawn only arbitrarily, according to individual judgment. In the *Brontops* phylum, for example, the species *Brontops brachycephalus* grades imperceptibly into the species *Brontops dispar* through gradual transitions in a great number of characters, as may be seen in the Hatcher collection in the United States National Museum. There is no evidence of brusque transitions, saltations, or jumps in any structure, such as are presupposed in the mutation theory of De Vries. By contrast, the mutations of Waagen are intergradations between arbitrarily defined species, and through these mutations species and genera pass imperceptibly one into another.

Evolutionary characters of each phylum.—Thus we reach a clear conception of a phylum of the titanotheres in its osteologic and dental characters. A phylum may be further defined as a succession of interbreeding (syngamic, Poulton) individuals of similar (synepigamic, Poulton) ancestry, which may or may not occupy a similar range of country (synpatric, Poulton), which follow in every structural character a similar line of evolution (synphyletic, Osborn) and adaptation (syntelic, Osborn).

In each horn, in each tooth, in every bone of the skull and skeleton, and by inference in all the hard parts as well as in all the soft parts, each phylum has its distinctive mode and rate of transformation in each character, as follows: (1) Distinctive hereditary proportion; (2) distinctive tendencies to change of proportion; (3) distinctive progressive changes of proportion; (4) distinctive retrogressive changes of proportion; (5) distinctive accelerations and retardations in ontogeny (individual development); (6) distinctive rates (velocities) of progression and retrogression in phylogeny in each character. In each phylum are consequently developed distinctive and ever changing proportions and ratios between different single characters and groups of characters, measurable by indices and ratios. Such indices express the degrees of broad-headed, long-headed, broad-footed, short-footed structure and proportion, and so on. Each phylum has also its distinctive but constantly changing indices and ratios of teeth to skull, of skull to body, of body to limbs, etc., which also are constantly changing as we pass from the lower to the higher geologic levels.

Old and new meanings of taxonomic terms.—In the following table a comparison is made between the old and the new meanings of the taxonomic terms used by mammalogists. The definitions given in the second column are those of the old "special creation" system—followed by Linnaeus—which is based on geographic distribution alone; the definitions given in the third column are those of the new phyletic system—that of Osborn—which is based on both geologic and geographic distribution. The new system was first used for the rhinoceroses (Osborn, 1900.192) and for the titanotheres (Osborn, 1902.208).

Comparison of the Linnaean and the phyletic systems of taxonomic terms

Term	Definitions	
	Old system	New system
Family	A contemporaneous group of similar subfamilies	Contemporaneous and ancestral phyla that exhibit similar family tendencies of evolution.
Subfamily	A smaller contemporaneous group of similar genera	A branch composed of one or more phyla which exhibit similar generic tendencies of evolution.
Genus	A still smaller contemporaneous group of similar or related species.	Part of a single phylum of successive species and mutations exhibiting similar tendencies.
Species	A group of related subspecies and geographic varieties.	A series of ascending mutations.
Mutation	Nothing corresponding to the geologic mutation of Waagen.	Geologic mutation (of Waagen); ascending substages within a specific phylum.

Desired harmony of mammalian paleontology and zoology.—The methods employed by all zoologists, paleontologists, and anthropologists in their observation and measurement of the hard parts of mammals should be the same. The methods pointed out above, first presented by Osborn (1914.412), are founded on the comparison in time of geologic ascending evolutionary phyla of mammals—such as the rhinoceroses and the titanotheres—with contemporaneous geographic series of species, subspecies, and varieties that may be grouped within a single genus. What applies to the systematic terms used in the classification and description of animals applies with equal force to those used for single characters, for it is the cumulative sum of evolutionary change in a very large number of single characters which makes up the mutation of Waagen, the species, or the genus, as the case may be.

SUMMARY OF DIFFERENCES BETWEEN OLD AND NEW SYSTEMS

To sum up: (1) The Linnaean genus or species is defined (statically) by the presence of certain proportions and by the presence or the absence of certain characters, whereas the phyletic genus or species is defined (dynamically) by the progressive evolution of certain proportions and by the gradual gain or loss of certain characters; (2) the Linnaean genus or species was clearly distinguished from a related genus or species, whereas the phyletic genus or species may gradually fade into its ancestor or successor, and the point where we make the dividing line is largely arbitrary; (3) consequently the phyletic genus actually has a new meaning, but to avoid innovation in nomenclature we apply the phyletic term genus to a number of species having a wide range in time and space, in the same manner that Linnaeus applied the term genus to a number of species having a wide range in space only.

STUDY OF THE EVOLUTION OF SINGLE CHARACTERS

In the hard parts of living as of extinct animals only three kinds of changes are observable—(1) changes of proportion, which the author terms "allometrons"; (2) the appearance of absolutely new characters, which the author terms "rectigradations"; (3) the disappearance or retrogression of characters.

Changes of proportion.—Changes of proportion (allometrons) make up by far the larger part of the evolution of the titanotheres, as of that of all other mammals. At least 95 per cent of the differences between the skeletons of *Eotitanops borealis* and *Brontotherium platyceras* are due to changes of proportion, and not more than 5 per cent to additions of absolutely new characters, such as horns. Consequently a very careful study has been made of allometry—that is, of the methods of calculating, measuring, recording, and describing changes of proportion—and the result has been the discovery of a number of general principles that apply to all mammals, extinct and living, including man. Probably also the undiscovered causes of changes in proportions are the same in all mammals, but their discovery constitutes a very difficult problem. (See Chap. XI.) In this difficult work the paleontologists may be greatly aided by the zoologists, especially by very precise field observers, such as Allen, Merriam, Miller, Osgood, and Sumner.

Although the mammalogists have demonstrated that there is an apparently causal relation, direct or indirect, between certain types of coloration and of size (harmonic increase or decrease) and the geographic environment, the relation between change of environment and changes in proportion (disharmonic) is very obscure. It is known that a harmonic increase or decrease in size of the entire mammal is correlated with certain differences in habitat, often for the obvious reason that a favorable environment favors development of larger races, whereas an unfavorable environment dwarfs growth. It remains to be determined, however, whether certain environments induce uniformly similar disharmonic changes of proportion. Anthropologists, for example, have failed to establish a definite causal relation between environment and the broad-headed (brachycephalic) or the long-headed (dolichocephalic) form of the human head.

The chief contribution that the paleontologist has made to this obscure matter is to show that when a proportionate change of head form is once established in a certain direction there is a tendency to go to extremes, so that, for example, extremely long heads or extremely broad heads tend to evolve longer or broader heads. These evolutionary tendencies are illustrated in the titanotheres.

Adaptive new characters.—The second mode of mammalian evolution—by the appearance of absolutely new characters—lies in a field where the paleontologist has a great advantage over the zoologist, because in a series of fossils a new character (rectigradation) can be traced back to its incipient, rudimentary stage, in which it is so inconspicuous that it would not attract the attention of the zoologist. Many characters that eventually may exert a most profound influence on the evolution of a race—that may, in fact, dominate all other characters—arise, so far as observed, from excessively minute beginnings. These origins of new characters are pointed out with great precision in Chapters V and VI, in which the evolution of the skull and teeth is described in detail as observed in the Eocene and lower Oligocene titanotheres. This very precise study of the origin and evolution of similar characters in many different lines of descent has led to the important discovery that phyla differ less through the possession of this or that new character than through the different rates of evolution at which the same character arises and evolves. In one phylum a new character like the horns will arise in an early geologic stage and evolve very rapidly, whereas in a related phylum it will arise relatively late in geologic time and will evolve very slowly. Thus a phyletic genus is defined not only by the characters which it exhibits but by the rate of the evolution of these characters. This principle, again, is observable only through paleontology.

The origin of new characters, as manifested in different ways in the members of twelve subfamilies of the titanotheres and as indicated by comparison with the origin of similar characters in other families of Perissodactyla, has accordingly been studied with great care.

Retrogressive characters.—The retrogression or disappearance of characters is illustrated in the history of the titanotheres by the features enumerated below.

1. Reduction of the canine teeth in many later titanotheres.
2. Reduction and occasional loss of incisors.
3. Reduction and frequent loss of first lower premolar.

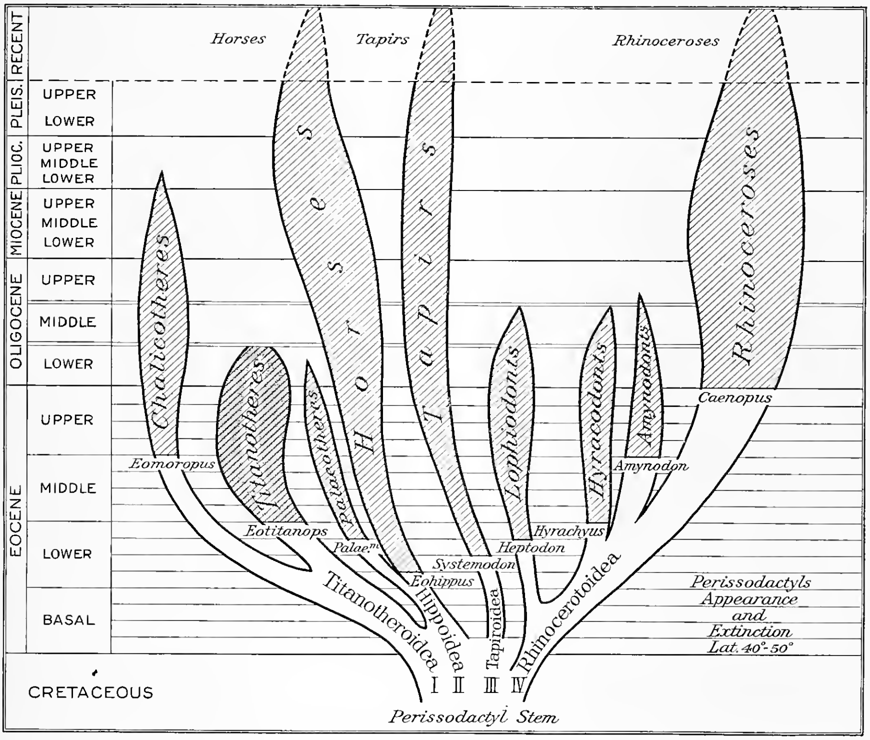

FIGURE 17.—Successive invasion of nine perissodactyl families in North America and western Europe between latitudes 40° and 50°

The chalicotheres (aberrant clawed perissodactyls with affinities to the titanotheres) are regarded as members of a separate superfamily, the Chalicotheroidea. Diagonal shading indicates the extent to which each phylum is represented by fossil remains.

4. Reduction and loss of protoconule and metaconule in upper molars.
5. Reduction of nasals and their coalescence with frontals.
6. Reduction of the trapezium in later titanotheres.

PHYLOGENY OF THE NINE TYPICAL FAMILIES OF THE PERISSODACTYLA

The competition of the titanotheres through natural selection was naturally closest with other members of the order Perissodactyla. As shown in the ordinal phylogenetic tree (fig. 17), we observe the successive appearance in North America and western Europe of members of nine different families of Perissodactyla, the odd-toed ungulates, which were probably all descended from a common ancestral or stem form which lived in Upper Cretaceous time. The probable characters of this stem form are fully described in Chapter X, where it is shown that the ancestral perissodactyl was a comparatively small and simple quadruped not exceeding half a meter in height, and that it was originally confined to a definite geographic area, feeding ground, and range, very possibly in northern Asia. The eight families that appear in North America and the paleotheres, which appear only in western Europe, were by no means equally distinct from one another. They were originally separated from the stem form not into nine branches but into five great main branches, termed superfamilies, as shown in Figure 17 and in the accompanying table.

Phyla of the odd-toed ungulates

Superfamilies	Families
1. Titanotheroidea	1. Brontotheriidae: The titanotheres, known chiefly in North America and in eastern Europe.
2. Chalicotheroidea	2. Chalicotheriidae: The chalicotheres, first known in Europe and North America; then in Asia.
3. Hippoidea: Horselike forms	3. Palaeotheriidae: The paleotheres, known in western Europe only. 4. Equidae: The horses, first known in Europe; then simultaneously in North America and Europe; subsequently in Asia, Africa, and South America.
4. Tapiroidea: Tapir-like forms	5. Tapiridae: The tapirs, first known in North America; then in Europe and Asia.
5. Rhinocerotoidea: Rhinoceros-like forms	6. Lophiodontidae: The lophiodonts, known in North America and Europe. 7. Amynodontidae: The amynodonts, aquatic rhinoceroses; first known in North America; then in Europe. 8. Hyracodontidae: The hyracodonts, cursorial rhinoceroses; upper Eocene and Oligocene of North America only, so far as known. 9. Rhinocerotidae: The rhinoceroses, the typical rhinoceroses; first known in North America and Europe; then in Asia and Africa.

In North America the horses (*Eohippus*) were the first perissodactyls to arrive. They were followed by the tapirs (*Systemodon*), which in turn were succeeded by the lophiodonts (*Heptodon*). It is possible that ancestral titanotheres were living in northern parts of the American continent, but apparently they did not reach the region near the fortieth parallel until it had become well populated with horses, tapirs, and lophiodonts. By middle Eocene time three more families had appeared—the paleotheres, in Europe only; the rhinoceros-like amynodonts (semiaquatic forms), which first appear in North America and subsequently in Europe; and the cursorial rhinoceroses known as hyracodonts (*Hyrachyus*), which appear in North America only and preceded the amynodonts. Toward the beginning of upper Eocene time there first appear in North America, as well as in Europe, ancestors (*Eomoropus*) of the chalicotheres, animals closely related in tooth structure to the titanotheres, which were separated into a distinct order (Ancylopoda) by Cope and are here regarded as forms somewhat parallel to the Titanotheroidea.

WIDE GEOGRAPHIC DISTRIBUTION OF THE PERISSODACTYLA

We are first struck with the remarkably wide holarctic distribution of the perissodactyls in Eocene and lower Oligocene time, a fact which points to facility of migration over the whole Northern Hemisphere. Only one family, the paleotheres, is exclusively European, and one other, the hyracodonts, is, so far as known, exclusively North American. The titanotheres were formerly believed to be exclusively North American, but two forms have been found in eastern Europe, which correspond very closely with the titanotheres of upper Eocene age from the Uinta Basin in northern Utah.

Members of all the other perissodactyl families—the chalicotheres, tapirs, lophiodonts, amynodonts, and rhinoceroses—probably ranged freely to and fro over the great northern continent of Eurasia and North America combined, the geographic region known as Holarctica.

The second important fact regarding the Perissodactyla is that, although the environment during middle and upper Eocene time, after the extinction of the archaic ungulates—the Condylarthra and Amblypoda—was especially favorable to the existence of the Perissodactyla, this order reached its maximum expansion in the lower Oligocene epoch, when all the nine families were existing and apparently flourishing at the same time. It would appear that in upper Eocene and lower Oligocene time Holarctica was dominated by perissodactyls. This period was immediately followed by a period when either the environment was adverse to the existence of the perissodactyls or competition with other types of ungulates was disastrous to them, because at or before the end of the lower Oligocene epoch five perissodactyl families suddenly disappeared—the titanotheres, paleotheres, lophiodonts, amynodonts, and hyracodonts. The aberrant chalicotheres, apparently through retreat to forested regions, survived in Europe and probably also in North America until the Pliocene epoch.

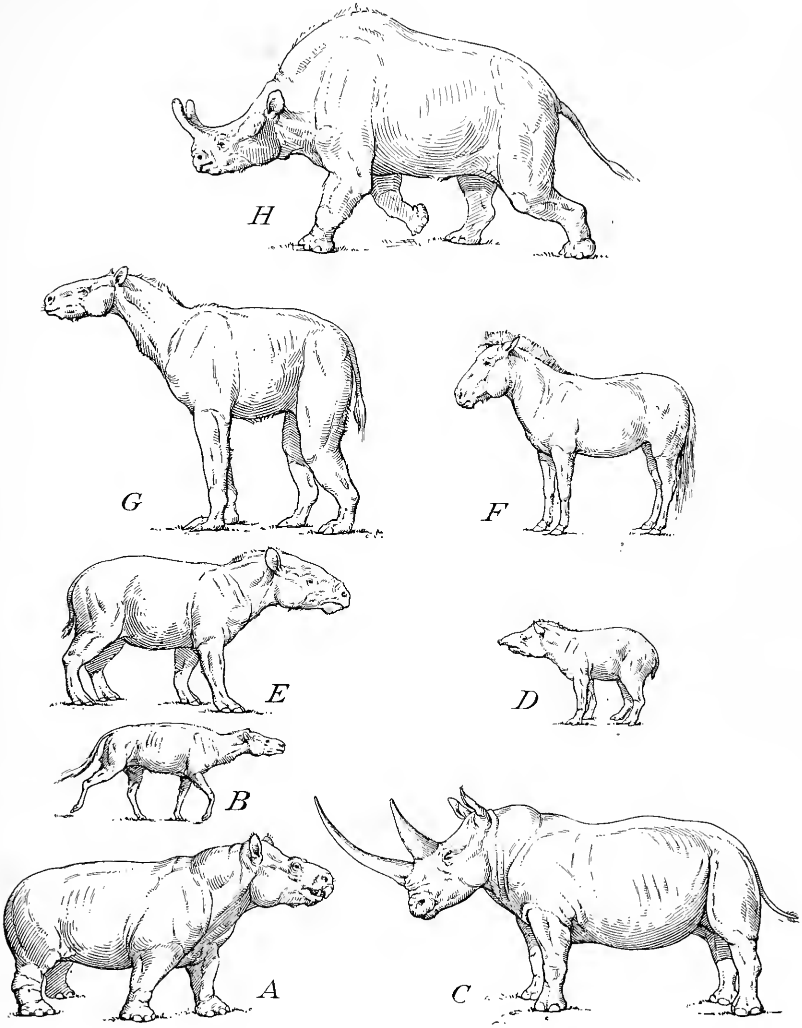

Figure 18.—Outlines of the body form of the perissodactyls, drawn to the same scale

The largest known member of each family is selected for comparison. The smallest known stem forms of each family are illustrated in Chapter X. The animals are grouped according to their natural relationships, as indicated especially by the pattern of the molar teeth, as follows:

Rhinocerotoid group: *A*, *Metamynodon;* family Amynodontidae; graviportal; aquatic; lower Oligocene. *B*, *Hyracodon*, family Hyracodontidae; cursorial; middle Oligocene. *C*, *Ceratotherium simum;* living white rhinoceros; family Rhinocerotidae; graviportal.

Tapiroid group: *D*, *Tapirus terrestris;* existing tapir; family Tapiridae; mediportal.

Hippoid group: *E*, *Palaeotherium;* family Palaeotheriidae; lower Eocene; mediportal. *F*, *Equus przewalskii;* existing horse; family Equidae; cursorial.

Chalicotheroid group: *G*, *Moropus;* family Chalicotheriidae; clawed perissodactyl; lower Miocene.

Titanotheroid group: *H*, *Brontotherium platyceras;* family Brontotheriidae; graviportal; lower Oligocene.

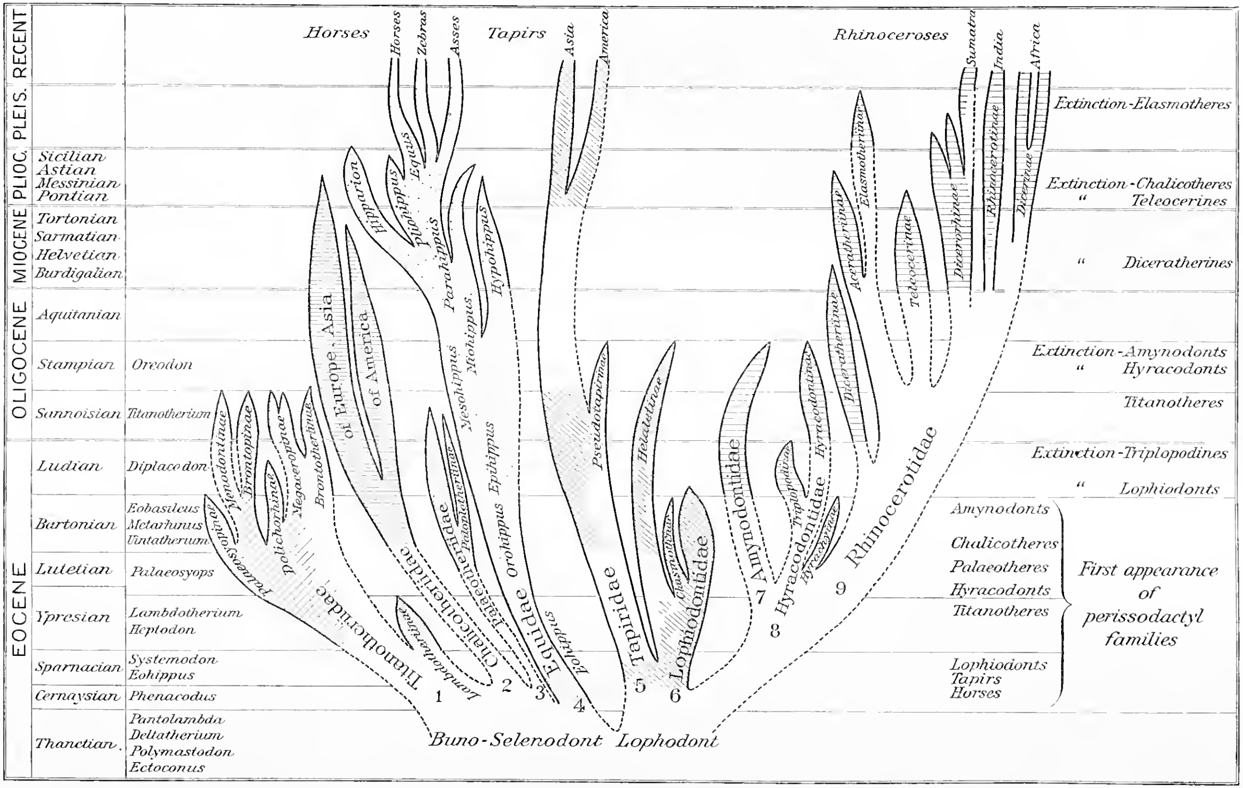

FIGURE 19.—The family tree of the Perissodactyla

Successive appearance in latitude 40° of representatives of the nine families. Successive extinction of six families. Survival of the three existing families—the horses, tapirs, and rhinoceroses.

Thus out of the nine original families of the great order of Perissodactyla only three—the horses, tapirs, and rhinoceroses—have survived to the present time, and these during the glacial epoch were greatly reduced both in numbers and in geographic distribution.

The consideration of these facts raises the whole problem of the origin and adaptive radiation of the perissodactyls (see Chap. X) and the general problem of the causes of the extinction of the perissodactyls and of other quadrupeds (see Chap. XI).

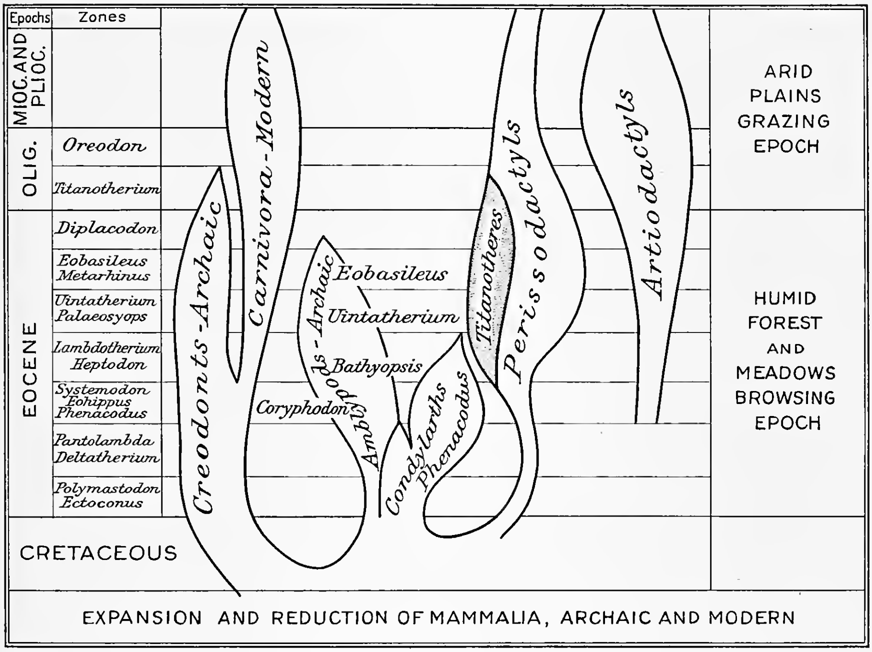

FIGURE 20.—Periods of expansion and extinction of the perissodactyls and contemporary forms

Showing that the expansion of the perissodactyls was coincident with the extinction of the archaic Condylarthra and Amblypoda and that the extinction of many perissodactyls was coincident with the expansion and adaptive radiation of the artiodactyls.

CAUSES OF EVOLUTION

There can be no doubt as to the survival value of certain finished types of tooth structure and limb structure (see pp. 880–881), a principle first formulated by the distinguished Russian paleontologist Kovalevsky (1873.1). Two important questions that the reader must keep in mind in considering the origin of innumerable new characters are (1) whether there is evidence of chance origins and chance rudiments of certain types of structure possessing sufficient survival value to establish themselves through the principle of the survival of the fittest, or natural selection; or (2) whether there is some other orthogenetic principle at work causing the definite and adaptive origin of new characters. The moment of origin of each new character is a very important moment in the history of that character. Does each new character arise fortuitously at this point or that, in an adaptive or inadaptive condition, or does each new character arise in a mechanically adaptive condition, although this condition may be merely incipient?

The biologic purpose of the long and dry descriptions and tables of measurements given in Chapters V, VI, and VII of this monograph is to direct observation continuously to this problem of the origin of new characters. Our general conclusions concerning these two questions are presented in Chapter XI.

ADAPTIVE EVOLUTION AND OVEREVOLUTION OF THE FORM OF SKULL, TOOTH, AND FOOT

Whatever may be the causes of evolution its results are definite. The visible evolution of all the hard parts of the body in herbivorous animals is originally mechanical and manifests general adaptation to two broad groups of purposes:

1. Prehension of food (lips, teeth, and jaws); comminution of food (teeth and jaws); conservation and transportation of stored food energy (body and limbs). These purposes involve all the mechanical changes of structure of skull and tooth.

2. Motion and locomotion; migration in search of food and to escape enemies; adaptation to perform the act of reproduction and to protect the young. These purposes involve all the mechanical changes of the structure of limb and body.

The operation of the principle that, under the dominance of these modes of mechanical adaptation each organ, structure, and character is adaptively evolved for some special service to the organism is not invariably evident in respect to all changes in the proportion of characters. Certain characters of proportion, such as extreme broad-headedness or extreme long-headedness, seem to interfere with adaptation; they appear to be carried so far in one direction as to render the animal less adapted to survive than its less specialized ancestral forms. In other words, certain tendencies of evolution may carry a phylum beyond its requirements in adaptation.

Aside from this question of the different degrees of survival or actual elimination value of certain tendencies of evolution, there can be little doubt that in its origin and development each character, sooner or later, responds and reacts independently to the conditions of the environment, quite apart from the question as to the causes of such response. The teeth react to the kinds of food; the feet and limbs to the kinds of soil.

The principles of the divergence of quadrupeds from each other in their independent adaptations in the skull, teeth, limbs, and feet are fully discussed elsewhere (see p. 123) in the treatment of the principle of adaptive radiation. Though they may have lived apparently in the same region and have been fossilized side by side in the same sediments, all distinct species of quadrupeds have locally different habits and habitats. The structure of the skull, jaws, and teeth responds to their habits and tastes; the structure of the feet and limbs responds to their habitats—the nature of the ground, etc.

PHYLETIC DIVERGENCE IN THE EVOLUTION OF NEW PROPORTIONS IN HORSES AND IN TITANOTHERES

All the families of an order of Perissodactyla start their career from a similarly proportioned ancestral stem form such as that described in Chapter X (p. 760) as the stem perissodactyl. Starting with the same complement of characters, divergence in proportions separates the families of perissodactyls more and more widely from one another. In the Equidae (horses), for example, the head form of the earliest known ancestor (*Eohippus*) is very similar to that of the earliest known ancestor (*Eotitanops*) of the family Brontotheridae. In both these primitive skulls the orbit is near the center of the head, and in the later forms it apparently moves backward or forward, but what really happens is that the skull is elongated in front of the orbit in the horse and is elongated behind the orbit in the titanothere. (See fig. 21.)

A comparison of the forms shown in Figure 21 with those shown in the following figures will demonstrate the marked similarity of the lower Eocene forms and the very wide divergence of the modern forms. The skulls of the ancestral tapir, horse, and titanothere (*Systemodon*, *Eohippus*, and *Eotitanops*) are in many ways much alike, the chief differences consisting in (1) the details of the characteristics of the dentition, (2) the relative position of the orbits, (3) the depth of the head through the back part of the lower jaw, and (4) the size of the muzzle. The primitive titanothere prophetically suggests the titanothere characters in the relatively heavy muzzle and stout lower jaw. The primitive horse *Eohippus* prophetically suggests the modern horse in the tapering form of the slender lower jaw and in the general contour of the skull, except that the eye is placed near the middle of the head, as in other primitive perissodactyls. The primitive perissodactyl *Systemodon*, regarded by Osborn as an ancestral tapiroid, had a somewhat longer, more pointed muzzle but was otherwise very similar to the contemporary horse *Eohippus*.

These differences of proportion between the facial region in front of the orbit and the cranial region behind the orbit are partly correlated in adaptation to the elongation (hypsodonty) of the crowns of the grinding teeth. In the horse and in most of the ruminant artiodactyls the face is elongated to accommodate the vertically elongated (hypsodont) grinding teeth. In the titanotheres, which are browsing animals, and in the browsing rhinoceroses of India and of Africa the orbit is directly above the grinding teeth and the cranium is slightly elongated, as shown in Figure 22. Thus it may be stated as a general principle of skull evolution that in browsing ungulates the cranium tends to be elongated and the face tends to be abbreviated, whereas in grazing ungulates, like the white rhinoceros of Africa, in which the grinding teeth are elongated, the face is elongated, and the cranium is abbreviated.

It follows that these respective proportions of the region in front and back of the eyes are adaptive; they are part of the general correlation of skull proportions with the functions of the grinding teeth employed in the prehension of food, as provided for chiefly in the shape of the upper and lower lips, which are obtrusible and flexible both in the browsing rhinoceroses and in the grazing horse, which occasionally browses. When the horse is browsing it extends its lips very much in the manner of the browsing rhinoceros, except that in the rhinoceros the independent motion and the pointing of the upper lip are more extreme. In the grazing white rhinoceros the upper lip is extremely broad and square. The animal subsists largely on grasses, which it crops with its square lips, exactly in the manner that the horse crops grass with its lips and front teeth. In all the rhinoceroses cropping front teeth are atrophied, the four pairs of incisors and the canines being reduced to a single large pair on either side and being thus analogous to those of certain titanotheres.

From these comparisons we deduce the structure of the mouth parts in the titanotheres as restored by Gregory. (See p. 704.) We also deduce the various adaptations to the browsing and grazing habit respectively in the different genera of titanotheres, for undoubtedly some were purely browsers and others tended toward grazing. Thus the orbits, the face, the grinding teeth, the front teeth, the lips, and the bones supporting these structures are respectively transformed in adaptation to the function of prehension and to browsing or grazing habits. The front part of the skull of the rhinoceros, with its terminal dermal horn, is comparable to that of the large-horned titanotheres, with their terminal bony horns. It will be observed that the entire front part of the head of the rhinoceros, in adaptation to the great strain of the horn used as a weapon of offense and defense, is correlated with a flat or a concave line along the top of the face, with a relatively short skull, and with a very powerful neck, a feature that is also especially characteristic of the titanotheres.

Thus there is a general resemblance between the side profile of *Brontotherium platyceras* and that of the Indian rhinoceros, which is due to analogous mechanical evolution, through the principles known as homoplasy, parallelism, or convergence. The titanotheres pass through a long lower and middle Eocene phase of tapir-like analogies, but when, in middle Eocene time, horns begin to appear the head region develops rhinoceros-like analogies. Similar analogous phases also occur to a greater or less extent in the feet of the rhinoceros and the titanothere.

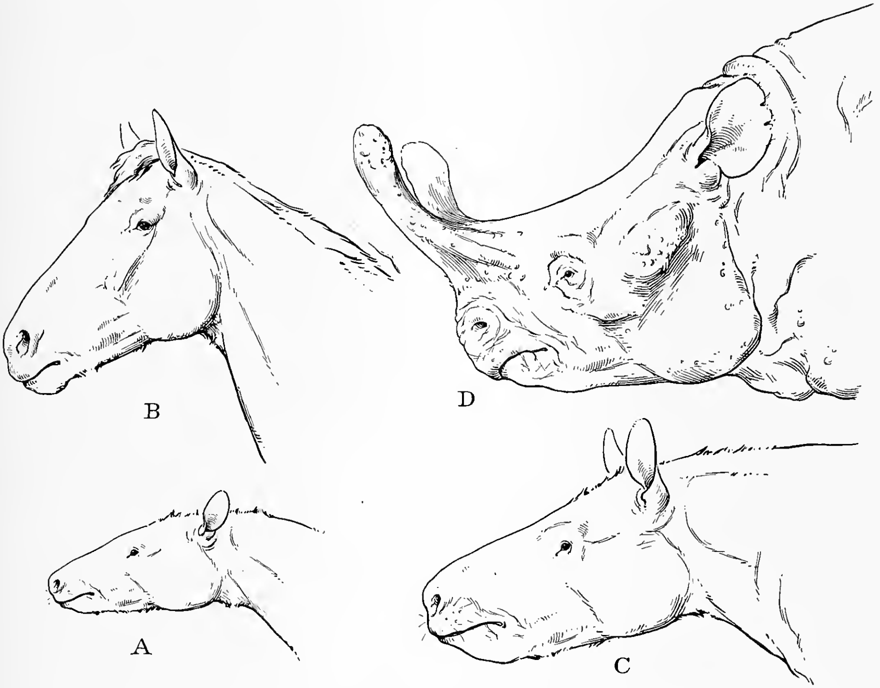

FIGURE 21.—Phyletic divergence in the evolution of new proportions in horses and in titanotheres

Lower Eocene ancestral horse *Eohippus* (A) and lower Eocene ancestral titanothere *Eotitanops* (C) (both with the orbit in the same relative position on the skull) compared with a modern horse (B) with face extended in front of the orbit and a titanothere of the latest stage (D) with skull extended behind the orbit. Thus two very similar heads (A, C) become increasingly dissimilar (B, D). Scales various.

On comparing the heads of the types of perissodactyls, ancient and modern, we observe that different modes of feeding and of offense and defense guide the dominant adaptations in evolution. The evolution operates under the principles of anatomical correlation and compensation, gain or loss in one part being mechanically balanced by gains and losses in every other part. This process includes the principle of physiologic compensation, whereby loss of function in

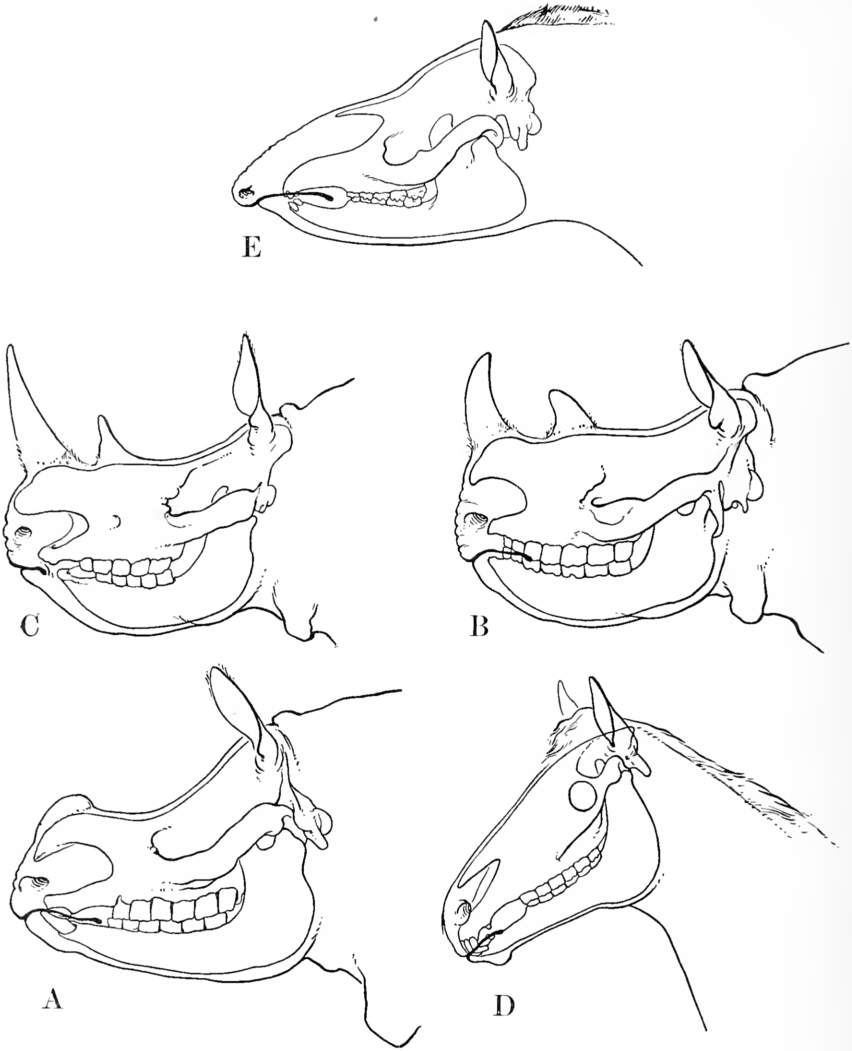

FIGURE 22.—Contours of the head and of parts of the mouth in browsing and grazing perissodactyls

A, Asiatic rhinoceros (*Rhinoceros*[5] *indicus*), chiefly a browser; B, black rhinoceros of Africa (*R.* (*Opsiceros*) *bicornis*), chiefly a browser; C, white rhinoceros of Africa (*R.* (*Ceratotherium*) *simum*), chiefly a grazer; D, domestic horse (*Equus caballus*), chiefly a grazer; E, American tapir (*Tapirus terrestris*), a browser.

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[5] The generic terminology of the rhinoceroses is not yet fully agreed upon by zoologists. The family tree, like that of the titanotheres, is polyphyletic.

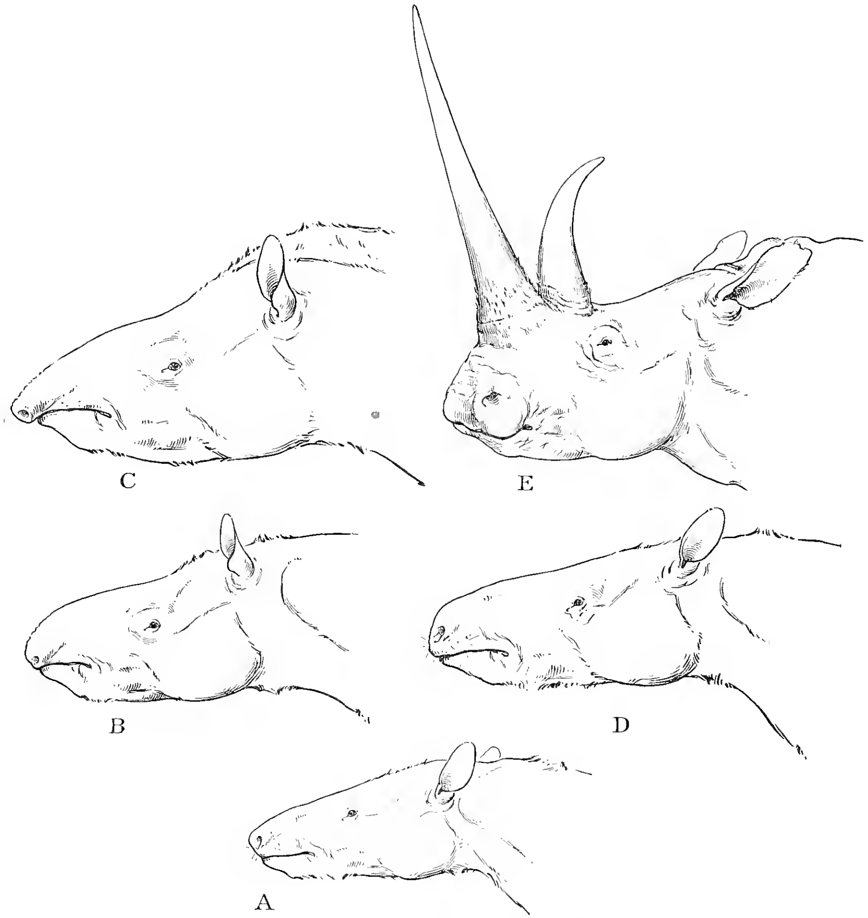


FIGURE 23.—Heads of lower Eocene and modern perissodactyls, showing changes of proportion and of the lip structure

Based on materials in the American Museum of Natural History. Scales various. A, Head of the lower Eocene tapiroid *Systemodon*, very similar to that of *Eohippus* and of *Lambdotherium;* B, head of middle Eocene tapir *Helaletes*, in which a prehensile upper lip first appears; C, head of the modern tapir *Tapirus*, whose prehensile upper lip forms a short proboscis; D, head of middle Eocene cursorial rhinoceros *Hyrachyus*, still of primitive proportions; E, head of existing white rhinoceros (*Rhinoceros* (*Ceratotherium*) *simum*) with extremely broad, grazing type of lip structure.

one part is taken up by some other part. For example, the loss of the function of the incisors in the prehension of food is compensated for by changes in the form and function of the lips.

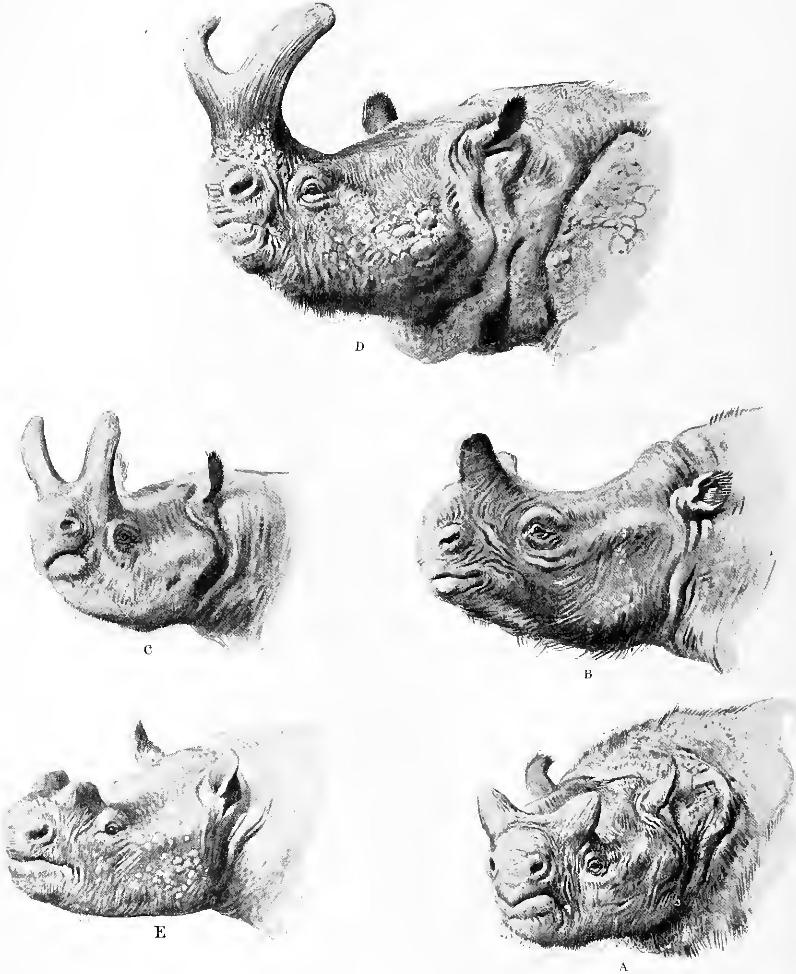


FIGURE 24.—Restorations to the same scale of the heads of some of the principal types of titanotheres

Drawn by Charles R. Knight, after models made by him under the author's direction. About one-seventeenth natural size. A, *Brontops robustus* Marsh, oblique view, middle *Titanotherium* zone; B, *Menodus giganteus*, upper *Titanotherium* zone; C, *Megacerops copei* Cope, partly oblique side view, summit of the *Titanotherium* zone of Colorado; D, *Brontotherium platyceras* Scott and Osborn, the final stage in the evolution of the horns of the titanotheres, summit of the *Titanotherium* zone of South Dakota; E, *Protitanotherium* sp., summit of the Eocene.

With the evolution of the lips the structure of the anterior parts of both the upper and lower jaws, of the anterior teeth, and the anterior nasal openings is closely correlated. The development of a prehensile upper lip like that of the tapir necessitates space for the superior retractor muscles, which curl the lip upward and backward. An example of the results of the evolution of the lower jaw may be seen by comparing *Eotitanops gregoryi* and *Brontotherium* (*medium*) *gigas*, the whole jaw of the former hardly exceeding in length a single posterior grinding tooth of the latter. (See fig. 25.)

EVOLUTION OF THE LIMBS AND FEET OF THE TITANOTHERES

The feet of the titanotheres, like their skulls, pass through a lower Eocene tapir-like phase, which is followed by a middle and upper Eocene rhinoceros-like phase and finally they attain a structure similar to that of the rhinoceroses, as shown in Figure 26, except that all the titanotheres, like the existing tapirs, retained four distinct and functional digits in the fore foot.

The fore foot of the tapir resembles the fore foot of the lower Eocene titanothere except that in the latter D. II, III, IV, V were all of nearly equal size, as shown in the diagram (B). This is known as the mediportal stage, for it is adapted to carrying a moderate amount of weight. The foot of the rhinoceros (C^1, C^2, C^3) is like that of the upper Eocene and lower Oligocene titanotheres except that in these there were four weight-bearing digits instead of three. This is known as the graviportal type of foot, in which a large cushion pad is developed at the back to relieve the shock of impact, and the end phalanges of the digits are incased in the horny sheath in front. In the tapir and rhinoceros the main weight passes directly through the center of the median phalanx (D. III), but in the tetradactyl titanotheres the main weight passes between D. III and D. IV. The concentration of the weight on the central digit of the horse and its resultant monodactylism, correlated with the expansion of the horny hoof and the contraction of the pad, is part of the evolution of a cursorial type of foot, which presents the widest contrast to the graviportal type.

In addition to comparing the head structure it was found necessary to compare the foot and limb structure of the titanotheres with that of all the other perissodactyls—not only the bony parts but the musculature. The work done on the musculature led to an exhaustive study of all that is known of the muscular anatomy of the members of the three existing families of perissodactyls. This study, which was directed by William K. Gregory, formed the basis of the restoration of the muscular anatomy of the giant *Brontops robustus* presented in Chapter VIII (pp. 722, 723). This restoration of an extinct animal is the first that has been based upon exact comparative study. It presents the titanothere as a superb example of the graviportal type of musculature and skeleton, surpassed only by the existing elephants.

The study of the structure of the foot led to a special investigation of the proportions of the limb bones in the ungulates. This investigation, directed by Osborn and cooperated in by Gregory, resulted in the striking discovery that the proportions of the upper and lower segments of the limbs and of the feet are invariably adjusted, first, to the weight that the limb must carry, and second, to speed of locomotion. These proportions are evolved, quite irrespective of ancestry, in adaptation to different modes of progression. Thus similar proportions of limb segments are observed not only in all mammals but in reptiles as well. A study, therefore, which was designed to disclose the habits of the titanotheres led to a thorough investigation of the principles of limb evolution in all the hoofed mammals in adaptation to various modes of locomotion and to various loads. This special study forms the subject of Chapter IX, in which acknowledgment is made to previous investigators.

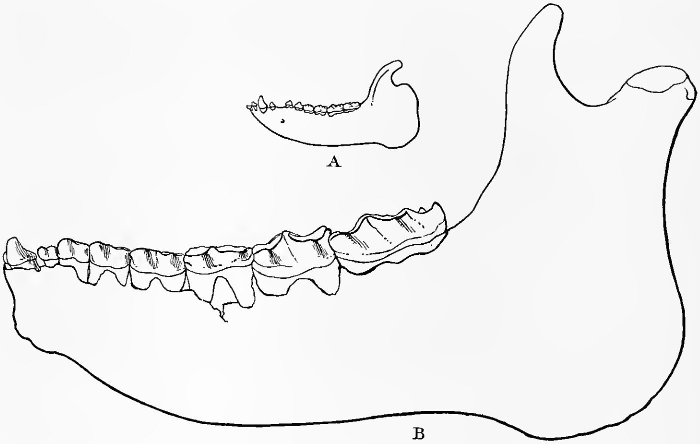


FIGURE 25.—Lower jaws of the first and the last of the titanotheres

One-sixth natural size. A, *Eotitanops gregoryi*, a small-jawed species from the Wind River formation (lower Eocene); B, *Brontotherium medium*, from Chadron C level of Chadron formation (lower Oligocene).

Not only the proportions of the upper and lower segments of the limbs but all the bones of the shoulder and pelvic girdles are gradually transformed from the subcursorial stages of *Lambdotherium* and *Eotitanops* through the mediportal tapir-like stages to the graviportal stages of the ponderous Oligocene titanotheres. This transformation is continuous, not sudden; it is brought about gradually by the simultaneous and correlated modification of all the bones and muscles involved in locomotion. Function (habit) is evidently far more potent than ancestry (heredity) in the determination of general form, yet in comparing the limbs of all the members of the different perissodactyl families with one another we can generally, by some family characteristic inherited from the ancestral stem form, distinguish the tapir type, the rhinoceros type, the titanothere type, etc. In the limbs, as in the skull and teeth, the titanothere, rhinoceros, or tapir ancestry respectively seems to keep the evolution of proportion and form within certain limits, so that, for example, the resemblance between the graviportal scapula of the titanothere and that of the rhinoceros, though it may be very close and deceptive, is never quite complete. The stages of muscular and skeletal evolution, arranged from latest to earliest, are as follows:

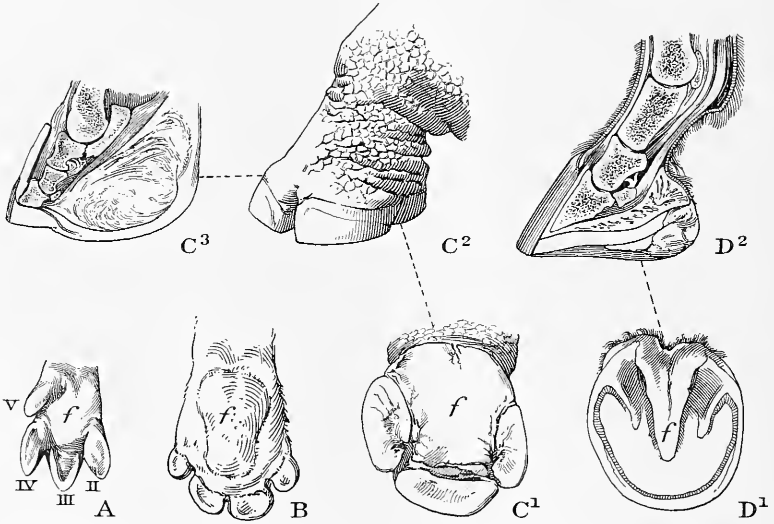


FIGURE 26.—Structure of the feet in extinct and living odd-toed ungulates (perissodactyls)

A, Sole of the left fore foot of a tapir (*Tapirus terrestris*), showing the tripod-like arrangement of digits II, III, and IV, and the reduced condition of V; B, sole of the left fore foot of an Eocene titanothere (*Mesatirhinus petersoni*), restoration based on Princeton Museum specimen No. 10013; C¹, sole of the fore foot of a rhinoceros, showing the enlarged hoofs of the three digits (II, III, IV); C², side view of same; C³, longitudinal section of same; D¹, sole of the fore foot of a horse, showing the expanded nail; D², longitudinal section of same. The central pad (*f*) in A, B, and C¹ is homologous with the relatively reduced pad or frog (*f*) in the foot of the horse (D¹). All but B after Eber.

4. Graviportal; ponderous, relatively slow-moving types, such as *Brontotherium, Rhinoceros* (*Ceratotherium*) *simum*.
3. Mediportal; of moderate weight and speed, such as *Limnohyops, Tapirus.*
2. Subcursorial; of light weight and relatively swift movements, such as *Eotitanops* of the lower Eocene.
1. Cursorial; swift moving, light frame, such as *Lambdotherium* of the lower Eocene.

ORIGIN OF NEW CHARACTERS AS DISTINGUISHED FROM CHANGES IN PROPORTION

The continuous gradual changes of proportion in the head, trunk, and limbs (allometrons), as already outlined, present a problem distinct from that of the origin of new characters (rectigradations). In this problem of the origin of new characters in the titanotheres we have two principal subjects of study, namely, the origin of horns on the skull and the origin of cusps on the grinding teeth.

In the evolution of the grinding teeth the titanotheres are very conservative; in them few new cusp elements originate, though several of the old cusp elements disappear. These animals thus present a striking contrast to the horses in the evolution of the grinding teeth, for in the horses a large number of new cusp elements are successively added. Yet the grinding tooth of the earliest titanotheres (*Lambdotherium* and *Eotitanops*) is in general similar to that of the earliest horses (*Eohippus*). In these lower Eocene contemporary mammals the grinding teeth are the same, cusp for cusp. In the horse all these cusp elements are preserved and utilized, and the highest degree of mechanical adaptation to the grazing habit is gradually evolved; in the titanotheres the browsing habit is generally conserved, and there is little marked increase of mechanical adaptation; in fact, mechanical inadaptation or imperfection of the grinders may have been one of the probable causes of the extinction of the titanotheres at a time when the conditions favorable to grazing gradually replaced those favorable to browsing.

The adaptive radiation of the grinding teeth in the several families of the Perissodactyla from somewhat similar ancestral forms is shown in Figure 29. The earliest members of every family had low-crowned (brachyodont) molar teeth, of relatively simple pattern, composed of six principal cusps ranged in three pairs—an external pair, the paracone and metacone; an intermediate pair, the protoconule and metaconule; and an internal pair, the protocone and hypocone.

In the titanotheres, chalicotheres, paleotheres, and horses the internal pair of cusps assume the conical, rounded shape (bunoid), whereas the two external cusps assume the double crescentic shape (selenoid), together forming a **W**, hence this type of tooth is termed bunoselenodont. These bunoselenodonts apparently formed originally a natural group from which the horses (*Eohippus*), the titanotheres (*Eotitanops*), and the chalicotheres (*Eomoropus*) gradually diverged very early in Eocene time. This is shown in Figure 30.

Another group of perissodactyls is the bunolophodonts, which includes the tapirs and lophiodonts, in which the internal and external pairs of cusps alike assume an elongate, crested, or lophoid pattern. This group has two main branches, the tapirs and the lophiodonts. The tapirs as forest-seeking animals escaped fossilization and are rarely found; only isolated remains of them have been found in Europe and America; yet they constituted one of the most persistent of all the perissodactyl phyla. The lophiodonts were tapir-like animals, in which the posterior outer molar cusps were flattened and thus are intermediate in shape between the tapir tooth and the rhinoceros tooth. These animals doubtless had a wide expansion in the luxuriant forests of Eocene France, and they attained very great size just before their extinction, which occurred contemporaneously with the extinction of the titanotheres in America—that is, in lower Oligocene time. Only one branch of the lophiodonts, the swift-footed Helaletinae, reached North America in lower Eocene time, soon after the arrival of the tapirs (*Systemodon*) and the horses (*Eohippus*).

The grinding tooth of the rhinoceroses is lophodont—that is, all the cusps are turned into elongate crests, of lophoid type, and the posterior outer cusps of the upper grinding teeth are elongated as well as flattened, producing an asymmetry of the cusps of the outer wall (ectoloph) of the crown. A grinding tooth of this kind is far more effective than that of the bunoselenodont titanotheres or of the bunolophodont tapirs. Such a tooth is a very efficient cutting instrument for an animal of either the browsing or the grazing habit. It is also capable of elongation (hypsodonty), and in two subfamilies of the rhinoceroses, the white rhinoceroses and the elasmotheres, the grinding teeth become hypsodont, greatly increasing the longevity and consequent reproductive power of each individual.

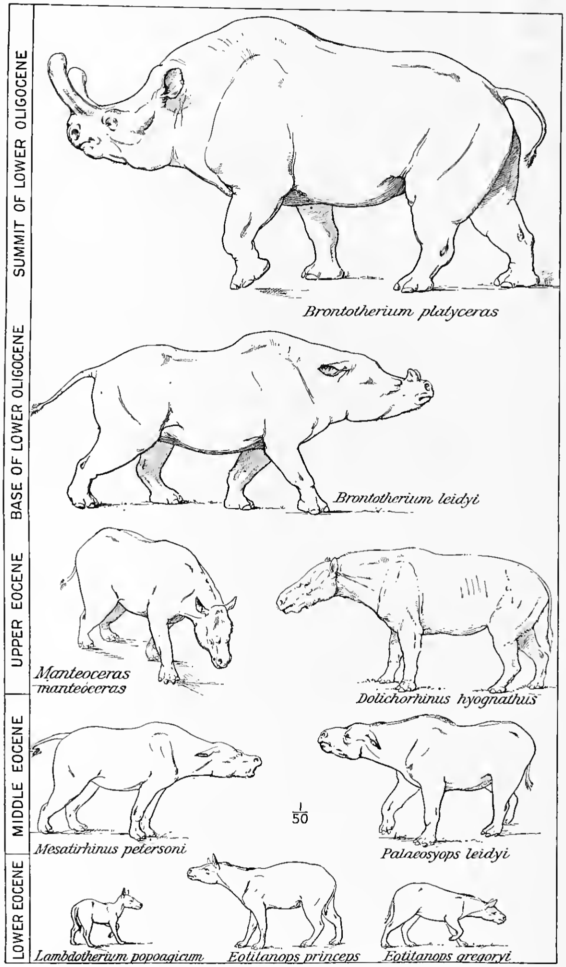


FIGURE 27.—Restorations of nine species of titanotheres from the lower, middle, and upper Eocene and the lower Oligocene

Drawn by Mrs. E. M. Fulda. About one-fiftieth natural size.

The rhinoceroses gave off at least twelve distinct branches (phyla) and were thus more plastic in adaptation than the titanotheres. These branches became adapted to every habitat, aquatic as well as terrestrial, to every mode of locomotion—cursorial, mediportal, and graviportal—and to every kind of feeding—browsing and grazing. Like the titanotheres some of the rhinoceroses passed from the mediportal to the graviportal stage of locomotion. In doing so they acquired an entirely new set of proportions, which are shown in detail in Chapter IX.

The teeth form the readiest means of distinguishing different branches and subbranches of the Perissodactyla from one another. The ancestral pattern, whether bunoselenodont or lophodont, is so marked and persistent that it is only partly modified through analogous adaptation. The manner in which the skeleton and limbs similarly became adapted independently to various modes of locomotion and thus assumed analogous forms and proportions is no less remarkable than the independent adaptation of the teeth to similar kinds of food.

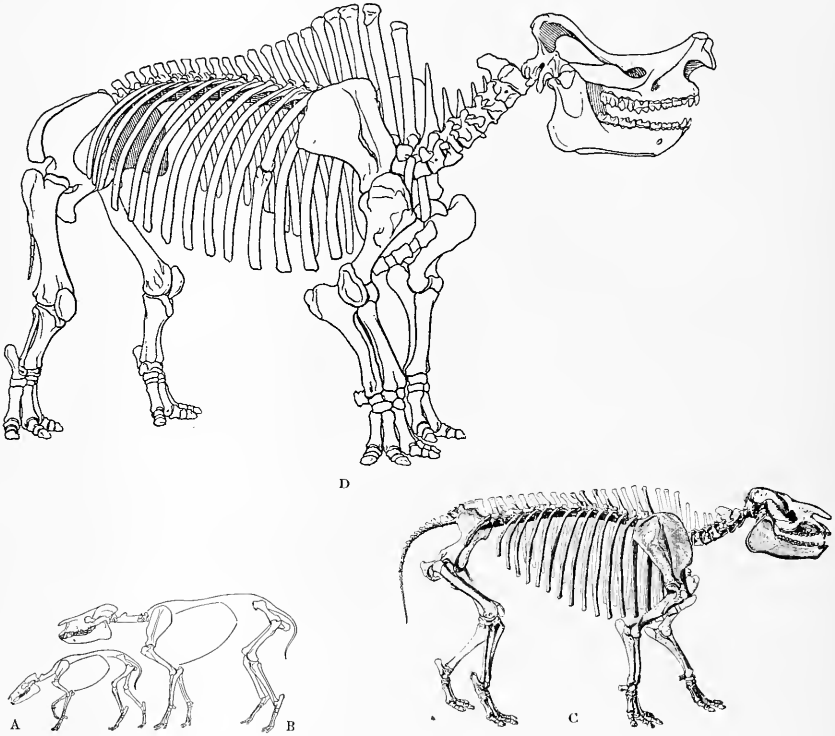
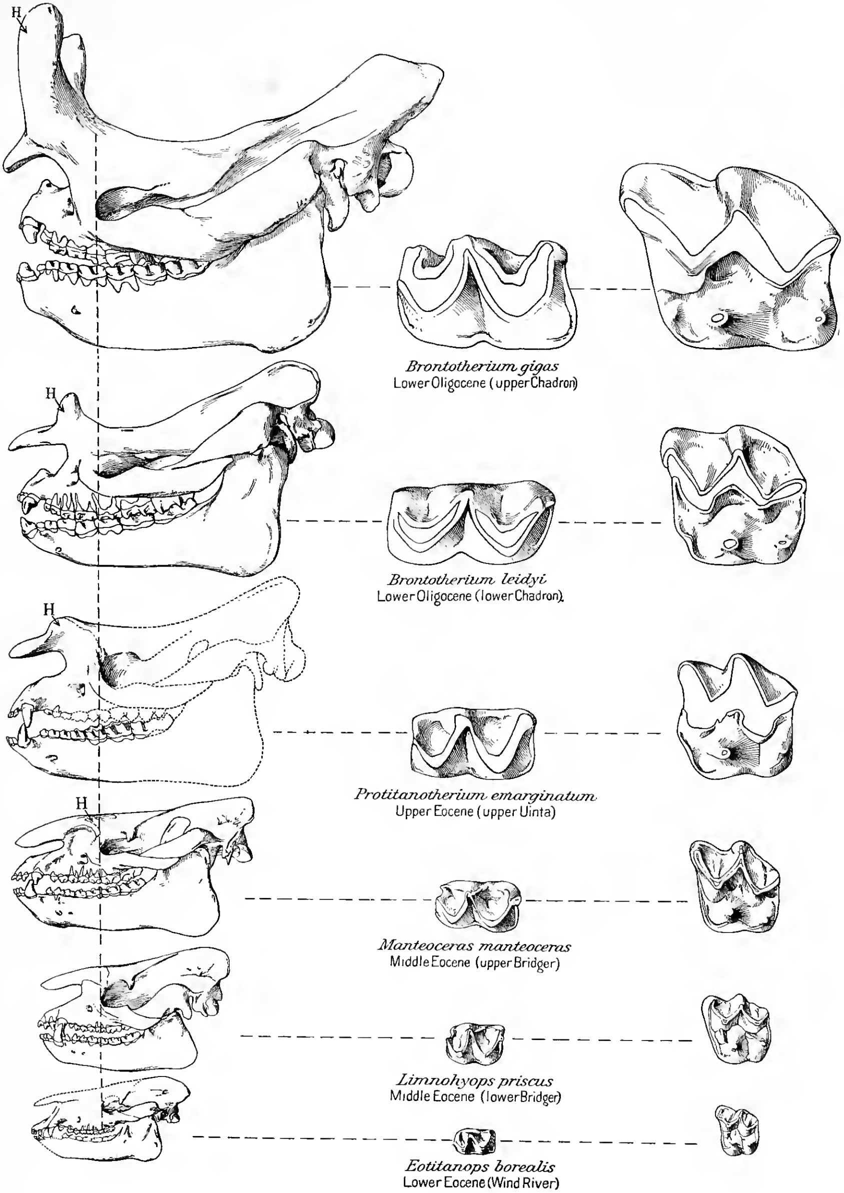


Figure 28.—Evolution of the skeleton of the titanotheres

A, First stage (subcursorial), lower Eocene, *Lambdotherium popoagicum;* B, second stage (subcursorial), lower Eocene, *Eotitanops borealis;* C, intermediate stage (mediportal), middle Eocene, *Palaeosyops leidyi;* D, final stage (graviportal), lower Oligocene, *Brontops robustus*. From one twenty-eighth to one-thirtieth natural size.

Of the nine typical perissodactyl families the horses alone are cursorial through the entire period of their evolution, and these give off one mediportal, forest-living branch, *Hypohippus*. The horses are paralleled by cursorial or subcursorial titanotheres, such as *Lambdotherium*, by cursorial paleotheres (*Palaeotherium* and *Paloplotherium*), mistakenly supposed by Huxley to be the ancestors of the horses, by two cursorial branches of the lophiodonts (the helaletids and the chasmotheres), and by two cursorial branches of the rhinoceroses (the triplopodines and the hyracodonts). It is shown elsewhere (see Chap. IX) how the cursorial habit, independently assumed in each of these subfamilies, modified not only the limbs but the skull and the entire skeleton into analogous forms that simulate real affinity. In Figure 32 all these cursorial branches, independently evolving in



Brontotherium gigas
Lower Oligocene (upper Chadron)

Brontotherium leidyi
Lower Oligocene (lower Chadron).

Protitanotherium emarginatum
Upper Eocene (upper Uinta)

Manteoceras manteoceras
Middle Eocene (upper Bridger)

Limnohyops priscus
Middle Eocene (lower Bridger)

Eotitanops borealis
Lower Eocene (Wind River)

FIGURE 29.—Evolution of the skull and molar teeth in the titanotheres

In *Eotitanops* the facial part of the skull is longer than the brain case (cranium). In *Brontotherium* the face is very short and the brain case is very long. The horn swellings (H) first appear in *Manteoceras* and become very prominent in the succeeding stages. The top of the skull becomes deeply concave. The outer wall and the V-shaped cusps of the upper molar teeth (paracone, metacone) become very deep, while the inner cusps (protocone, hypocone) retain their low, conical form. The lower molars retain the W-shaped crown throughout, which increases considerably in depth.

different perissodactyl families, are indicated by different kinds of shading.

Forest-living habits among perissodactyls are somewhat more rare, especially the extreme adaptation to forest living, consisting of relatively slow locomotion and marked special adaptation to browsing on the leaves of trees. Types that are more or less fully adapted to forest living are represented, we believe, among the chalicotheres, among certain forest-living horses (*Hypohippus*), and among certain forest-living tapirs (*Tapirus terrestris*), all relatively slow in movement and all without conspicuous weapons of offense or defense, except that the chalicotheres, such as *Moropus*, are provided with heavy claws.

Aquatic branches of the perissodactyls are also more or less readily distinguishable. Among the titanotheres we have a group of swamp or river living forms, with short limbs and spreading feet, whose remains are preserved in many river-channel sandstones, namely, the genera *Dolichorhinus* and *Metarhinus*, which are clearly distinguished from all other titanotheres by their apparent adaptations to river-border or aquatic life. Certain tapirs frequent river borders and swim freely for long distances, but they do not acquire distinctive aquatic adaptations. Among the rhinoceroses the pronounced aquatic division is the amynodonts, which have marked aquatic features about the head, simulating those of the hippopotami.

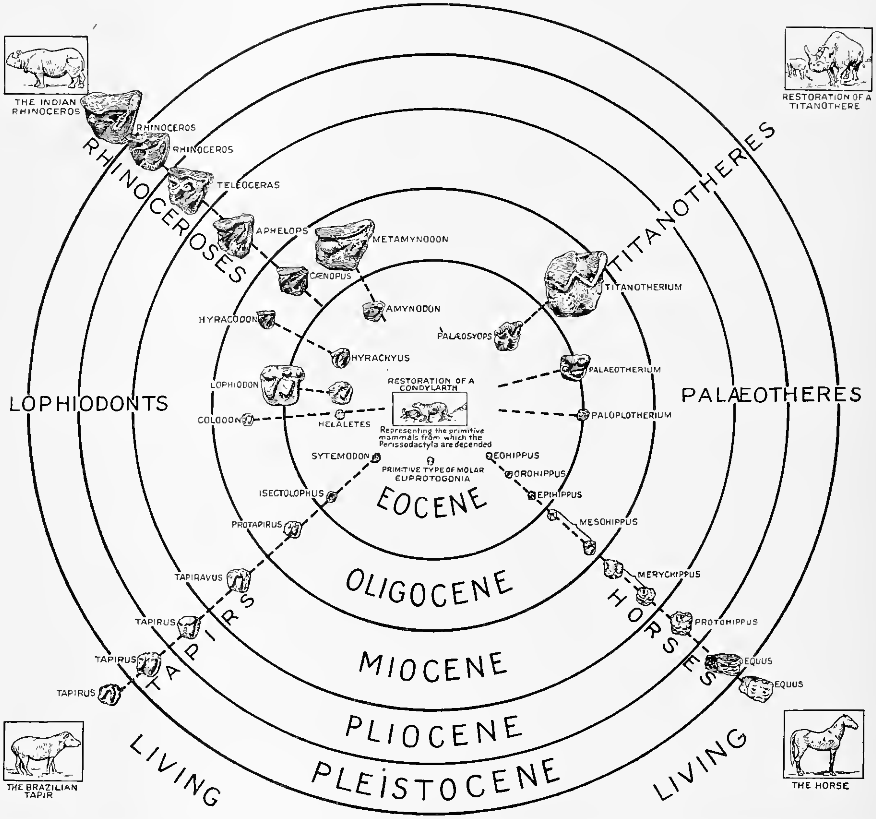


FIGURE 30.—Adaptive radiation in the evolution of the upper molar teeth in the odd-toed hoofed mammals (perissodactyls)

After W. D. Matthew. The earliest members of each family had low-crowned (brachyodont) teeth, of relatively simple pattern. In the titanotheres and paleotheres the internal cusps remain low and the two outer main cusps form a **W**. In the horses (hypsodont) the whole surface of the crown is thrown into complex crests and ridges and the crown becomes very long. In the tapirs (brachyodont) the molar crown takes the form of two sharp cross crests. A somewhat similar pattern is seen in the lophiodonts, except that in this family (brachyodont) the outer cusps form an irregular outer wall. In the rhinoceroses (brachyodont to hypsodont) the outer wall (ectoloph) becomes very much flattened, elongate, and oblique, and the cross crests also become oblique.

The great family tree of the perissodactyls may be interpreted as shown below.

Family tree of the perissodactyls

Primitive ancestors	Ancient branches	Families, extinct and living
Perissodactyls of Upper Cretaceous and basal Eocene time: four digits on the fore foot, three on the hind foot; six rounded cusps on the upper grinding teeth.	A. Bunoselenodont branch of basal Eocene time: inner cusps bunoid, conical; outer cusps selenoid, crescentic.	1. Titanotheres. 2. Chalicotheres. 3. Paleotheres. 4. Horses.
	B. Bunolophodont branch of basal Eocene time; inner cusps crested, outer cusps symmetrically crested and more or less flattened.	5. Tapirs. 6. Lophiodonts, mediportal and graviportal; confined to Europe. Helaletids, cursorial lophodonts; reaching America.
	C. Lophodont branch of upper Eocene time; inner cusps crested, outer cusps asymmetrical, greatly flattened.	7. Amynodonts (aquatic). 8. Hyracodontidae (cursorial and mediportal). 9. True rhinoceroses (mediportal and graviportal), variously adapted to browsing and grazing; distinguished by variations in the evolution of the horns.

The mediportal structure, in which the skeleton and limbs are adapted to moderate speed and weight, embraces those intermediate stages in several different families in which there was moderate body weight and moderate speed, as in the tapirs. In the tapirs this is the last term of evolution, but in the titanotheres and in many rhinoceroses the mediportal stage is simply a gateway to the graviportal stage, in which the proportions of the limbs and trunk are adapted to weight bearing, more or less rapid progression, and active offense and defense.

The interpretation of these phenomena of analogous, parallel, and convergent evolution under the principle of adaptive radiation, presented on pages 121–127, simplifies the problem of the anatomy of the group as a whole as well as of the several adaptations seen in the skull, skeleton, limbs, and teeth. Each perissodactyl family appears to exhibit an innate potentiality to evolve in many different directions and thus to meet new conditions of life. In this sense each family is plastic. Here we are not witnessing the direct action of the environment: we are witnessing the direct response of the organism, through largely unknown causes, to develop its potential heredity characters along certain new lines. If the supply of new potential characters is exhausted, if a mechanical stage is reached out of which no additional stages can be developed, the animal will tend to become extinct unless it can retire to the recesses of the forests, as did the chalicotheres, and thus escape a struggle for existence in competition with more plastic forms, better adapted to the grazing life. The interpretation of these processes, however, has been the most difficult and baffling of all the problems that have arisen in the research made for this monograph.

The interpretation of the modes and causes of the origin and evolution of new characters and of new proportions in response to new conditions of life (see pp. 834–849) is extremely difficult. Explanations that at first seem obvious appear on close analysis not to be explanations at all. As this monograph is the most exhaustive and most detailed study thus far made of any group of mammals it seems important to show the bearing of all the observations on each of the current theories of evolution. It appears that, as is fully set forth in Chapter XI, we are still very far from even a preliminary understanding of the causes of many of the processes of mammalian evolution.

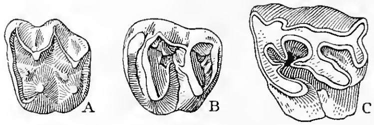


Figure 31.—Three types of teeth of members of nine typical families of perissodactyls

Bunoselenodont (A), bunolophodont (B), and lophodont (C) types of teeth displayed in the short-crowned (brachyodont) stage.

VELOCITY IN THE DEVELOPMENT OF CHARACTERS AND IN PHYLOGENY

The earliest explanations of evolution were purely mechanical; we are now passing through a phase of chemical explanations; but it appears that we may be led to the adoption of certain physical conceptions and the use of certain physical terms (Osborn, 1917. 462) for what has been described above as the rate of evolution of certain characters as distinguishing genera. For the term "rate" we will substitute the term "velocity."

Ontogenetic velocity.—The velocity of the evolution of certain characters in embryonic development—in fact, throughout the whole course of individual development—has long been a very familiar feature of adaptation. From the embryo onward a character may be either hurried along or slowed down in its rate of development, and in consequence it will appear in earlier or later stages of individual life. For example, certain adult proportions of the limbs are needed at birth in all cursorial animals; these adult proportions are consequently hurried forward during the foetal life, so that the animal is at birth able to run immediately with almost the same speed as the parent. This kind of velocity of development is called ontogenetic; it is appurtenant to every character in every stage of its development, it is closely connected with the survival of certain young organisms, and we shall see that the most plausible explanation of it thus far offered is the theory of natural selection proposed by Darwin.

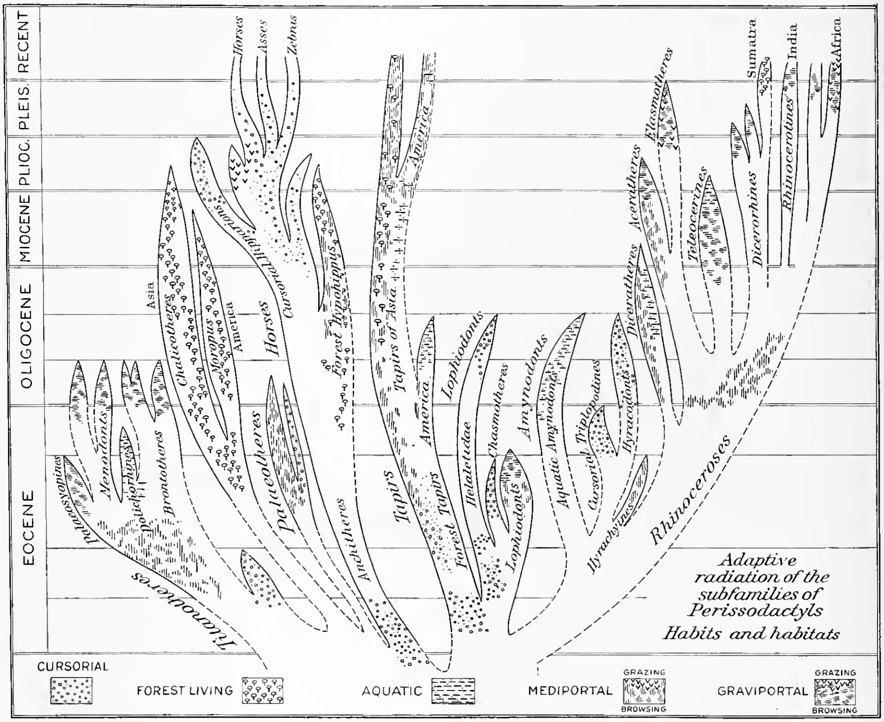


FIGURE 32.—The family tree of the perissodactyls, showing adaptive radiation of the nine families and thirty-five subfamilies

Exhibiting their divergence in limb and foot structure into cursorial, forest-living, mediportal, and graviportal types and in tooth structure into browsing and grazing types.

Phylogenetic velocity.—Another kind of velocity, however, may be noted in the perissodactyls and may be measured and calculated with great precision in the numerous phyla of titanotheres here considered. This velocity may be called phylogenetic velocity. Its postulation rests upon the fact that a given character may evolve much more rapidly in the members of one phylum than in the members of a related phylum, although the environment of both phyla may be the same. For example, in twelve subfamilies of titanotheres we observe homogeneous characters evolving independently—the same cusps on the teeth, the same horns on the skull. How, then, do the subfamilies differ from one another? They differ because the evolution of each character in each phylum proceeds with its distinctive velocity. In a phylum that is evolving rapidly a certain character appears early in geologic time; in a phylum that is evolving slowly the same character appears late in geologic time. The titanotheres of one phylum may at a particular geologic period be completely hornless, whereas those of a contemporaneous phylum may have well-developed horns. In the former the horns may appear much later and may never acquire very great momentum in development. We can thus note the incipiency of the differences between the short-horned titanotheres and the long-horned titanotheres.

This principle of unequal phylogenetic velocity in the development of the same characters enables us to distinguish different genera and species. In one genus the development of the internal cusps of the premolar grinding teeth shows high velocity; in another genus it shows low velocity. Apparently these internal cusps are useful adjuncts of the tooth; they make the tooth more effective for grinding up food. Similarly the horns are useful adjuncts of the head in warding off enemies. Yet these characters evolve so slowly in certain phyla that it is unreasonable to believe that utility and natural selection are the prime causes of their evolution. There would seem to be physiological and physical (or chemico-physical) causes of these different velocities. It is the data on the different velocities of the development of the same characters in related phyla which give the principal biologic value to the long series of detailed measurements and justify the large number of figures that are presented in Chapters V and VI. This suggests a summary of the biologic aspects of the problems of this monograph and of the features that distinguish this particular field of biologic research.

SUMMARY OF THE EVOLUTION OF THE TITANOTHEREG

The known titanotheres were confined to a relatively small area near the fortieth parallel in western North America and to Europe and Asia. The direct lines of descent and the continuous changes in many branches in different or successive life zones were complicated by the occasional incursion of new families from outside larger regions, probably from northern America and perhaps from northern Asia. (See appendix.) Nevertheless the localities in western North America where the remains of titanotheres have been found were apparently near the main geographic center of the evolution of the family, for the series of known fossils enables us to follow almost every step in the slow transformation of forms that were small and defenseless to forms that were huge and well armed.

The remains of the titanotheres now collected represent the most complete evolutionary series of mammals thus far discovered except those of the horses. The horses, however, are much less highly differentiated. In the titanotheres we see the growth of a great and vigorous family tree, giving off numerous branches (phyla), which diverge in characters and habits while retaining hereditary resemblances and certain hereditary trends and tendencies of transformation. Each of these branches is made up of slowly transforming successive stages (mutations of Waagen), which appear to be the more continuous and unbroken by sudden change the more thoroughly we explore the geologic levels where they successively occur. The evolution of the soft parts can only be inferred. The hard parts evolve in a variety of ways, chiefly through increase of size, through changes in proportion, through addition of new parts, and in less measure through loss of parts. Actual addition or loss of parts in the titanotheres is rare; general increase in size is almost universal, though in a few branches the size is diminished or arrested.

Changes in the proportions (allometrons) of structure were brought about by different velocities of phylogenetic evolution (acceleration and retardation) in the skeletal framework as a whole and in each of its parts. No less important is the definite and successive addition of new characters (rectigradations), each developing from infinitesimal beginnings until it reaches a stage of usefulness and each apparently having its individuality (biocharacter) and its separate history.

Throughout this wonderful transformation, which is in general adaptive, there were certain manifest germinal (hereditary) tendencies and certain unknown interactions between these germinal changes and the external, habitudinal, and environmental influences. The more carefully we study the detailed characters in each branch the more evident it becomes that the causes of evolutionary development are neither exclusively external nor exclusively internal but are to be sought hypothetically in the interactions between germinal, habitudinal, and environmental forces. The changes in the proportions of the skeletal characters and the new elements added to the teeth and skull, which are the outward expressions of these hypothetic germinal and environmental reactions, become visible more or less contemporaneously but not simultaneously in all members of the branches and subbranches of the great family tree—that is, the same characters appear, but at different periods and with different velocities of development. The whole process is an orderly one, which is, however, not predetermined in the germinal constitution of the titanotheres but results from certain innate or germinal potentialities of evolution, which are evoked in response to certain environmental and habitudinal conditions.

The struggle for existence, or natural selection, is operating continuously and more or less strongly on every single character according as its survival value is greater or less. In each successive geologic level we witness alterations of the family tree—its impoverishment through the extinction of certain branches or its augmentation through the survival of other branches and the immigration of branches which evolved in other regions. The individual members of all the branches (with two exceptions) become more imposing and more diverse as time goes on. Finally, at the climax of the general trend of transformation and at the very height of the grandeur of development, we observe the apparently simultaneous extinction of the whole titanothere family, seemingly through failure to cope with changed environmental conditions or to compete successfully with other herbivorous types.

This contribution to biology is therefore important chiefly as a study of the actual modes of evolution as observed in the skeleton and teeth of many different members of a great family of extinct animals which existed throughout a long period of geologic time—from the early Eocene through the early Oligocene—a time reckoned as hundreds of thousands of years. It is merely suggestive as to the causes of evolution.

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CHAPTER II

ENVIRONMENT OF THE TITANOTHERES AND EFFECT OF ADAPTIVE RADIATION ON THEIR VARIATION

SECTION 1. GEOLOGY AND GEOGRAPHY

CORRELATION OF EARLY TERTIARY EVENTS IN THE ROCKY MOUNTAIN REGION WITH THOSE IN WESTERN EUROPE

The recorded history of the titanotheres extends from the upper horizons of the lower Eocene series (upper Ypresian or upper Wind River horizon) through the middle and upper Eocene to the top of the lower Oligocene (Sannoisian or Chadron horizon), covering a period estimated at 450,000 to 600,000 years. This estimate is based on the assumption that 9,000 to 12,000 feet of sediment was deposited during the period from basal Eocene to lower Oligocene time and that the average rate of deposition was 1 foot in every 100 years.

The Eocene type formations (Wasatch, Bridger, etc.) of the Rocky Mountain region in North America have gradually acquired a time significance, similar to the stages (étages) into which the Eocene and lower Oligocene of Europe are divided, as shown in the following table. The correlation in time between France and America is close for some periods, as, for example, between the Sparnacian and lower Wasatch and between the Sannoisian and Chadron. For other periods the correlation is provisional, because the faunal relations are interrupted.

Provisional correlation of European and American geologic stages and life zones of the titanothere epoch

Epochs	Stages (étages) of Europe	Type formations of America	Major type life zones	Maximum thickness of sediments in feet, deducting overlaps
Lower Oligocene.	Sannoisian.	Chadron (Nebraska and South Dakota).	(Extinction of titanotheres.) *Titanotherium-Mesohippus.*	500
Upper Eocene.	Ludian.	Uinta (northeastern Utah).	*Diplacodon-Protitanotherium-Epihippus.*	600
	Bartonian.	Bridger (southwestern Wyoming).	*Uintatherium-Manteoceras-Mesatirhinus.*	1,875
Middle Eocene.	Lutetian. Ypresian (upper).		*Palaeosyops paludosus-Orohippus.* *Eometarhinus - Trogosus - Palaeosyops fontinalis.*	
Lower Eocene.	Ypresian (lower). Sparnacian.	Wasatch (western Wyoming).	*Coryphodon.* (First titanotheres.)	2,025
Transition.	Cernaysian.			
Basal Eocene.	Thanetian.	Fort Union (Montana): Torrejon (northwestern New Mexico).	*Pantolambda.*	6,000
		Fort Union (Montana): Puerco (northwestern New Mexico).	*Polymastodon.*	Total 11,000
Cretaceous.[a]	Montian. Danian.	Lance (=in part Laramie and Denver).[a]	*Triceratops.*	

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[a] The United States Geological Survey classifies the Lance formation as Tertiary (?), the Laramie formation as Upper Cretaceous, and the Denver as Eocene. The author of this monograph believes that the Lance formation is equivalent in part to the Laramie and Denver formations and that it is of Cretaceous age.

All estimates of geologic time are highly provisional, because they involve two unknown quantities—the amount of overlap and the relative rate of deposition. The rate of the deposition of sediments varies enormously. For example, certain Fort Union sediments of Montana, aggregating 6,000 feet in thickness, are at present considered contemporaneous with Torrejon sediments of New Mexico, which aggregate only 385 feet. It would therefore appear that sedimentation in Montana was more than thirteen times as rapid as in New Mexico. The only sedimentary stage which appears fairly uniform in several geographic localities is the Wasatch, which exhibits beds of approximately the same thickness in many different regions.

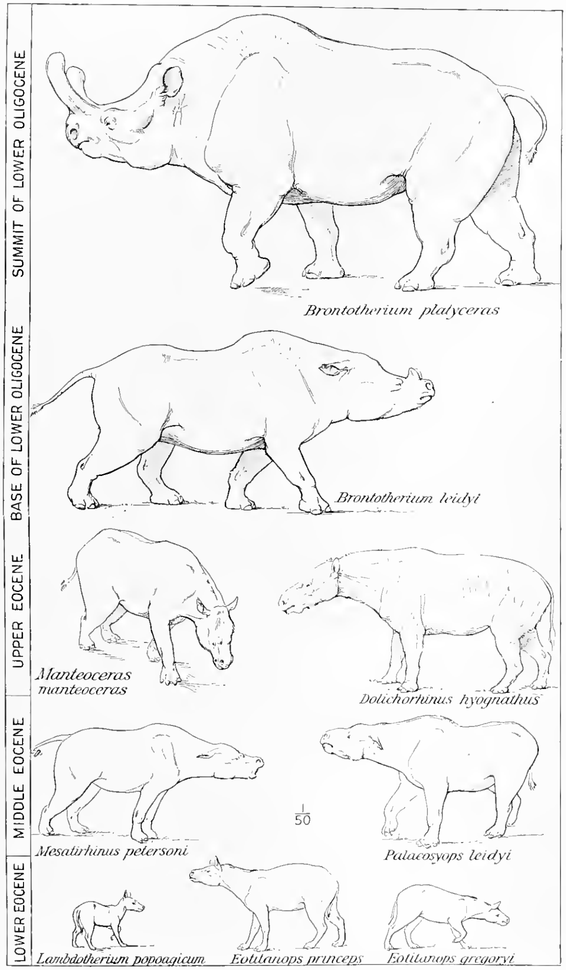

FIGURE 33.—Outlines of the bodies of titanotheres at different stages of evolution

If an average rate of deposition of a foot in a century is assumed, the period from basal Eocene to lower Oligocene time, inclusive, is estimated as not exceeding 1,100,000 years, a moderate estimate considering the great biologic changes that took place in the titanotheres and other groups during this period. The epoch of the titanotheres is roughly estimated at 500,000 years or more, during which they steadily increased in size, from the geologically earliest animals, which are no larger than a sheep, to some of the latest members of the race, which exceeded in size the largest rhinoceroses, standing over 8½ feet at the shoulders.

The recorded history of the titanotheres is nearly unbroken, but there have been two evolutionary gaps, one between the lower and the middle Eocene, which was filled in 1918 by explorations of the Huerfano (Osborn, 1919.494), and one between the upper Eocene and the lower Oligocene, which will be filled by the exploration of the upper part of the Uinta formation (theoretic faunal zone 16, still unknown). The record also shows sudden transitions caused by invasions of animals from other regions.

The geographic range of the titanotheres was probably continent wide in America and also extended across Asia into the Balkan region of southeastern Europe. In the relatively small Rocky Mountain and western plains region, where most of the fossil remains have been discovered, we observe the successive invasion of new kinds of titanotheres, which had apparently evolved previously in other regions, probably in areas to the north and east.

The geologic age of the little-known European titanotheres is somewhat uncertain. The type and only known specimen of *Brachydiastematherium*, an animal about the size of *Diplacodon*, is recorded from a formation in eastern Hungary that was originally assigned to the lower Eocene, but this animal is in a stage of evolution corresponding to that of the uppermost Eocene titanotheres of America, and the same European formation has yielded remains of a primitive rhinoceros (*Prohyracodon*) of upper Eocene or even lower Oligocene type. *Brachydiastematherium* is therefore probably not of lower Eocene age. The animals described as *Menodus rumelicus* and *Titanotherium bohemicum* are in all respects similar to American titanotheres of lower Oligocene age, but as the localities and horizons from which these fragmentary specimens were obtained are in doubt they may be imported American fossils to which a European origin has been erroneously imputed.

The correlation of the chief geographic, geologic, climatic, and faunistic events during the Tertiary period in the Rocky Mountain region with those in western Europe has been studied by the author continuously during the last 20 years, with the cooperation of Depéret in France and of Matthew, Merriam, Granger, Brown, Peterson, Douglass, Riggs, Darton, Stanton, Berry, Knowlton, and others in this country. The theoretic correlations reached are shown in the accompanying tables (pp. 43, 48). The comparison of similar stages in the evolution and migration of floras and faunas is partly independent of changes in the surface of the earth and in climate and is partly related to them. The general succession (Osborn and Matthew, 1909.321; Osborn, 1910.346) of the four Eocene and Oligocene life phases of North America is as follows:

Phase IV (*lower Oligocene*), *approximation.*—A similar mammal fauna in western America and western Europe. Extinction of archaic fauna and invasion of modern fauna.

Phase III (*upper and middle Eocene*), *estrangement.*—Independent mammal fauna of western America and western Europe; gradual diminution of archaic fauna.

Phase II (*lower Eocene*), *approximation.*—Closely allied and similar fauna of western America and western Europe; first invasion of modernized fauna.

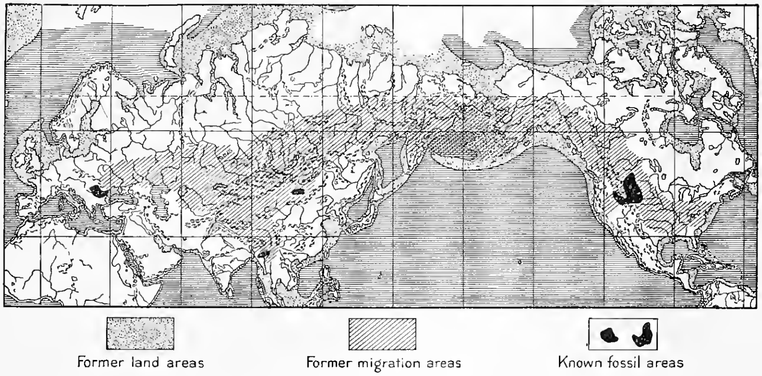

FIGURE 34.—Map showing the known areas (black) and the hypothetical areas (oblique lines) of titanothere migration and habitat

Phase I (*basal Eocene*), *approximation.*—Partly similar archaic mammal fauna of western America and western Europe.

Final Mesozoic phase.—Gradual extinction of the upper Cretaceous dinosaur fauna and appearance of ancestors of the archaic Eocene fauna.

This alternate approximation and estrangement of the mammal life of western America and western Europe points to periods during which conditions favored intermigration and intervening periods when geographic, climatic, or forest barriers may have stood between these widely separated regions. The basal Eocene American forests—those of the Fort Union epoch, for example—were very luxuriant and were unfavorable to migration.

LATE CRETACEOUS AND EARLY TERTIARY CLIMATES

End of the Cretaceous period.—The initial point in the correlation of geologic time in both the Eastern and the Western Hemisphere is the end of Cretaceous deposition. (See table on p. 48.) Some geologists place this after the first Rocky Mountain (Laramide) revolution in post-Laramie time—that is, after the end of typical Laramie deposition in Colorado. Others, among them the author of this monograph, place it at the time of the extinction of the great land and marine reptiles of Europe and America—that is, after Lance time.[6] The Fox Hills formation, which underlies the Lance, represents the end of uniform widespread marine sedimentation. At some places the Fox Hills is continuous with overlying freshwater deposits known as Laramie; at others it is continuous with overlying deposits known as the Lance. Thus Laramie time and Lance time, in our opinion, are in part the same—that is, they overlap at some places.

Lance and Fort Union flora.—New physiographic and climatic conditions arose during the initial period of the Rocky Mountain uplift, when uplands and plateaus were formed. Knowlton and Berry have shown that the Fort Union flora extends back into Lance dinosaur time, regarded by the author as late Cretaceous. The Lance flora is prevailingly a relatively warm temperate flora as compared with the antecedent Laramie and other Upper Cretaceous floras in the same region, and the climate in Lance time was about like that of the present Atlantic Coast States from North Carolina southward. In the Rocky Mountain province (Berry, 1914.1, pp. 153–154), in the zone of transition from the Cretaceous to the Eocene, a large number of local floras appear, such as those in the Arapahoe and Denver formations of Colorado, the Livingston formation and the Lance formation ("Hell Creek beds") of Montana, and the typical Lance formation of Wyoming. The formations in which they occur consist of lacustrine, fluviatile, and terrestrial deposits eroded from the rising land area of the Rocky Mountain province. These early so-called post-Laramie floras are said to

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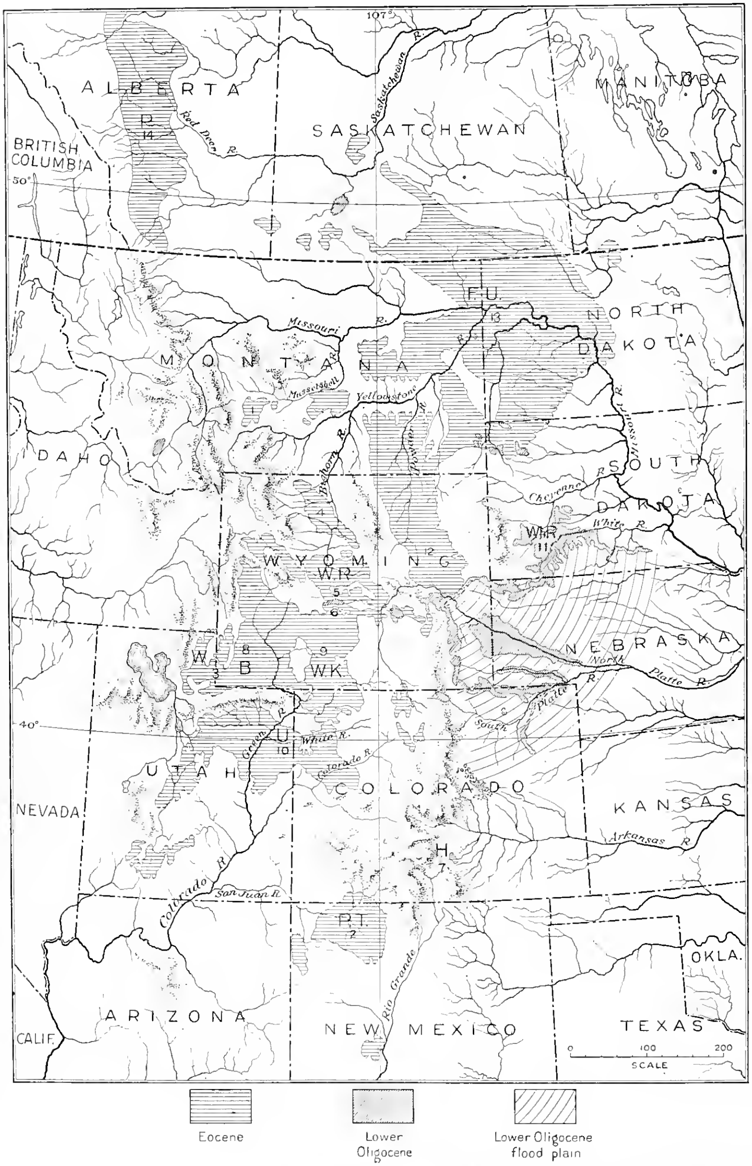
[6] The United States Geological Survey classifies the Lance formation as Tertiary (?). The author of this monograph regards it as Cretaceous.



1. Sweet Grass County, Mont. Fort Union formation.
2. P. T., San Juan Basin, N. Mex. and Colo. Puerco and Torrejon formations and "Tiffany beds."
3. W., near Evanston, Wyo. Typical Wasatch group.
4. Big Horn Basin, Wyo. Wasatch formation.
5. W. R., Wind River Basin, Wyo. Typical Wind River formation.
6. Beaver Divide, Wyo. Eocene and Oligocene section.
7. H., Huerfano Basin, Colo. Typical Huerfano formation.
8. B., Bridger Basin, Wyo. Typical Bridger formation.
9. W. K., Washakie Basin, Wyo. Typical "Washakie formation" of Hayden.
10. U., Uinta Basin, Utah. Typical Uinta and older Eocene deposits.
11. Wh. R., White River, S. Dak. Typical White River group.
12. Powder River and Pumpkin Buttes, Wyo. Fort Union and Wasatch formations.
13. F. U., Fort Union, N. Dak. Typical Fort Union formation.
14. P., Red Deer River, Alberta. Paskapoo formation.

FIGURE 35.—General geologic sketch map of the Rocky Mountain region, showing existing topography and drainage areas and their relation to areas of Eocene and lower Oligocene sedimentation

Each of the numbered areas except 13 and 14 is also represented in geologic section in this chapter. Topography after the United States Geological Survey, 1911 (See tables on pp. 48, 57, 58.)

be distinct from those of the true Laramie and to be more closely allied to those of the true Fort Union above.

The true Fort Union floras of basal Eocene (Thanetian) age include between 500 and 600 species of trees, which were apparently derived from areas farther north, certainly not from areas farther south. These forests, which were contemporaneous with the Puerco and Torrejon mammals, indicate a climate in the Rocky Mountain region between the fortieth and fiftieth parallels that was far from tropical, yet moderately warm and humid, with mild winters, favorable to the growth of palm, fig, and camphor trees, as well as other warm-temperate trees, including ginkgos and sequoias. This flora, which is characteristic of the early uplift period of the Rocky and Uinta Mountains in Colorado and Wyoming, indicates a somewhat cooler climate than that of the subsequent lower Eocene (Green River) epoch in the same region and a much cooler climate than the subtropical climate of the South Atlantic States in early Eocene time. In fact, both in the Rocky Mountain region and farther south the American climate became milder and more tropical as the Eocene epoch advanced.

EOCENE GEOGRAPHY OF WESTERN NORTH AMERICA AND ITS RELATION TO FAUNAL MIGRATIONS

GEOGRAPHIC DIVISIONS AND THEIR BEARING ON MIGRATION

The main topographic features of western North America were established between late Cretaceous and middle Eocene time. In late Cretaceous and early Eocene time certain routes of migration connected the animal life of the central Rocky Mountain region with that of Eurasia and probably with that of South America. The key to these routes of migration and to the geographic distribution of these animals is afforded by the results of researches made since 1853 by the geological surveys of the United States and Canada. The foundation of the descriptive geologic history of the Rocky Mountain region is laid in the report of F. B. Meek and F. V. Hayden (Meek and Hayden, 1862.1).

The entire Cordillera region extends from Bering Strait to the Isthmus of Tehuantepec, a distance of 4,500 miles, and has an average width of 500 to 600 miles. The main geographic divisions of the Cordilleran region, named in order from east to west, are the following:

- Rocky Mountain Range, Bering Sea to Colorado, including—
  - Front or eastern range, facing the Great Plains.
  - Rocky Mountain basins between the eastern and western ranges, forming the central north and south migration routes of mammals.
  - Westerly ranges, facing the interior plateaus.
- Central interior plateaus, intermontane belt region (main migration routes of herbivorous mammals):
  - Northern interior plateaus, Alaska to Washington.
  - Columbia Plateau.
  - Nevada-Sonora Plateau (Great Basin).
  - Colorado Plateaus.
  - Mexican Plateau.
- Pacific mountain system, British Columbia:
  - Sierra Nevada.
  - Pacific mountain basins between the Sierra Nevada and the Coast Ranges. Coastal migration routes of mammals.
  - Pacific Coast Range.

A transverse section of the Cordillera on the 41st parallel exhibits clearly the main confines of these mountain ranges, basins, and plateaus. The great plateaus and the mountain basins may have presented bordering forests and central grassy plains and jungles, interspersed with swamps, marsh lands, rivers, and lakes similar to those in the plateau and mountain (Kenya, Kilimanjaro) region of equatorial Africa to-day. Migration from north to south or from south to north was possible along three routes.

Our only knowledge of the late Cretaceous and Eocene mammal life of North America is afforded by the remains of mammals of the Rocky Mountain basins and foothills from Alberta to northern New Mexico. During the Oligocene epoch the life of the Columbia Plateau is revealed in the John Day formation of Oregon. The life of the Great Plains first appears in the lower Oligocene formations in South Dakota, Wyoming, Nebraska, and Colorado, which border the Rocky Mountains on the east. The Eocene mammalian life of the country that stretches eastward from the Rocky Mountain Front Range to the Mississippi and the Atlantic coast is entirely unknown.

Correlation of late Cretaceous and early Tertiary stages in Europe and in North America

Epochs	European stages	Rocky Mountain and Plains formations	Changes in flora and climate	Chief forms of reptile and mammal life
Upper Eocene.	Ludian. Bartonian.	Uinta formation (*Diplacodon* zone), upper part of "Washakie" formation (Washakie B), and (?) upper part of Bridger formation (Bridger E).		Ancestors of horned titanotheres.
Middle Eocene.	Lutetian. Upper Ypresian.	Lower part of Bridger formation (Bridger A, B, C, and D), lower part of "Washakie" formation (Washakie A), and upper part of Huerfano formation (Huerfano B).		Rapid evolution of titanotheres (upper Bridger).
		Post-Wasatch and post-Green River uplift, Uinta Mountains, Utah.		
Lower Eocene.	Lower Ypresian. Sparnacian.	Wind River, Green River, and Wasatch formations and lower part of Huerfano formation.	Green River flora, showing affinity to tropical flora of the south; climate warmer than Fort Union.	Appearance of titanotheres (Wind River time). Appearance of modernized families (lower Wasatch time).
Transition.	Cernaysian.			
		Post-Fort Union mountain uplift, Montana and Colorado.		
Basal Eocene.	Thanetian.	Fort Union, Torrejon, and Puerco formations. Swamp, lagoon, forested flood-plain sediments; lignitic and coal deposits.	Fort Union flora of modernized types.	Archaic mammals of Puerco, Torrejon, and Fort Union time. Extinction of the dinosaurs and large marine reptiles.
Uppermost Cretaceous.[a]	Montian.	Lance (upper part), Denver and Arapahoe formations. Rising land area of Rocky Mountain region; brackish-water estuarine, fluviatile, and channel sediments.	Fort Union flora. Warm and humid climate similar to that of southeastern coastal States; mild winters, flora not tropical. Low-lying forested swamps in the plateau region. Open flood plains surrounding the mountain slopes.	*Triceratops-Tyrannosaurus* fauna. Mammals of Lance time. Ancestors of Puerco and Torrejon placentals, marsupials, multituberculates. Paskapoo mammal fauna of Alberta (more recent).
		Beginnings of Laramide revolution; Rocky Mountains (Colo.), Uinta Mountains (Utah), Wasatch Mountains (Utah).		
Upper Cretaceous.	Danian. Maestrichtian.	Uppermost of the conformable series sediments of Rocky Mountain and Plains region: Laramie formation (= lower part of Lance). Fox Hills sandstone. Pierre shale.	Edmonton flora of Alberta (similar to Fort Union). Laramie flora transitional to modern. Upper Cretaceous flora. Climate warmer than Fort Union.	Edmonton dinosaur (*Leptoceratops*) fauna (succeeding Belly River), of Fox Hills (?) age; Ojo Alamo (N. Mex.) dinosaur fauna similar to Judith River fauna; Judith River (Mont.) and Belly River (Alberta) dinosaur fauna; *Monoclonius* of Pierre age.

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[a] The Lance formation is classified by the United States Geological Survey as Tertiary (?) and the Denver and Arapahoe formations as Eocene.

NOTE.—Near the end of Cretaceous time the chief uplift of the Laramide revolution in the Rocky Mountains began in the Front Range of the Colorado Rockies after the Laramie and before the Arapahoe. In the northern (the Montana) Rocky Mountains the chief uplift occurred at the end of the Fort Union. In southern Colorado and in northern New Mexico uplifts occurred both before the Puerco and after the Torrejon. (Ransome, 1915.1, pp. 360–362.)

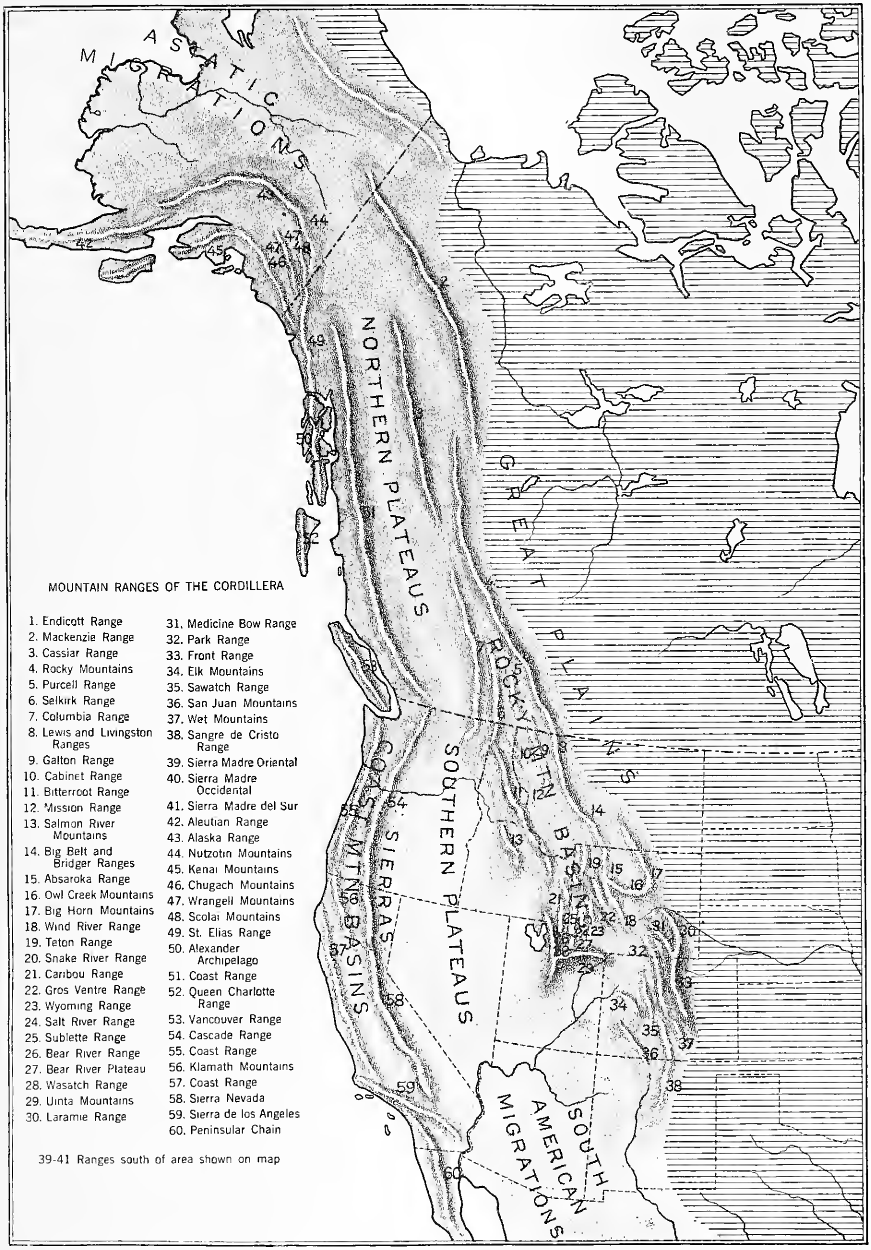

FIGURE 36.—Map of western North America showing supposed routes of migration of animals

This map shows the general early Tertiary topography of the Great Plains, mountain ranges, northern and southern plateaus, and coast basins and illustrates the supposed lines of Asiatic migration from the north and South American migration from the south. Modified after F. L. Ransome (1915.1).

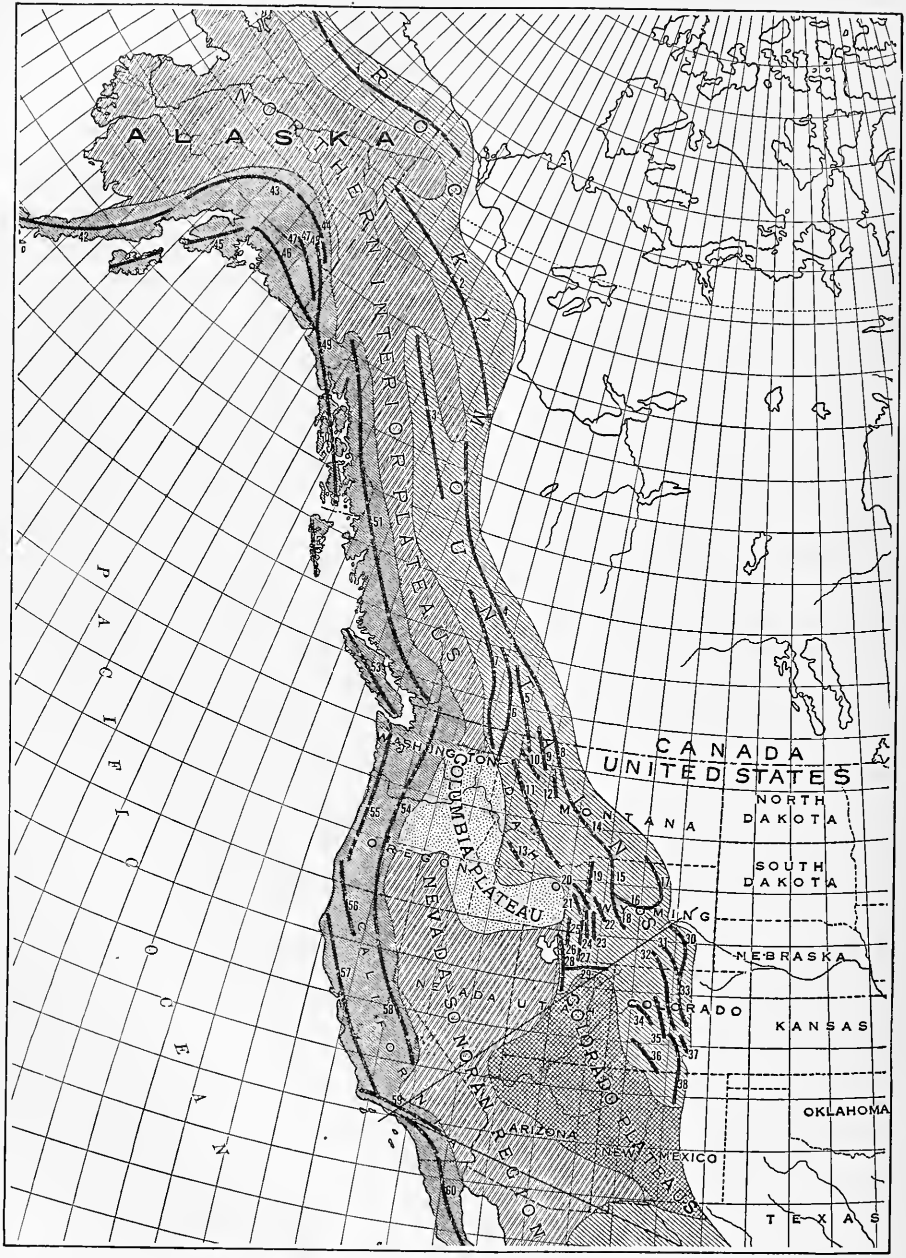

FIGURE 37.—Map showing the orogeny of the western mountain and plateau region

After F. L. Ransome (1915.1). Key to the numerals is given in Figure 36.

CHARACTER OF THE MOUNTAIN-BASIN, PLATEAU, AND PLAINS REGIONS

The geographic history of the mountain-basin region and of the Plains region presents some resemblances and some contrasts. Both regions were subject to slowly progressive elevation during this period. Nearly all the Eocene deposits of the mountain basins were laid down in broad, flat valleys and on mountain plateaus, which were drained largely by the same great river systems that drain them to-day, whereas those of the Plains region were widely scattered over broad flood-plain areas in which the rivers frequently changed their courses, the present river courses being comparatively modern. In the mountain basins, from the basal Eocene of the Fort Union, Puerco, and Torrejon formations to the summit of the upper Oligocene as represented in the John Day formation of the Columbia Plateau, the older Tertiary rocks were at very few places worked over into newer deposits, but at many places deposition was continuous. Despite continuous erosion since Oligocene time large areas of the historic Eocene sediments of the mountain-basin region have been preserved in their original purity and continuity for the geologist and paleontologist. By contrast, in the Plains region large areas of the original Oligocene strata were in part worked over to form Miocene strata, and part of these in turn were eroded to form Pliocene strata; again all three contributed to the Pleistocene strata; and finally all four are now contributing to the alluvium of the Great Plains.

EOCENE TOPOGRAPHY IN THE ROCKY MOUNTAIN REGION, MONTANA TO NORTHERN NEW MEXICO

By middle Eocene time the topography of the Rocky Mountain region from Montana to northern New Mexico had become broadly similar to that of to-day. The existing sharply sculptured ranges of the Big Horn, Wasatch, Uinta, and San Juan Mountains are remnants of much loftier ranges, which had their birth in late Cretaceous and early Eocene time. The two great drainage systems of the region—(1) Big Horn, Yellowstone, and Missouri Rivers on the north and (2) Green, White, San Juan, and Colorado Rivers on the south—were probably well established at the end of Eocene time.

According to Ransome (1915.1) and Lindgren (1915.1) the general uplift of the land in the Rocky Mountain region near the end of Cretaceous time was not uniform at different points either in its inception or in its intensity. Apparently the earliest movement occurred after the deposition in the Denver Basin of the conformable series of Cretaceous beds that is now called the Laramie formation, which overlies the Fox Hills sandstone. The Front Range of central Colorado arose at this time, before the deposition of the Arapahoe formation of Colorado (Ransome, 1915.1, p. 361). Andesitic tuffs and flows occur in the Denver formation, which immediately overlies the Arapahoe. At the south end of the Rocky Mountains, in northern New Mexico, great uplifts occurred both before and after the deposition of the basal Eocene Puerco and Torrejon formations. In contrast, in the typical Rocky Mountains of Montana the principal uplift appears to have taken place at the end of Fort Union time—that is, subsequent to basal Eocene time. In the Park Range province of Colorado there was uplift and vigorous erosion at the end of the Cretaceous period and renewed uplift after the deposition of the lower Eocene Wasatch and Green River sediments.

The separate history of the great mountain ranges in the basin region also shows that the upward movements began early in Eocene time. The Big Horn Range of northern Wyoming (Darton, 1906.1) arose as an anticline from the nearly horizontal strata of the Plains to a height of 9,000 feet in early Eocene time. Its uplifted peaks were truncated, and the larger features of the present topography were outlined. The major uplift of the Wind River Mountains, which produced a broad, low, somewhat broken anticline, also took place in early Eocene time (Fisher, 1906.1). In the Wasatch Range of western Wyoming, an eastward-dipping monocline cut off along its western side by a great fault, there was only a slight uplift at the end of the Jurassic, the main uplift taking place at the end of the Cretaceous (Boutwell, 1907.1). Subsequent movement took place in post-Eocene time. East of the Wasatch Range is the exceptional east and west anticline of the Uinta Mountains, which extends eastward and westward as a broad central plateau, 150 miles long and 30 miles wide, forming a dividing line between the Bridger and Uinta Basins. The formation of the Uinta arch began at the end of the Cretaceous period (Emmons, 1907.1, p. 302), as is shown by the fact that the flanking Tertiary beds lie unconformably over the upturned edges of the older strata, which stand at angles of 30° or more. The Eocene formations—the Wasatch, Green River, Bridger, and Uinta—are upturned against the flanks of the Uinta Mountains, in a position which means that the continued rise of the mountain mass has dragged up the edges of the adjoining beds.

Powell estimated that the summit of the Uinta anticline rose 25,000 feet above the level of the adjacent country—the Bridger and Uinta Basins. This altitude is equivalent to that of the Himalaya Mountains. Certainly in Eocene time the Uinta was a lofty, majestic range. The Colorado Front Range arose between the time of the deposition of the Laramie and Arapahoe formations, to the south, and the San Juan Mountains arose at the end of Cretaceous time and again after the deposition of the basal Eocene Puerco and Torrejon formations.

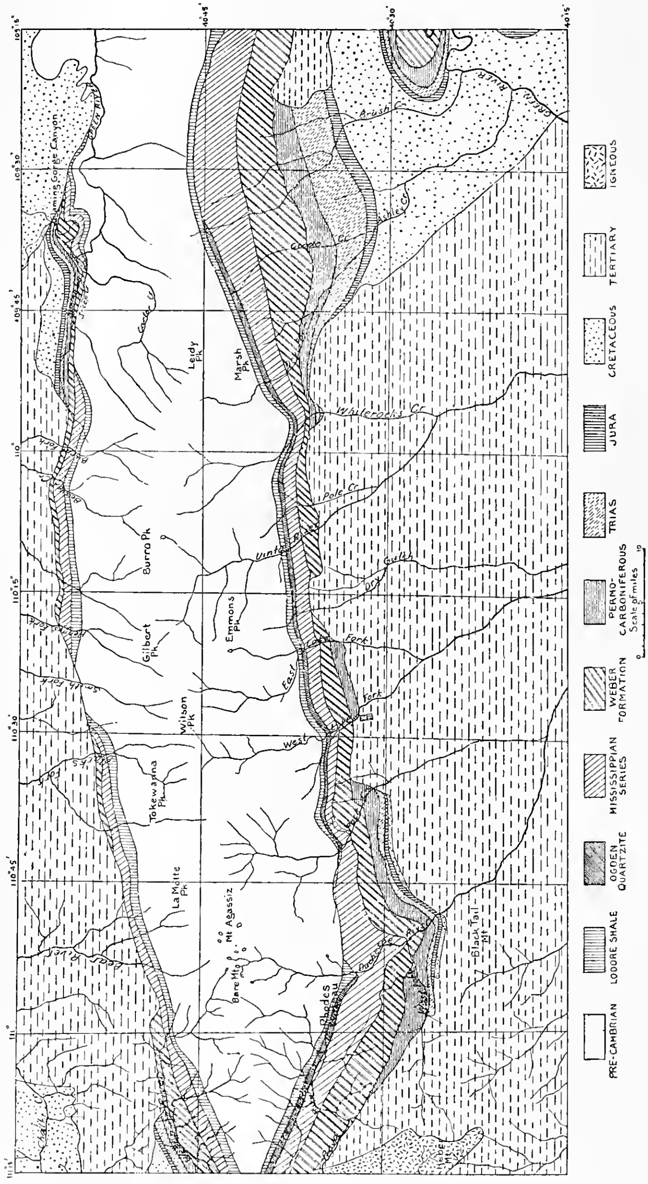

FIGURE 38.—Geologic map of the Uinta Range, showing the Tertiary sediments of the Bridger Basin, Wyo., at the north, and of the Uinta Basin, Utah, at the south

Rocks of lower to upper Eocene age are included in both areas. After Weeks (1907.1).

The entire topography of the mountain-basin region was thus broadly defined at the end of the Cretaceous period and was accented by uplifts during and after Fort Union (Puerco and Torrejon) time; also after Wasatch and Green River time, following which, from the present Canadian border to northern New Mexico, there was a continuous very gradual uplift. In general this uplift was earlier and more rapid in Colorado and New Mexico—that is, it occurred before the Fort Union epoch—and more retarded in Montana, where it occurred after the Fort Union epoch. In the Huerfano Basin the upturn of the western edge of the Huerfano beds amounts to 84°, and although this uplift is local it indicates a considerable movement in the Sangre de Cristo Range after Wind River time (W. Granger, letter, 1919). Ransome (1915.1, p. 362) believes that a large part of the Rocky Mountain uplift followed the deposition of the Fort Union formation.

CONTRAST IN PHYSIOGRAPHIC CONDITIONS EAST AND WEST OF THE ROCKY MOUNTAIN FRONT RANGE

During and after the deposition of the conformable Cretaceous formations (such as the Fox Hills and the Laramie) the country bordering the Rocky Mountain range on the east presented a marked physiographic contrast to that lying within the Rocky Mountain basins. Sedimentation east and west of the Rockies was not contemporaneous.

East of the Rockies.—On the east flanks of the Front Range great river flood-plain systems began in the north in Pierre time and extended toward the south after Fox Hills time. Thus on the western borders of the present Great Plains region rivers had long been spreading out sand over their flood plains in Alberta, forming such deposits as the Belly River sandstone in Pierre time and the Edmonton sandstone in Fox Hills time, and extending southward through Montana to deposit the Judith River sandstone in Pierre time, the Laramie formation of Colorado, the "Hell Creek beds" of Montana, the great Lance sandstones of Converse County, Wyoming, and the Denver and Arapahoe formations of Colorado after Fox Hills time.

The fact that the Lance sandstones were laid down at the end of Cretaceous time[7] is shown by the remains of the horned and carnivorous dinosaurs found in them, especially *Triceratops* and *Tyrannosaurus*. At about the same time *Triceratops alticornis* flourished east of the Front Range of Colorado, during the deposition of the Denver formation, which overlies unconformably (by erosion and uplift) the Laramie, the topmost formation of the "conformable Cretaceous series." These great flood-plain deposits, correlated both by their dinosaurs and by flora of the older Fort Union type, mark the beginning of the Rocky Mountain revolution as it affected the country to the east. At certain localities, notably along Hell Creek, Mont., south of the Missouri, these fans of much disturbed channel sand and gravel are contemporaneous with undisturbed beds that appear to be lithologically exactly like those of the Fort Union; consequently Fort Union sedimentation began in some regions early in post-Laramie time.

This long period of mountain erosion and sedimentation east of the Rockies came to an end either through heavy forestation or high-gradient river erosion, which deposited materials farther east. It is a very significant fact that in the region east of the Rocky Mountains, between South Dakota and northern New Mexico, only sparse lower Eocene sediments (Huerfano A and Cuchara) are known between Fort Union (basal Eocene) and Chadron (lower Oligocene) time, whereas in the region west of the Front Range sedimentation continued through the entire Eocene epoch.

West of the Rockies.—In the mountain-basin region from southern Montana to New Mexico the conditions during Lance time were very different from those that prevailed east of the Rockies. There was apparently erosion and rapid transportation rather than deposition. Within the mountain basins—except around Medicine Bow, near Laramie, and around the *Agathaumas sylvestris* locality, near Black Buttes, Wyo.—relatively few deposits of Lance age (*Triceratops* zone) have thus far been identified by means of fossils. The Evanston formation, above the Adaville formation, in the typical Wasatch section of southwestern Wyoming, according to Berry, contains plants of Fort Union and of Wasatch rather than of Denver age. Similarly the oldest Eocene deposits of the San Juan Basin (the Puerco and Torrejon) are comparable with the Fort Union and not with the older Lance formation; they overlie unconformably beds of probable Montana age. In brief, few deposits of Lance time (*Triceratops* zone) have thus far been identified within the mountain-basin region, although they may be found hereafter. At many places the oldest sediments of the mountain basins lie upon the eroded surfaces of unquestioned Cretaceous and older formations with pronounced unconformity.

Physiographic conditions again changed, apparently, for after Lance time sedimentation began vigorously in the mountain-basin region and continued throughout the Eocene until it formed deposits having a combined thickness of 9,000 to 11,000 feet. (See table on p. 43.) Not until Oligocene time, when the deposition of these mountain-basin beds probably ceased, was great fluviatile and flood-plain sedimentation resumed east of the Front Range, forming the lower Oligocene Chadron beds.

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[7] The United States Geological Survey classifies the Lance formation as Tertiary(?), but the author regards it as of Upper Cretaceous age.

LATERAL AND MAIN RIVER SYSTEMS IN THE MOUNTAIN-BASIN REGION

The great mountain-basin valley.—The contour lines of the basal Eocene and lower Eocene sediments of the mountain-basin region in northern New Mexico and Montana are very illuminating. They show the presence of a series of broad, relatively level basins—a chain of flat uplands or valleys—in which the products of erosion and the volcanic dust that were gathered by streams from the surrounding mountains were spread wide, indicating that although the mountain streams had high gradients and great erosive power the larger rivers had low gradients and little transporting power. The uniform elevation of the mountain-basin region at the north and the south and the low river gradients were favorable to sedimentation. We observe, moreover, that in basal Eocene time the conditions of climate and of sedimentation were somewhat uniform in the Puerco and Torrejon deposits of the San Juan Basin in New Mexico, laid down by tributaries of Colorado River, and in the typical Fort Union deposits of Montana, laid down by tributaries of Missouri River. The rates of sedimentation were different. Similar basal Eocene sediments probably underlie some of the Wasatch (lower Eocene) deposits in the intermediate basins of Wyoming and Utah, for they have been exposed in the San Juan Basin only by the removal of the overlying Wasatch. A new sedimentary phase was begun in Wasatch time, and a third phase in Bridger time.

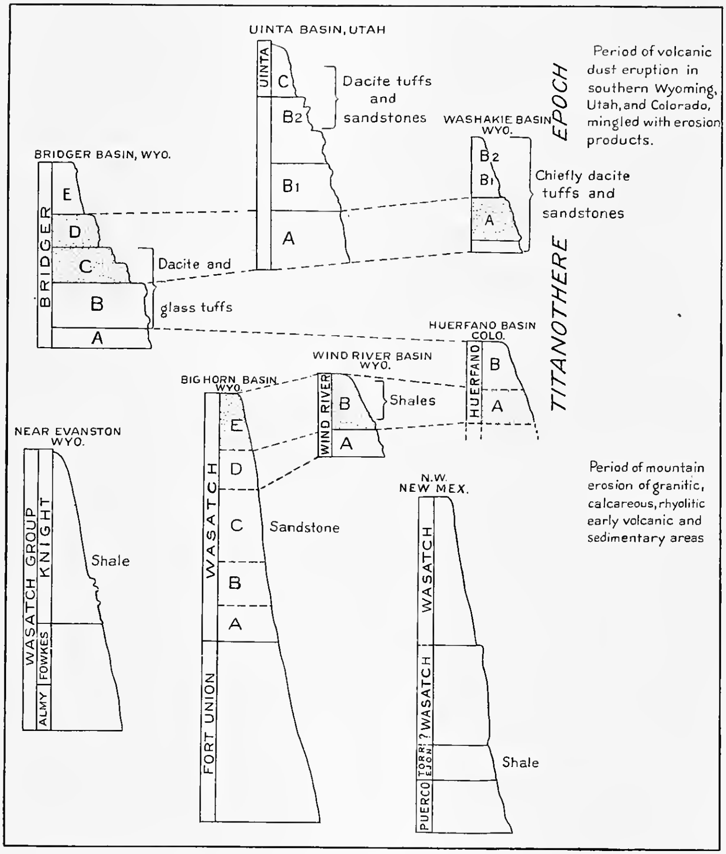

FIGURE 39.—Chronologic relations of formations in the mountain-basin region

This diagram exhibits the overlapping of sediments and the falls of volcanic ash in eight widely separated areas (Nos. 2-5 and 7-10, fig. 35), which, when combined, cover the entire Eocene epoch.

The contrast in the physiographic conditions east and west of the Front Range has a very important bearing upon the paleontologic records. The mountain-basin sediments afford a marvelous and almost unbroken record of mammalian evolution in the Eocene, but little or nothing in the Oligocene, doubtless because large areas of Oligocene sediments have been eroded away. Only two spots remain—Bates Hole and Beaver Divide, in Wyoming.

Piedmont, flood-plain, and lacustrine deposits.—King led the earlier geologists in presenting the theory that the mountain basins were once filled with a chain of lakes. This theory was adopted by Marsh, Cope, Scott, and Osborn. Leidy, as early as 1869, cast doubt upon the lake theory as applied to the White River group east of the mountains. The lake theory has gradually been replaced by the flood-plain theory through the studies of Haworth (1897.1), Gilbert (1896.1), Matthew (1899.2), Davis (1900.1), Johnson (1901.1), and Hatcher (1902.3).

For the highly diversified mountain-basin region throughout the very long period of the Eocene, with its considerable climatic vicissitudes, no single theory of deposition is adequate. We have seen that in the basal Eocene, during Fort Union, Puerco, and Torrejon (Thanetian) time, there were doubtless great level areas, heavily forested, with dense undergrowth, favorable to the formation of peat and lignitic deposits and subject to heavy silting of fine sediments from annual floods. These were like the flooded areas of the forest belt in the Amazon delta. Such still-water areas were contemporaneous with areas in the piedmont regions close to the mountains, where stream erosion was active. The conditions that prevailed in general during Wasatch (Sparnacian) time are nearly paralleled by those now found in the flood plains of Parana, Paraguay, and Uruguay Rivers, which are carrying down vast masses of gravel, sand, and clay from the mountain chains of Brazil, as reported by John Ball in his "Notes of a naturalist in South America" (1887.1). The annual rainfall in these mountains ranges from 100 to 136 inches, and it rapidly disintegrates the yielding rocks and discharges a vast quantity of detrital matter over the broad plains of Argentina and Uruguay. The mountain streams have thus built up wide, level areas in these countries, and the lower rivers, ploughing their channels through the vast deposits over which they must make their way, extend their banks with every increment and thus continually make additions to the outskirts of the formation they are depositing. In this way deposits covering an area of 200,000 square miles have been formed from the mountains of Brazil.

The period of flood-plain and piedmont deposition in the Rockies was followed by the great lacustrine period of Green River time and of Wind River (Ypresian) time, in which the climate was much warmer. In the same region there ensued the flood-plain period of the Bridger.

Eocene basin deposition of another kind and climatic change are indicated in the widespread horizontal "white layers" that divide the Bridger into several geologic and faunistic levels. These white layers indicate periods of lagoon leveling by annual uniform flooding and evaporation, similar to that of the existing playa lakes of the Great Basin in Nevada.

In middle Eocene time new conditions of forestation and erosion and the presence of volcanic atmospheric dust in the Bridger and Washakie Basins are indicated. Sinclair showed (1906–1909) that the Bridger formation was composed chiefly of volcanic material that has been more or less rearranged by stream action, and that clouds of volcanic dust doubtless filled the atmosphere during the Bridger epoch (middle and upper (?) Eocene). This interesting discovery was confirmed by thorough analyses made by Johannsen in 1914. The rocks of the upper and middle Eocene formations consist chiefly of volcanic tuff. Although the minerals of this tuff are those of a dacite (quartz andesite), the quartz grains may be of sedimentary origin and the volcanic rock may be andesite (Johannsen, 1914.1, p. 210). The presence of dacite tuffs in the lower Bridger levels (B and C) indicates that the atmosphere was charged with volcanic dust, which also settled upon the contemporaneous deposits of the Washakie Basin, 100 miles to the east, as well as on the Uinta Range, 60 miles to the south. Thus during middle and upper Eocene time the atmosphere over the present Bridger, Washakie, and Uinta region was at times charged with volcanic dust. Specimens of lower and basal Eocene rocks indicate sediments of more normal type, and whatever volcanic material they contain is so much altered by re-sorting and mixing with normal sediments that it is not clearly recognizable.

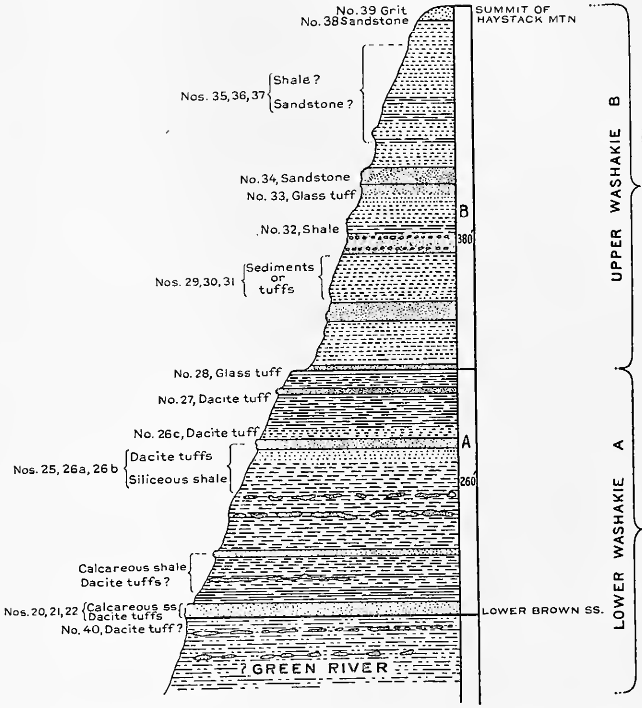

FIGURE 40.—Section of deposits near Barrel Springs, Washakie Basin, southern Wyoming (No. 9, fig. 35)

Showing alternating beds of tuff, siliceous and calcareous deposits, and sandstone. Johannsen (1914.1), after Granger, with modifications. The numbers refer to lithologic specimens examined by Johannsen.

The manner in which the layers of dacite and glass tuffs alternate with the heavy river-channel sandstones is clearly displayed in the analysis of sediments from the Washakie Basin by Johannsen. Tuffs are also scattered, but more sparingly, through the earlier Torrejon, Wasatch, and Wind River formations, along with river-borne material derived from the decay and erosion of older rocks.

SECTION 2. EOCENE AND LOWER OLIGOCENE FORMATIONS AND FAUNAL ZONES

FIRST FAUNAL PHASE (BASAL EOCENE)

SEVENTEEN LIFE ZONES

Largely as the result of explorations and researches made for this monograph, the major Eocene and Oligocene type life zones that were recognized by Leidy, Cope, and Marsh up to the year 1900, such as the "*Coryphodon* beds," "*Uintatherium* beds, "*Diplacodon* beds," and "*Titanotherium* beds," have gradually been differentiated, through the work of Osborn, Granger, and Matthew, into 16 known life zones, each distinguished by the presence of a highly varied mammal fauna and by the appearance or disappearance of certain groups of mammals and reptiles. There is also one theoretic life zone, between known upper Eocene and known lower Oligocene time, making 17 in all. Each of these life zones corresponds with a series of sediments ranging in thickness from 300 to 600 feet. Many of them correspond with changes in climate, temperature, and forestation, and some of them are clearly defined and sharply demarcated from others. A single generic name, such as *Coryphodon,* rarely suffices to distinguish them, because many genera and even certain species may survive for long periods of time.

Each of these faunal zones is defined paleontologically by one or more of the life forms it contains, geologically by the locality where it is best preserved, to some extent botanically by the flora it contains, and lithologically by the character of its rocks as shown by microscopic analyses. Thus, for example, we have the typical upper Wind River zone—the "Lost Cabin" or *Lambdotherium-Eotitanops-Coryphodon* zone, a rather cumbersome designation, which indicates that only during this period did these three types of mammals exist together. In this zone *Lambdotherium* is the most distinctive genus. Sediments in different geographic basins are correlated in such a manner as to present the whole life story of the Eocene epoch, as shown in the accompanying diagram. Of the two chief faunistic gaps that have been recognized, that between the Wind River and the Bridger has now been filled by explorations of the Huerfano, so that there remains only that between the Uinta and the White River. These 16 known life zones will doubtless be multiplied to 20 or more by future discovery. They are shown in the following table:

Synopsis of life zones

Epoch	Life zones	Horizon	Characteristic species and genera
Lower Oligocene.	17. Titanotherium-Mesohippus.	Chadron C	Brontops robustus, Menodus giganteus, Brontotherium platyceras, Allops crassicornis.
		Chadron B	Brontops dispar, Menodus trigonoceras, Allops marshi, Brontotherium hatcheri.
		Chadron A	Brontops brachycephalus, Menodus heloceras, Brontotherium leidyi.
Upper Eocene.	16. Theoretic zone (no fauna)	Uinta C 2.	
	15. Diplacodon-Protitanotherium-Epihippus.	Uinta C 1	Diplacodon, Protitanotherium, Epihippus, Protoreodon.
	14. Eobasileus–Dolichorhinus	Uinta B 2 and Washakie B 2.	Eobasileus, Dolichorhinus.
	13. Metarhinus	Uinta B 1 and Washakie B 1.	Metarhinus, Amynodon.
Middle Eocene.	12. Uintatherium-Manteoceras-Mesatirhinus.	Washakie A and Bridger C and D.	Uintatherium, Manteoceras, Mesatirhinus.
	11. Palaeosyops paludosus-Orohippus.	Bridger B	Palaeosyops paludosus, Orohippus.
	10. Eometarhinus-Trogosus-Palaeosyops fontinalis.	Bridger A and Huerfano B.	Palaeosyops fontinalis, Eometarhinus.
Lower Eocene.	9. Lambdotherium-Eotitanops-Coryphodon.	Huerfano A, Wind River B, and Big Horn E.	Lambdotherium, Eotitanops, Coryphodon, Meniscotherium.
	8. Heptodon-Coryphodon-Eohippus.	Big Horn (Wasatch) D and Wind River A.	Heptodon, Eohippus, Coryphodon.
	7. Systemodon-Coryphodon-Eohippus.	Big Horn (Wasatch) C	Systemodon, Eohippus, Coryphodon.
	6. Eohippus-Coryphodon.	Big Horn (Wasatch) B	Eohippus, Pelycodus, Coryphodon.
Transition basal Eocene to lower Eocene.	5. Phenacodus-Nothodectes-Coryphodon.	Big Horn (Wasatch) A	Phenacodus, Nothodectes, Coryphodon, Champsosaurus.
Basal Eocene.	4. Pantolambda	Torrejon B	Pantolambda, Tetraclaenodon, Claenodon.
	3. Deltatherium	Torrejon A	Deltatherium, Mioclaenus, Haploconus.
	2. Polymastodon	Puerco B	Polymastodon, Oxyclaenus.
	1. Ectoconus	Puerco A	Ectoconus, Champsosaurus.
Cretaceous.[a]	Triceratops-Tyrannosaurus	Lance and Denver formations.	Triceratops, Tyrannosaurus, Champsosaurus, Meniscoëssus.
	Monoclonius	Judith River and Belly River formations.	Monoclonius, Deinodon, Eodelphis.

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[a] The United States Geological Survey classifies the Denver formation as Eocene and the Lance formation as Tertiary (?).

Lower Tertiary geologic horizons and life zones and their hoofed mammals

Epoch	Geologic horizon	Chief life zones. (Titanotheres, horses, and other mammals.)	Chief titanotheres and other perissodactyls
Oligocene.		Leptauchenia, Miohippus, and Oreodon.	**Extinction of titanotheres**
	Chadron A, B, and C.	17. Titanotherium-Mesohippus.	Giant titanotheres—Menodus, Brontops, Brontotherium, etc.
Upper Eocene.	Uinta C.	16. Theoretic zone (fauna unknown). 15. Diplacodon-Protitanotherium-Epihippus.	Protitanotherium, early horned titanotheres.
	Washakie B and Uinta B.	14. Eobasileus-Dolichorhinus. 13. Metarhinus.	Dolichorhinus cornutus, Mesatirhinus.
Middle Eocene.	Bridger C and D and Washakie A.	12. Uintatherium-Manteoceras-Mesatirhinus.	Manteoceras, ancestors of Oligocene titanotheres.
	Bridger B.	11. Palaeosyops paludosus-Orohippus.	Palaeosyops and numerous other titanotheres.
	Bridger A and Huerfano B.	10. Eometarhinus-Trogosus-Palaeosyops fontinalis.	Palaeosyops fontinalis (primitive).
Lower Eocene.	Big Horn E ("Lost Cabin"), Wind River B (typical Wind River of Cope), and Huerfano A.	9. Lambdotherium-Eotitanops-Coryphodon.	**Appearance of titanotheres**
	Big Horn D ("Lysite") and Wind River A.	8. Heptodon-Coryphodon-Eohippus.	
	Big Horn C ("Gray Bull").	7. Systemodon-Coryphodon-Eohippus.	Earliest tapiroids, Tapiridae.
	Big Horn B ("Sand Coulee").	6. Eohippus-Coryphodon.	Earliest Equidae (horses).
Transition.	Big Horn A ("Clark Fork") of Wyoming and "Tiffany beds" of southwestern Colorado.	5. Phenacodus-Nothodectes-Coryphodon.	Earliest Phenacodus (condylarths). Earliest Coryphodon. Nothodectes, similar to Pleisiadapis of Cernay.
Basal Eocene.	Upper horizon of Torrejon formation.	4. Pantolambda.	Ancestors of the Amblypoda.
	Lower horizon of Torrejon formation.	3. Deltatherium.	
	Upper horizon of Puerco formation.	2. Polymastodon.	Multituberculata.
	Lower horizon of Puerco formation.	1. Ectoconus.	Earliest known Taligrada.

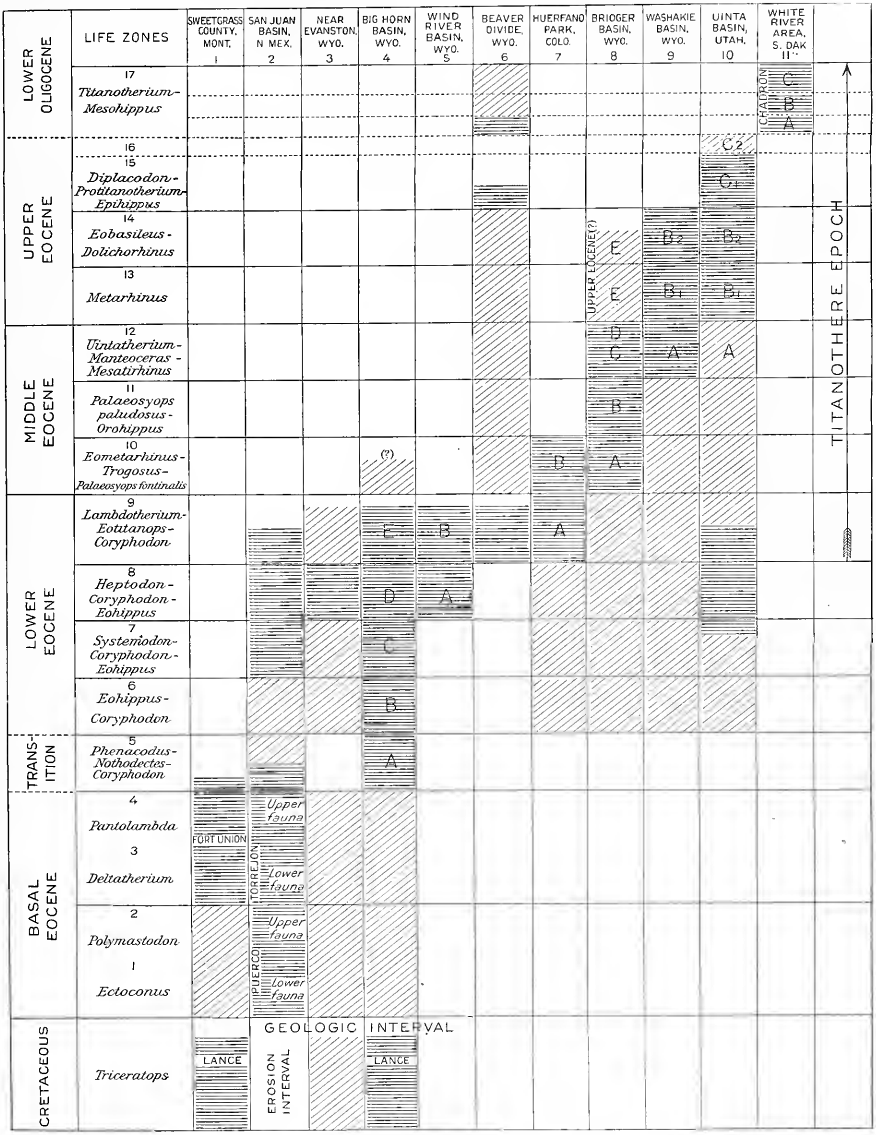

Figure 41.—Eocene and lower Oligocene mammalian life zones in eleven typical correlated areas in New Mexico, Colorado, Utah, Wyoming, South Dakota, and Montana, located as shown on the general geologic map (fig. 35)

Arranged by Osborn (1919) after original studies made in the field, chiefly by Granger, but also by Hatcher (Oligocene), Hills, Peterson, and Gidley (Eocene). The 16 known life zones numbered 1 to 15 and 17 are indicated in the diagram by dark horizontal lines. The nonfossiliferous areas are indicated by light oblique lines. These life zones and sections also correspond with the detailed geologic sections in this chapter. The United States Geological Survey classifies the Lance formation as Tertiary (?), Eocene (?). The author of this monograph regards it as Cretaceous.

BASAL EOCENE TIME IN MONTANA AND NEW MEXICO

Fort Union formation of Montana.—The typical Fort Union formation of Hayden (Meek and Hayden, 1862.1, p. 433), at the junction of Yellowstone and Missouri Rivers, lies east of the center of an ancient forested swamp in which was laid down the upper part of Hayden's "Great Lignite Group." One of the most interesting results of discoveries made in 1901 (Douglass, 1902.1) is revealed in an exposure of the Fort Union in Sweet Grass County, Mont., near the headwaters of the Musselshell, containing a rich fauna of the archaic species of basal Eocene animals, some of which are identical with those found on the headwaters of San Juan River, in northern New Mexico, a thousand miles to the south. Both lie near the one hundred and seventh meridian. The presence in large numbers of animals belonging to similar species shows that uniform climatic and physiographic conditions existed in this great mountain-basin region for a very long time, because similar generic forms of life (*Claenodon, Pantolambda*) persist through 3,000 feet of Fort Union sediments. The remains of the oldest of these mammals are found immediately above the dinosaur-bearing beds at a level which is here identical with that of the Lance formation; and the present opinion is that sedimentation may have been continuous throughout Upper Cretaceous and basal Eocene time in this region in Montana.

The mode in which these Fort Union beds were formed has not yet been positively determined, but the masses of fresh-water shells which they contain in certain localities indicate that they were in part laid down in shallow lagoons and swamps, which were in some places crossed by river channels. At some places the beds contain multitudes of leaves, which give us a complete record of the forest life of the time. Vast areas of warm-temperate and more hardy trees were interspersed with areas where swamp vegetation accumulated rapidly enough to form great beds of lignite. Amid the glades of these forests there wandered swamp turtles, alligators, and especially the choristoderan reptiles of the characteristic genus *Champsosaurus.*

Puerco and Torrejon formations of New Mexico.—A southern center of this archaic mammal life is the type locality of the Puerco formation, on the divide between the Rio Grande and the San Juan, in northwestern New Mexico, a formation described by Cope (1875.1) as the "Puerco marls." Cope listed the first mammalian fauna from those beds in 1881, opening a new epoch in mammalian paleontology. In 1885 he assigned to the formation a thickness of 850 feet and distinguished it from the underlying beds, which he supposed to be Laramie but which have since been divided into the Ojo Alamo sandstone, the Kirtland shale, and the Fruitland formation, all probably of Montana age, older than Laramie. The Puerco of Cope appears to be a single formation geologically, deposited with apparent conformity between the upper and lower divisions, but it is sharply divided faunistically into two main life zones, a lower, which retains the name Puerco, and an upper, to which the name Torrejon was given by Wortman in 1895 (Osborn and Earle, 1895.95, pp. 1–3A). In 1910 Gardner (1910.1) applied the name Nacimiento group to both divisions. In 1897 Matthew (1897.2) separated the mammal fauna of the two levels, and in 1912 and 1913 Sinclair and Granger (1914.1) established in this group no less than four faunistic levels, which are shown in the accompanying section (fig. 43). Two faunistic levels were observed by Wortman in the Puerco, and two distinct faunistic levels are distinguished by Granger, Sinclair, and Matthew in the Torrejon.

These four successive changes in the archaic fauna occurred during a period of continuous sedimentation, for no unconformity has been observed between the Puerco and Torrejon. The rate of deposition of the 800 feet of Puerco and Torrejon sediments was relatively slow as compared with that of the deposition of the 6,000 feet of the corresponding Fort Union sediments to the north. As the mammals distributed through 4,000 feet of the northern part of the Fort Union deposits correspond chiefly with those of the Torrejon, it appears possible that the underlying Puerco fauna may belong in part in upper Lance time. We observe that the Fort Union was deposited upon the Lance continuously, without recognized notable unconformity, whereas the Puerco lies upon the eroded surface of the Ojo Alamo, which, because of its dinosaur fauna, is considered of probable Judith River and Belly River age.

The close resemblance of the crestless trachodont dinosaur, *Kritosaurus navajovius*, from the Ojo Alamo, to a corresponding form from the Belly River formation of Alberta also suggests a close correlation in time.[8]

In 1912 and 1913 Sinclair and Granger thoroughly explored the basal Eocene deposits of the San Juan Basin, with the results enumerated above.

SUMMARY OF FAUNAL EVENTS OF BASAL EOCENE TIME

In addition to the four fossiliferous zones observed in the Puerco and Torrejon formations, all distinctively basal Eocene, there is an overlying zone in the "Tiffany beds," beyond the border of Colorado, determined by Gidley (1909) and Granger (1916). These beds contain a fifth fauna, which is strictly intermediate between basal Eocene and lower Eocene. This transitional basal-lower Eocene zone is described on pages 64–65. The basal Eocene mammalian life

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[8] See Parks, W. A., The osteology of the trachodont dinosaur *Kritosaurus incurvimanus:* Univ. Toronto Studies, Geol. series, 1920.

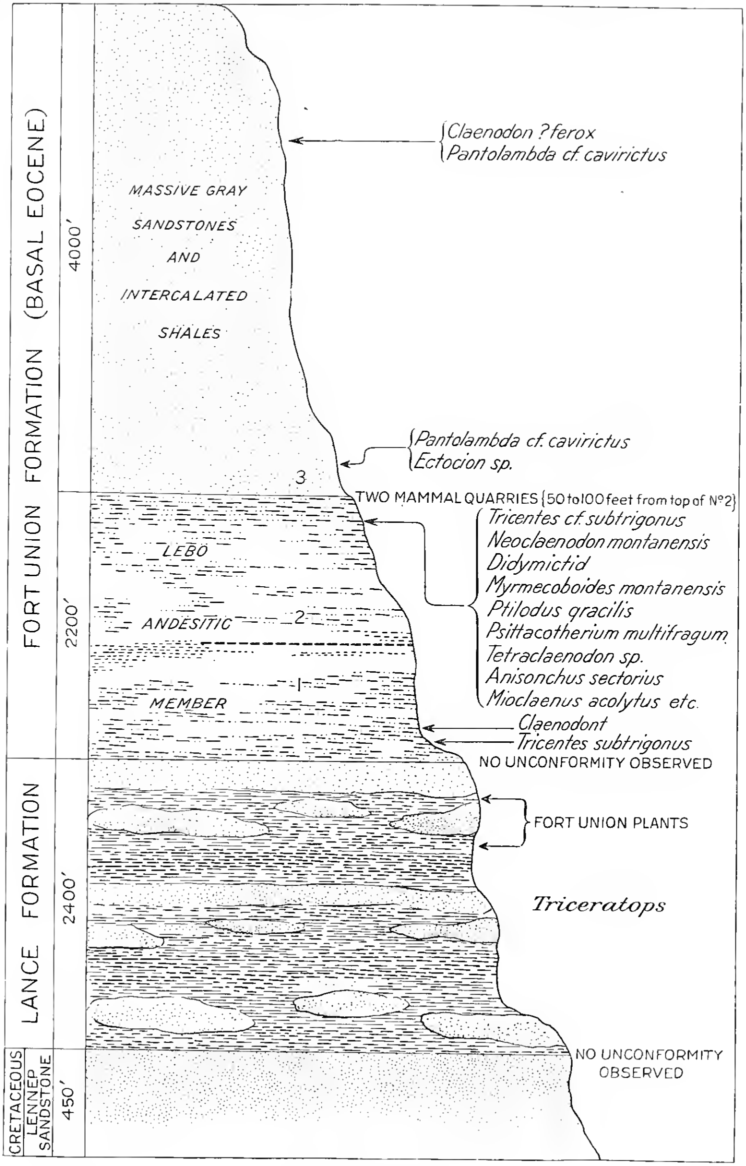

FIGURE 42.—Section of Upper Cretaceous and basal Eocene (Fort Union) deposits in Sweet Grass County, Mont.

After Stanton (1909.1), Stone and Calvert (1910.1), and Gidley (1919). This very significant exposure (No. 1, fig. 35) is in an outlying area of the Fort Union formation and its mammal fauna corresponds broadly with that of the Torrejon formation of northwestern New Mexico, although the section has not yet been divided into separate life zones. It affords the most satisfactory means of correlating the Fort Union and Puerco and Torrejon formations. The United States Geological Survey classifies the Lance formation as Tertiary(?), but the author of this monograph regards it as of Upper Cretaceous age.

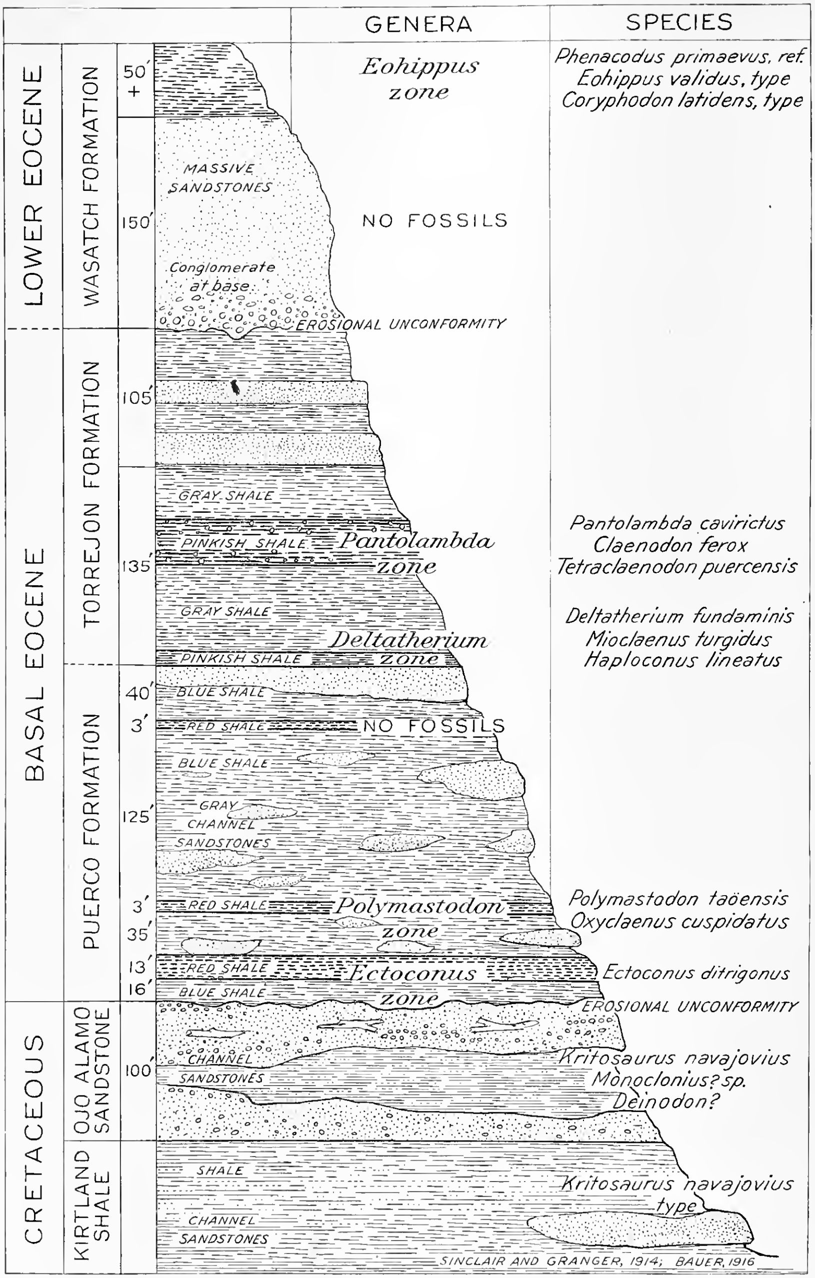

FIGURE 43.—Section of Eocene deposits in the San Juan Basin, northwestern New Mexico (No. 2, fig. 35), showing the base of the Puerco formation resting upon the eroded surface of the Ojo Alamo sandstone, as observed by Sinclair and Granger (1914.1)

This section displays the close geologic continuity of the Puerco and Torrejon beds, which are subdivided faunistically into four distinct life zones, named, in ascending order, (1) *Ectoconus* and (2) *Polymastodon* zones, Puerco formation; (3) *Deltatherium* and (4) *Pantolambda* zones, Torrejon formation. The Ojo Alamo sandstone is perhaps of Judith River age.

of the Puerco and Torrejon formations in northwestern New Mexico and southwestern Colorado is accordingly related as follows:

Transition epoch:
  5. *Phenacodus-Nothodectes-Coryphodon* zone. Represented in the "Tiffany beds" of southwestern Colorado and in the Wasatch formation (horizon Big Horn A, "Clark Fork") of Big Horn Basin, Wyo.

Basal Eocene epoch:
  4. *Pantolambda* zone. Represented in the upper levels of the Torrejon formation of northwestern New Mexico and in the upper part of the Fort Union formation of Montana.
  3. *Deltatherium* zone. Represented in the basal part of the Torrejon formation and in part of the Fort Union formation of Montana.
  2. *Polymastodon* zone. Represented in the upper part of the Puerco formation of northwestern New Mexico. Not yet recorded in the Fort Union formation.
  1. *Ectoconus* zone. Represented in the lower part of the Puerco formation. Not yet recorded in the Fort Union formation.

BASAL EOCENE FAUNAL ZONES

ZONES 1 AND 2: ECTOCONUS AND POLYMASTODON ZONES

[Puerco fauna; part of Thanetian of Europe]

No equivalent of the most ancient Puerco fauna has thus far been discovered in the Fort Union beds of the North or in Europe; it is at present unique.

Puerco mammals and reptiles.—The Puerco mammals are extremely archaic, mostly Meseutheria (Osborn) or paleoplacentals (Matthew), representing groups of placentals that became extinct during the Eocene. The Puerco contains no remains of modern orders or families of mammals except three, one (Miacidae) which is related to the doglike Carnivora, a second which is related to the primitive Insectivora, and a third which is related to the primitive Edentata. No rodents or lemuroid primates have been discovered, and certainly no perissodactyl or artiodactyl ungulates were in this region at this time. Matthew (1914.1, p. 383) is of the opinion that most of these archaic placentals have no known predecessors in the Lance formation.

About 10 per cent of the fauna consists of rodent-like multituberculates, an extremely ancient order related to the existing monotremes or to the marsupials. These animals are nearly related to ancestral forms in the Lance. Didelphiid marsupials are also present.

Similarly the reptiles all belong to families that originated in Belly River or Pierre time (Upper Cretaceous) or earlier. The Choristodera (*Champsosaurus*) became extinct in basal Eocene time. Noteworthy is the absence of the prevailing Tertiary families of chelonians (Emydidae, Testudinidae), which, with the modernized mammals, first appear in the lower Eocene.

On comparing the life of the Puerco with that of the Lance we find a mammalian fauna that indicates no very wide gap in time—a fauna that is somewhat more ancient than the Torrejon and known Fort Union, also more ancient than the Cernaysian and upper Thanetian of France. It is therefore probable that the Puerco corresponds with the lower Thanetian of France, but its life has no known equivalent either in Europe or in this country.

The opinion of Cope that the ancestry of the modernized mammals should be sought among these Puerco forms lacks adequate confirmation. The opposite opinion—that the Puerco mammals are not ancestral to the modern mammals—was developed by Osborn (1893.82, 1894.89) when he applied to them the name Mesoplacentalia (Meseutheria), indicative of their archaic or Mesozoic characteristics. They represent the first known adaptive radiation of the placentals into archaic flesh eaters and herbivores. We note the presence of three families of archaic Carnivora (Creodonta) and remote relatives (*Psittacotherium*) of the Edentata. Among the archaic ungulates we find one varied family (Periptychidae) of the Amblypoda (Taligrada) and two families (Phenacodontidae, Mioclaenidae) of the Condylarthra.

Puerco sedimentation and physiography.—The Puerco formation is not separated from the overlying Torrejon formation by any lithologic or stratigraphic break. (Sinclair and Granger, 1914.1, p. 308.) The absence of erosional unconformity between the Puerco and Torrejon was also observed by Gardner (1910.1, pp. 722–723) and by Bauer (1916.1, p. 277). That the Puerco and Torrejon formations represent a very long period of geologic time is demonstrated by the recorded 6,000 feet of Fort Union sediments, which have yielded the Torrejon fauna alone; and, like the Fort Union, they represent a very long period of uniform conditions of climate and sedimentation. The presence of fish, crocodiles, turtles (*Trionyx*), and other genera in the same strata with the bones of mammals and at the same level shows conclusively that these deposits were formed by water. That the streams were of low gradient is shown by the complete absence of pebbles in the Puerco and by the wide horizontal extent of some of the clay bands. Bogs, apparently formed in back waters in the channels, were filled with accumulations that preserved impressions of the leaves of figs (*Ficus*), plane trees (*Platanus*), poplars (*Populus*), relatives of the bread fruit (*Artocarpus*), and numerous shrubs (*Paliurus*, *Viburnum*). The quantity and variety of these plant remains, together with the abundant large drift logs in the clays, indicate a heavy growth of vegetation along the streams. The species of *Ficus*, *Paliurus*, *Viburnum*, and *Artocarpus* are also found in the Denver and Raton formations of eastern Colorado; and other species indicate Fort Union age (Knowlton, cited by Sinclair and Granger, 1914.1, p. 306). The mode of occurrence of the fossils in the still-water clays and occasionally in the river-channel sandstones shows that some of the skeletons may have been washed into the streams during heavy rains and scattered by the action of crocodiles, carnivores, turtles, and fish. Other skeletons show traces of gnawing, probably by small Ptilodontidae, which proves that many of the bones lay for some time on the surface of the ground before reaching the streams or being covered in flood time by water-borne sediments.

ZONES 3 AND 4: DELTATHERIUM AND PANTOLAMBDA ZONES

[Torrejon and Fort Union faunas; in part Thanetian of Europe]

The mammals of the Torrejon formation of northwestern New Mexico, whose remains are found in a stratum about 250 feet above the base of the Puerco mammal-bearing level, are somewhat larger, considerably more diversified (perhaps because more fully known), and of slightly more progressive type. They show very close affinity to the Fort Union mammals of Montana and some affinity to the Cernaysian forms discovered in the conglomérat de Cernay, near Rheims, France.

The multituberculates, which occur in the Holarctic region in upper Triassic (Rhaetic) time, now make their last appearance abundantly; of the Ptilodontidae, *Ptilodus* (or *Neoplagiaulax*) is found in New Mexico, Montana, and Cernay; the large *Polymastodon* that distinguishes the upper Puerco zone does not recur.

Here also are five families of archaic carnivores (Creodonta), among which, in the Miacidae, there is a genus (*Didymictis*) which appears to lead through the civet and doglike forms of the lower and middle Eocene into forms related to the modern Carnivora. Among the three Torrejon families of Insectivora the existing Centetidae (tenrecs) are possibly related to the genus *Palaeoryctes*, a very primitive form resembling the modern Cape golden moles (*Chrysochloris* of South Africa, *Necrolestes* of South America). The ancestors of the modern edentates are highly diversified (Edentata, Ganodonta) and include slothlike animals, indicative of present or former migrations into South America. Of the families of archaic ungulates two (Phenacodontidae and Mioclaenidae) represent the Condylarthra, and two (Periptychidae and Pantolambdidae) represent the Amblypoda. Of the Amblypoda *Pantolambda cavirictus*, which is also found in the Fort Union, is very characteristic. Of the bearlike Creodonta (Arctocyonidae) *Claenodon ferox*, which is closely related to the *Arctocyon* of the Thanetian of France, occurs also in the Fort Union of Montana.

Most of these mammals of the Torrejon, like those of the Puerco, were ancient adaptive radiations of the Mammalia. They were small-brained, had defective foot structure, and were unfitted to compete with the ancestors of the modernized mammals, which begin to appear immediately above the *Nothodectes* zone. Six families approached extinction at the end of the Torrejon—the Plagiaulacidae of the Multituberculata; the Oxyclaenidae of the Carnivora; the Conoryctidae of the Edentata; the Periptychidae and Pantolambdidae of the Ambyploda (which, however, are related to the succeeding coryphodons); and the Mioclaenidae of the Condylarthra. The Plagiaulacidae and Oxyclaenidae, however, survive into the early Wasatch, the Periptychidae into the "Tiffany beds." Torrejon time thus ends with the extinction of a large number of families of archaic mammals, though several families survived, passing into the succeeding lower Eocene.

Unconformities of the Torrejon with the underlying Puerco have not been found. (Sinclair and Granger, 1914.1, p. 312; also Gardner, 1910.1, p. 722, and Bauer, 1916.1, pp. 273–277.) There is no doubt about the aqueous origin of either the Puerco or the Torrejon deposits. The Torrejon carries less petrified wood than the Puerco, but it contains *Unio*-bearing beds, which occur repeatedly in the gray clays, and abundant shells of land mollusks (*Pupa*), which are found in the clays that contain bones of mammals. Lithologically, the Torrejon closely resembles the Puerco, except that gravels of quartzite, jasper, red shale, etc., occur in some of the channel sandstones. Mammals appear principally in the zones filled with small rusty calcareous concretions, which occur in clays that range in color from red mottled with green to gray. The upper boundary of the Torrejon is everywhere marked by the presence of *Tetraclaenodon* (ancestor of *Phenacodus*) and of the two amblypods *Periptychus rhabdodon* and *Pantolambda*. The total thickness of the Torrejon differs at different places, ranging from 240 to 660 feet, whereas the approximately contemporaneous Fort Union of Montana, which possibly also represents the Puerco, attains a thickness recorded as nearly 6,000 feet.

The top of the Torrejon is in unconformable contact with sandstone that indicates a cycle of deposition of coarse sediments and alluvial fans, attributed to Wasatch time.

SECOND FAUNAL PHASE (LOWER EOCENE)

TRANSITIONAL BASAL EOCENE FAUNAS

ZONE 5: PHENACODUS-NOTHODECTES-CORYPHODON ZONE

[Base of Wasatch formation of Big Horn Basin, first Wasatch life zone, Big Horn A; Cernaysian of Europe]

The first Wasatch life zone is represented in the "Tiffany beds" of southwestern Colorado, in the basal part of the Wasatch formation (horizon Big Horn A = "Clark Fork") of the Big Horn Basin, Wyo., and probably in the summit of the Fort Union formation of Montana. In southwestern Colorado, near the headwaters of the San Juan, are the "Tiffany beds" of Granger, which contain a fauna characterized by the last appearance of *Periptychus* and by the first appearance of *Phenacodus* and of *Coryphodon*, a genus characteristic of the Sparnacian of France. *Nothodectes* of the "Tiffany beds" is particularly interesting because of its structural affinity to *Plesiadapis* of the Cernaysian of France. The multituberculates are represented in Wyoming by *Ptilodus* ("Sand Coulee" and "Clark Fork"?). Of the four specimens of ptilodontids from Wyoming, one found by Granger was from the Big Horn B horizon ("Sand Coulee beds"). Three found by Stein were probably from the same horizon but may have been from the underlying Big Horn A horizon (the "Clark Fork beds"). Undoubtedly ptilodontids occur in the "Clark Fork," but we can not furnish any positive evidence (W. Granger, 1919).

This mammal fauna as a whole actually resembles that of the Torrejon more closely than that of the lowest overlying horizon (Big Horn B, "Sand Coulee") of the Wasatch. A significant discovery in the *Nothodectes* zone is *Zanycteris*, a bat showing affinities with the vampires (Phyllostomatidae) of South America.

The *Nothodectes* zone ("Tiffany" and "Clark Fork") is basal Eocene, as indicated by the absence of the four orders Primates, Perissodactyla, Artiodactyla, Rodentia; it is lower Eocene, as indicated by the presence of *Phenacodus* and *Coryphodon*.

The mammalian life of the "Clark Fork" beds in the Big Horn Basin of Wyoming, to the north, is very similar (Granger, 1914.1, p. 204) to that of the "Tiffany beds" in Colorado. These "Clark Fork beds," 500 feet in thickness, are characterized by the predominance of the Condylarthra (*Phenacodus* and *Ectocion*), remains of which constitute three-fourths of the fossils collected from them. The amblypod ungulates are represented by *Coryphodon* and by the first appearance of an animal (*Eobathyopsis*) ancestral to *Bathyopsis*, of the Wind River formation, which in turn is ancestral to the horned *Uintatherium* of the Bridger formation. Among the Reptilia is the last surviving *Champsosaurus* from the Fort Union and the Cretaceous, a distinctively basal Eocene type.

EARLY EOCENE TIME

General correlation.—Lower Eocene (Wasatch) time began, it may be said, with the first appearance of *Coryphodon* and *Phenacodus* in the "Clark Fork" and "Tiffany beds" described above as the *Phenacodus-Nothodectes-Coryphodon* zone, in which is found the first phase of the *Coryphodon* fauna. The modernization occurred later, in the "Sand Coulee beds" (*Eohippus* zone), which overlie the "Clark Fork."

The Sparnacian of Europe is broadly parallel with part of the Wasatch formation (*Coryphodon* zone) of America. It is typified in France by the deposits of Soissons, Meudon, and Vaugirard; in England by the Woolwich beds, which contain a rich flora. In these fluviomarine, lagoon, and lacustrine deposits of Europe mammals are rare, and homotaxis with America is afforded through the large coryphodons, the perissodactyl *Lophiodon*, and the creodonts *Palaeonictis* and *Pachyaena*. This sparse European fauna, which in its early stages lacks Equidae (*Hyracotherium*), has almost a counterpart in that of the *Nothodectes* zone of the Rocky Mountain region.

The two upper zones of the lower Eocene (Wasatch) are correlated with the Ypresian of Europe.

Wasatch and Sparnacian floras.—According to Berry (1914.1, p. 148) the earliest Eocene beds of Europe (Sparnacian and Ypresian stages) contain the flora found in the Oldhaven, Woolwich, and Red beds of England, largely unstudied, and the small flora from the Paris Basin recently described. The Woolwich beds have yielded the fig (*Ficus*), the locust (*Robinia*), the tulip tree (*Liriodendron*), and *Grevillea*, a proteaceous plant now confined to Australia. Berry believes (letter to the author, April 1, 1918) that in lower Wasatch time the Fort Union flora persisted over the Rocky Mountain basin region. This belief implies that the climate was then prevailingly warm-temperate but that there were occasional incursions of trees of subtropical type.

Sedimentation during Wasatch time.—As the Sparnacian stage of Europe, which is equivalent to part of the Wasatch, derives its name from Épernay (Latin Sparnacum), so the Wasatch stage of mammalian life derives its name from the typical Wasatch group of Hayden in western Wyoming, a single mammal-bearing member of which is the Knight formation (Veatch, 1907.1), 1,750 feet in thickness, containing Cope's types of *Eohippus index*, *E. vasacciensis*, *Phenacodus primaevus*, *Coryphodon radians*, *C. semicinctus*, *C. latipes*. These species of mammals do not represent the oldest Wasatch fauna; they are of the same age as the species found at the "Lysite" horizon (life zone No. 8) of the Big Horn Basin.

Among the chief sources of Wasatch mammals are the following:

	Feet
1. Knight formation (Veatch), top of typical Wasatch group (Hayden), southwestern Wyoming; red and yellow sandy clays	1, 750
2. Wasatch formation, Big Horn Basin, Wyo.; red, brown, and gray sandstones and clays	2, 025
3. Wasatch formation ("Bitter Creek" of Powell and "Vermilion Creek" of King), Washakie Basin, Wyo.; red and gray clays and sandstones	4, 000–5, 500
4. Wasatch formation of the San Juan Basin, N. Mex	1, 500
5. Wasatch formation of the Uinta Basin, Utah (White, 1878)	2, 000
6. Wasatch formation of the Powder River Basin, Pumpkin Buttes, Wyo	2, 400

The estimate made by King (1878.1) of the thickness of the sediments in the Washakie Basin (4,000–5,500 feet) is considered high (Granger). It is interesting to note that the mean thickness (about 2,300 feet) of the Wasatch sediments in the six areas listed above exceeds somewhat that of the Bridger formation (1,875 feet).

The earliest Wasatch sediments are those in the Big Horn and Clark Fork Basins of northern Wyoming, from which we obtain the whole range of lower Eocene fossil mammals, beginning with the end of basal Eocene time.

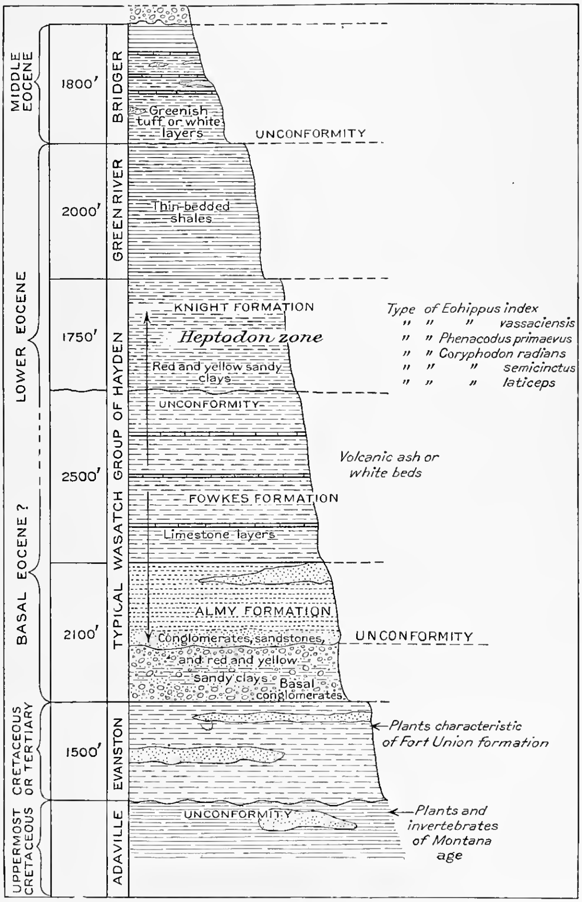

FIGURE 44.—Columnar section of Cretaceous and Eocene sediments exposed along Bear River near Evanston, in extreme southwestern Wyoming (No. 3, fig. 35), showing the typical Wasatch group of Hayden (1869). Chiefly after A. C. Veatch (1907.1)

Mammals similar to those in zone 8 (*Eohippus*, *Phenacodus*, *Heptodon*, and *Coryphodon*) occur in a narrow fossiliferous stratum which may be referred to the *Heptodon-Coryphodon-Eohippus* zone. Above are Green River and Bridger beds; below are 4,600 feet of beds (without mammals) belonging to the Wasatch group (Fowkes and Almy formations), which are underlain by the Evanston formation, containing Fort Union plants, and the Adaville formation, containing Montana plants and invertebrates. The author of this monograph regards the Evanston formation as uppermost Cretaceous.

Similar heavy and continuous sedimentation also occurred during Wasatch time, in both the northern and the southern Uinta region, in the Bridger and Washakie Basins on the north, and in the great Uinta Basin south of the mountains. Few of these vast masses of sediment have thus far yielded mammalian fossils. Douglass found a considerable fauna in the Wasatch of the Uinta Basin. *Systemodon* occurs there. Wortman has reported (letters) a *Coryphodon* from the Wasatch of the Washakie Basin. To the south, in the San Juan Basin, there were laid down, over the Torrejon, thick beds of sand and fluviatile sediments, which form the New Mexico Wasatch. These beds, which are divided by Granger (1914.1) into an upper ("Largo") and a lower ("Almagre") division, have a combined thickness of 1,500 feet, throughout the greater part of which mammalian fossils are found. These Wasatch beds in New Mexico have much the same general appearance as the Wasatch in other localities, consisting of red, gray, and ocherous bands of shale and sandstone, without evidence of unconformity throughout the series. The most recently identified Wasatch sediments are those of Pumpkin Buttes, in the Powder River Basin, Wyo.

The correlation of the faunal horizons in these sedimentary areas by the species of mammals which they contain was determined with remarkable precision by the American Museum expedition under Granger, as shown in the accompanying table (p. 67).

Wasatch physiographic and climatic conditions favorable to modernized fauna.—All the Wasatch sediments indicate a profound and somewhat abrupt change in the physiographic and climatic conditions of the mountain-basin region from those that prevailed during Fort Union, Puerco, and Torrejon time. In general, still-water sedimentation in level forests and lagoons ceased. Fluviatile, flood-plain, fluvial-fan, and channel deposits containing a larger percentage of coarser materials were widespread. There is evidence of open stretches of country exposing sand, gravel, and clay, subject to occasional desiccation and aridity.

The Wasatch of the Big Horn Basin represents the filling of an intermontane trough of downwarp. (Sinclair and Granger, 1912.1, p. 66.) Materials were transported by streams from the surrounding mountains, as shown by the lithology of the gravel, sand, and clay. The underlying Fort Union was uplifted before sedimentation began, and the synclinal basin was inclosed more or less completely to the east, south, and west by anticlinal mountains. Erosion from the mountain rocks represents all the members of the typical section from the Archean to the Fort Union, usually by stream transportation and deposition in river channels and over broad flood plains. No beds of volcanic ash have been found, nor is there evidence of transportation by wind. The deposits of clay show a more or less regular alternation of red and bluish-gray layers, which may be due to climatic changes.

The excess of iron salts in the red clays may have accumulated and oxidized to hematite during dry climatic cycles; the blue clays were probably deposited in a moister climate, which is less favorable to the concentration and oxidation of the iron. Similar alternations of red and blue clays in the desert basins of Lop and of Sewistan have been described by Huntington, who also associates the colors with the recurrence of moist and arid climatic cycles. Sinclair and Granger (1914.1) ascribe the color banding of the Wasatch and Wind River clays to a similar cause—the alternation of moist and dry climatic conditions—but they have not found any other evidence of excessive aridity, the fauna of the red and blue bands being the same. The fact that the blue clays of the Wasatch are here and there lignitic and are at some places associated with skeletal remains suggests that they may have been formed during cycles of rather abundant rainfall, when the surface of the intermontane basin was prevented from drying out rapidly. That these climatic and physiographic conditions were not local is shown by similar color banding in the Wasatch of all the mountain-basin regions. The name "Vermilion Creek" was applied by King to the Wasatch because of the red color of the rocks through which that creek flows in southern Wyoming and northwestern Colorado.

Microscopic examination of the feldspars in the Wasatch deposits of the Big Horn Basin does not favor the idea of luxuriant subtropical forests and a warm, humid climate, with the formation of a deeply decayed humus, but rather suggests a dry, not necessarily arid climate, with rapid changes of temperature, favorable to splintering of the ledges of hard rock; rapid transportation of the fragments for short distances; and burial of these beyond reach of carbonated waters.

A cursorial ungulate fauna.—This conception of a drier lower Eocene climate in the basins during Wasatch time accords with the successive appearance in this region of four families of the modernized types of perissodactyl mammals—horses, tapirs, lophiodonts, and titanotheres—with light, cursorial limb and foot structure adapted to rapid locomotion and wide seasonal migration.

Correlation of lower Eocene life zones of Wyoming and New Mexico (after Granger, with modifications)

Epoch	New Mexico (Wasatch—"Largo" and "Almagre")	Evanston (typical Wasatch)	Wind River Basin (typical Wind River)	Big Horn and Clark Fork Basins	Remarks
Lower Eocene		Green River.	Lambdotherium zone ("Lost Cabin"; typical). Hyrachyus, Eotitanops, Lambdotherium, Heptodon, Eohippus, Meniscotherium.	Lambdotherium zone ("Lost Cabin"). Lambdotherium, Heptodon, Eohippus, Ambloctonus.	End of lower Eocene. First titanotheres appear.
	"Largo" (typical). Eohippus, Meniscotherium, Ambloctonus.	Knight (typical). Heptodon, Eohippus.	Heptodon zone ("Lysite"; typical). Heptodon, Eohippus.	Heptodon zone ("Lysite"). Heptodon, Eohippus, Anacodon.	First lophiodonts appear.
	"Almagre" (typical). Eohippus, Anacodon.			Systemodon zone ("Gray Bull," typical). Systemodon, Eohippus.	First tapirs appear.
	Unconformity between Wasatch and Torrejon. In southern Colorado "Tiffany" (typical). No perissodactyls.			Eohippus zone ("Sand Coulee," typical). Eohippus (abundant), etc., first artiodactyls, rodents, and primates.	First horses appear. Arrival of modernized mammals.
Basal Eocene	Torrejon. No perissodactyls. Fauna more primitive than in "Clark Fork."			Phenacodus zone ("Clark Fork"; typical). No perissodactyls, artiodactyls, rodents, or primates. Fauna more advanced than in Torrejon.	End of basal Eocene. Archaic mammals only.

A very significant fact, clearly presented in the table on page 67, is that these small, light-limbed, cursorial ungulates appear not simultaneously but at successive horizons. At the lowest level are the horses (*Eohippus*); at a higher level the pseudotapirs (*Systemodon*); at a still higher level the lophiodonts (*Heptodon*); and then, toward the end of the lower Eocene, the titanotheres (*Lambdotherium*).

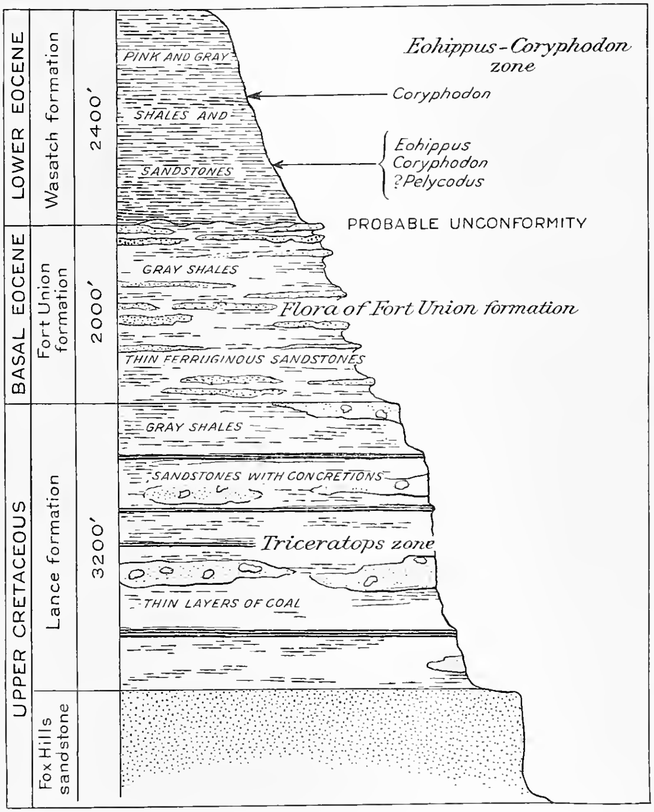

FIGURE 45.—Generalized section through Upper Cretaceous and basal and lower Eocene deposits near Pumpkin Buttes, Powder River Valley, Wyo. (No. 12, fig. 35)

Adapted from C. H. Wegemann (1917.1).

Though the results of our observations may be modified by further discoveries the successive rather than simultaneous appearance of these advancing waves of perissodactyl migration is what a study of modern migrations should lead us to expect. All these animals, as shown elsewhere in this monograph, have similar cursorial foot structure, which indicates extensive areas of dry land and open meadow, in which the small, defenseless Herbivora could easily escape the attacks of the Carnivora.

Habitat of Wasatch mammals.—The conditions that prevailed in Wasatch time have been determined very interestingly by Loomis in his "Origin of the Wasatch deposits" (1907. 1, pp. 356–364). In adaptation to various habitats the known species of vertebrates are divided as follows: Aerial, 3 per cent; cursorial, terrestrial, and arboreal, 75 per cent; amphibious, 12 per cent; aquatic, 10 per cent. The light-limbed horse, *Eohippus*, typical of a plains or partly open country, alone makes up 32 per cent of the total collections from the *Systemodon* zone ("Gray Bull" horizon). All the other odd-toed ungulates are light-limbed, including the tapiroids (*Systemodon*), lophiodonts (*Heptodon*), and primitive titanotheres (*Lambdotherium*), as well as the surviving archaic condylarths (*Phenacodus* and *Ectocion*). The feet of all these animals indicate dry rather than swampy or forested land, because they are more slender than those of the modern tapir. On the other hand, the coryphodons were certainly marsh dwellers and perhaps in part stream dwellers. The small percentage of species of truly aquatic animals, such as crocodiles, fishes, and turtles, whose remains are mingled with those of the prevailing land animals, probably became stranded in lagoons far from the rivers. The presence in the rivers of rather large fishes is shown by the remains of the large *Clastes*. Remains of river-living turtles (*Trionyx*) have also been found in the Wasatch.

LOWER EOCENE FAUNAL ZONES

ZONE 6: EOHIPPUS-CORYPHODON ZONE

[Second Wasatch life zone, Big Horn B; lower Sparnacian of Europe]

Below the *Eohippus-Coryphodon* zone in the Clark Fork Basin of Wyoming lies the first Wasatch life zone (*Phenacodus - Nothodectes - Coryphodon* zone) described on pages 64–66. Near the head of the Big Sand Coulee, on the Clark Fork of the Yellowstone, which adjoins the Big Horn River basin on the west, is a series of about 200 feet of red-banded shales, which overlie the *Phenacodus* zone ("Clark Fork beds," transition basal Eocene) and contain a mammalian fauna that is radically different from that of the underlying "Clark Fork." These beds (the "Sand Coulee beds" of Granger) mark the first appearance in the Rocky Mountain basin region of four modernized orders of mammals—the lemuroids, rodents, artiodactyls, and perissodactyls. Of the Perissodactyla only one family occurs, the Equidae, represented by a primitive specific form of *Eohippus* (*E. borealis*). There are two or possibly three species of *Eohippus* in these "Sand Coulee beds," which are not yet separable from the species found in the "Gray Bull" horizon above. Here also occurs *Palaeanodon*, an ancestral armadillo, which left descendants in lower and middle Eocene time.

This lower Eocene horizon, described by Granger (1914.1, p. 205), appears to constitute the beginning of Sparnacian time in the Rocky Mountain region. It contains the oldest known modernized fauna (perissodactyls, artiodactyls, rodents, etc.) found in America. The antiquity of these beds is indicated by the last recorded appearance of the primitive order Multituberculata, as represented by remains of *Ptilodus?* sp. The horizon is also distinguished by the absence of tapirs (*Systemodon*). Here occur the first known species of the primitive lemuroid Notharctidae (*Pelycodus*) and the peculiar ungulate *Hyopsodus*, now regarded as a condylarth. No other exposures containing this very primitive Wasatch fauna have thus far been discovered.

ZONE 7: SYSTEMODON-CORYPHODON-EOHIPPUS ZONE

[Third Wasatch life zone, Big Horn C; upper Sparnacian of Europe]

The "Gray Bull beds" of Granger (1914.1, pp. 203, 204), in the Big Horn Wasatch, lie at a horizon that is distinguished by the presence of the earliest tapirs—the pseudotapirs (*Systemodon*). These beds were at first called the Ralston,[9] a name that had been preoccupied. They are exposed principally in the Clark Fork and Big Horn Basins south of the Yellowstone (Pl. V, *B*) and are at least 600 feet thick. They may be correlated with part of the "Almagre" of the Wasatch of New Mexico. As this is the first appearance of the tapirs, and as their remains are mingled with those of horses, this horizon may be known as the *Systemodon-Coryphodon-Eohippus* zone. These beds are exposed chiefly along the south side of Greybull River, where they extend over many miles. From this horizon was made the larger part of Cope's collection from the lower Eocene of the Big Horn Basin, including the classic skeleton of *Phenacodus primaevus*, as well as the skeleton of *P. copei* [10] and that of *Eohippus*, besides many species of *Coryphodon*. One of the most common forms is the pseudotapir *Systemodon*, which includes the species *S. tapirinum*, and it is noteworthy that this genus, which is indirectly related to true tapirs, does not appear in the overlying beds.

ZONE 8: HEPTODON-CORYPHODON-EOHIPPUS ZONE

[Fourth Wasatch life zone, Big Horn D and Wind River A; lower Ypresian of Europe]

To zone 8 belong the "Lysite beds" (Pl. V, *A*) of the Big Horn Basin Wasatch, Wyoming (Big Horn D); the lower level of the Wind River formation (Wind River A); a part of the Knight formation of the typical Wasatch group; and parts of the "Almagre" and "Largo" of the New Mexico Wasatch. In this life zone *Heptodon* takes the place of *Systemodon*, which disappears or is not thus far recorded. The graceful lophiodont *Heptodon* appears at the very summit of the underlying "Gray Bull beds," is abundant in the "Lysite," and continues into the "Lost Cabin," its presence being one of the means of correlating the fauna of these beds with that of the typical Wasatch group in the Knight formation. This Knight fauna occurs in the *Coryphodon*-bearing layer, which Cope describes as 500 feet above the base of this division of the typical Wasatch of the Evanston region, or about the middle third of the formation according to Granger.

The typical *Heptodon* zone (="Lysite") of the Wind River beds, 350 feet in thickness, is distinguished by the absence of titanotheres (*Lambdotherium*, *Eotitanops*), which are very abundant in the superimposed "Lost Cabin beds." The "Lysite" or *Heptodon* zone in the Big Horn Basin is 400 feet thick. *Anacodon*, one of the arctocyonid creodonts, which has flattened or pavement-like teeth, is characteristic of the *Heptodon* zone. This zone is faunistically but not lithologically separated from the overlying *Lambdotherium* zone.

ZONE 9: LAMBDOTHERIUM-EOTITANOPS-CORYPHODON ZONE

[Fifth Wasatch life zone, Big Horn E, Wind River B, and Huerfano A; upper Ypresian of Europe]

Geology and fauna.—To zone 9 belong the typical Wind River of Hayden and of Cope in the Wind River Basin, Wyo. (=the "Lost Cabin" of Granger and Sinclair); the "Lost Cabin" (Granger) of the Big Horn Basin Wasatch; part of the "Largo beds" (Granger) of the San Juan Wasatch of New Mexico; part of the Green River lacustrine formation of Wyoming; and the lower level of the Huerfano formation (Hills) of Colorado or Huerfano A. This is the typical Wind River life of all the literature of Cope. (See Pl. VI.)

The *Lambdotherium* life zone is distinguished by the arrival in the Rocky Mountain basin region of the first titanotheres, which are abundantly represented in remains of the smaller, cursorial *Lambdotherium* and the larger, mediportal *Eotitanops*. It includes the

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[9] "Ralston" was the name given by Sinclair and Granger (1912) to the Clark Fork beds. "Clark Fork" was substituted by Granger (1914) because "Ralston" had been previously used otherwise. Sinclair and Granger (1912) referred the beds between the "Lysite" and the "Ralston" to the "Knight" formation. Granger (1914) separated the "Knight beds" into two horizons, which he called "Gray Bull" and "Sand Coulee." The "Gray Bull" and the overlying "Lysite" of Buffalo Basin constitute the "Big Horn Wasatch" of Cope and Wortman. The "Gray Bull" is exposed almost entirely in the Big Horn Basin, although a small area of it overlies the "Sand Coulee" beds at the head of Big Sand Coulee in the Clark Fork Basin (Granger, 1919).

[10] The type of *Phenacodus wortmani* is from Wind River. Cope's reference of the small Big Horn skeleton to this species is not correct. Granger (1915) renamed the skeleton *P. copei*.

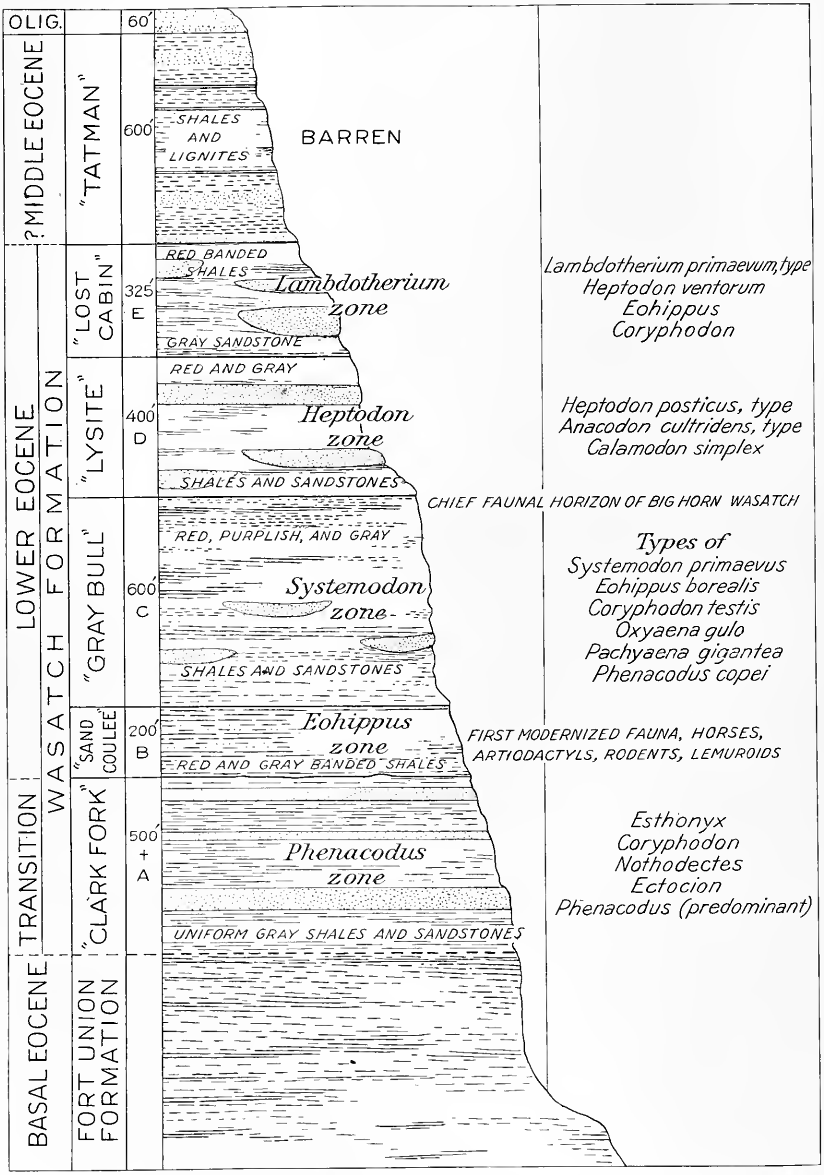


FIGURE 46.—Composite section of the Eocene deposits of the Big Horn and Clark Fork Basins, Wyo.

This section contains the entire Big Horn Basin Wasatch of Cope's descriptions, which is now divided into very clearly defined ascending life zones, as follows: 5, *Phenacodus-Nothodectes-Coryphodon* zone; 6, *Eohippus-Coryphodon* zone; 7, *Systemodon-Coryphodon-Eohippus* zone; 8, *Heptodon-Coryphodon-Eohippus* zone; 9, *Lambdotherium-Eotitanops-Coryphodon* zone. A few characteristic species of mammals from each horizon are indicated in the right-hand column. Chiefly after Granger (1918).

last surviving species of *Coryphodon* and of the condylarth *Phenacodus* among the archaic ungulates. The presence of the condylarth *Meniscotherium* serves to correlate the Wind River with the upper levels ("Largo beds") of the Wasatch of New Mexico.

While the Wind River life on the whole represents a continuation of that of the preceding stages of the Wasatch, with which it possesses several genera and eleven species in common, it also includes nine new genera that survive in the Bridger formation of middle Eocene time. The Wind River marks the end of the lower Eocene, the last period of certain highly distinctive lower Eocene forms like *Coryphodon*, but it is also prophetic of the middle Eocene in the presence of lemuroids like *Notharctus*, *Anaptomorphus*, and *Shoshonius;* of true doglike or civet-like carnivores like *Viverravus* and *Vulpavus;* or of rodents like *Sciuravus* and *Paramys*. Remains of Equidae are rather rare and are represented by several species of *Eohippus*, of which *E. venticolus* is the most progressive, and those of titanotheres, especially *Lambdotherium*, are very abundant.

Lambdotherium, one of the earliest titanotheres, was a small, light-limbed form, about the size of a coyote (*Canis latrans*). It represents a distinct cursorial side branch of the titanothere family, resembling the contemporary horses and lophiodonts in its light limb and foot structure. *Eotitanops* ("the dawn titanothere") was a true and very primitive titanothere about the size of a sheep (*Ovis aries*), somewhat like a slender, diminutive tapir in body proportions. In skull structure and dentition *Eotitanops* foreshadows the true titanotheres of the middle Eocene; its feet are more slender than those of its successors, and it was doubtless a more agile animal.

The special life conditions surrounding these early titanotheres are more fully set forth in the descriptions of the Wind River titanotheres in Chapter V, section 3.

Climate and physiography during the deposition of the Wind River and Green River sediments.—For Wind River life in general the reader is referred to section 3 of this chapter. Here we may speak of the whole basin region.

While fluviatile and flood-plain sediments were being deposited in the Wind River Basin of northern Wyoming there lay to the south a large, shallow lake, covering about 5,000 square miles, in which were deposited 800 feet of impure limestone at the base, followed by about 1,200 feet of thin, fissile calcareous shale. (King, 1878.1, p. 381.) The deposition of these lake sediments (Green River) began near the end of Wasatch time. They contain abundant and well-preserved remains of insects and fishes. The presence of sting-rays and other fishes of marine or coastal type indicates that these originally marine forms had become landlocked, as did the existing marine survivors in the Caspian Sea and Lake Titicaca. Many of the fishes of the Green River shales are related to forms now found chiefly in the southern continents, especially South America.

FIGURE 47.—A typical "Lost Cabin" locality, on the north side of Alkali Creek about 8 miles east of Lost Cabin, Wind River Basin, Wyo.

Lambdotherium-Eotitanops-Coryphodon zone (Wind River B). A characteristic view of the red-banded beds that have yielded the greater part of the fauna of the *Lambdotherium* zone. (Compare Pl. VI, *B*.) After Granger (1910.1), Am. Mus. negative 17792.

Green River forests.—Our present knowledge of the Green River flora, which, according to Berry (1914.1, p. 164) was mid-Eocene, indicates a considerably warmer climate than that of the basal Eocene Fort Union, for it includes such types as *Acrostichum* and *Arundo*, which are also represented in the contemporaneous Eocene flora of Georgia, as well as the genera *Ficus* and *Sapindus*. The Green River lake-border forests differed from the tropical forests of the Georgia coast in the presence of genera like *Ilex*, *Juglans*, *Myrica*, *Planera*, *Quercus*, *Rhus*, *Salix*, and *Zizyphus*, most of which are temperate types. Thus the Green River exhibits a commingling of warm-temperate and tropical trees such as are now found in subtropical forests in regions where there is a mean annual temperature of about 14° C., uniform humidity, and an

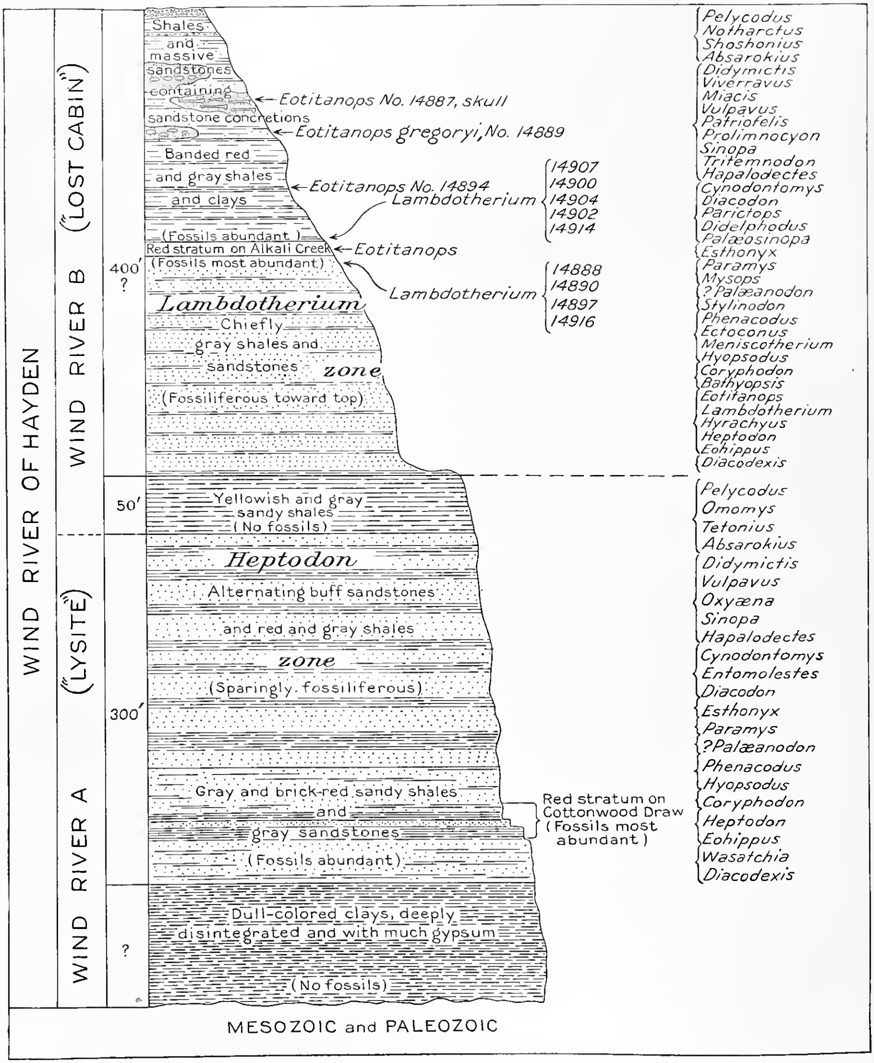


FIGURE 48.—Section through the Wind River formation (lower Eocene) near Lost Cabin, Wind River Basin Wyo. (No. 5, fig. 35)

A complete list of genera from each horizon is given in the right-hand column. First appearance of the primitive titanotheres *Lambdotherium* and *Eotitanops*. Chiefly after Granger (1910.1) and Sinclair and Granger (1911.1).

annual rainfall exceeding 200 centimeters. This flora is not very different from that found in the upper Ypresian of France.

These forests are so interesting in respect to the environment of the first titanotheres which appeared in North America that the principal genera cited by Berry may be quoted in full. The figures appended to the names of the genera show the number of species in each genus.

Acrostichum, 1.
Alnus, 1.
Ampelopsis, 1.
Aralia, 1.
Arundo, 2.
Brasenia?, 1.
Cheilanthes, 1.
Cissus, 1.
Cyperus, 1.
Equisetum, 1.
Eucalyptus?, 1.
Ficus, 4.
Ilex, 2.
Juglans, 3.
Leguminosites, 1.
Lygodium, 1.
Manicaria, 1.
Musophyllum, 1.
Myrica, 1.
Phragmites, 1.
Planera, 2.
Quercus, 2.
Rhus, 1.
Sabal, 1.
Salix, 2.
Sapindus, 1.
Sphaeria, 1.
Zizyphus, 2.

The Green River flora is the only described middle Eocene flora known from latitude 40°. The nearly contemporaneous Claiborne flora of Georgia shows (Berry, op. cit., p. 161) that the main elements of the modern flora of tropical America reached at least as far north as latitude 33° and, in the middle Eocene, probably several degrees farther north.

Wasatch and later events.—In areas that lay north of the great lake in this region in Wasatch time were laid down the sediments of the Wind River and Big Horn Basins, the deposition of which began in the first phase of Wasatch time and probably continued into middle Oligocene time. (Sinclair and Granger, 1911.1, p. 85.) The Wind River sandstones in the vicinity of the Beaver Divide are stream-channel deposits, probably laid down in broad, shifting streams of low gradient which flowed across clay-covered flats, into which they sunk their channels or over which in seasons of flooding they spread coarse detritus. The materials composing these sandstones were derived from the granites and other pre-Tertiary rocks of the surrounding mountains. Below the *Lambdotherium* zone at other localities, interstratified with Wind River clays and sandstones, there are layers of white volcanic tuff, 13 feet thick, indicating the presence of active volcanoes. The floor of the Big Horn Basin, to the north, was modified by erosion that took place subsequent to the main uplift of the Big Horn Mountains, which occurred after the deposition of the Fort Union formation. (Sinclair and Granger, op. cit., p. 105.) There is evidence also of an uplift of the Big Horn Range subsequent to the deposition of the Wasatch. In the Wind River Basin material washed down from the mountains continued to be spread over the basin floor by streams until the end of upper Eocene time.

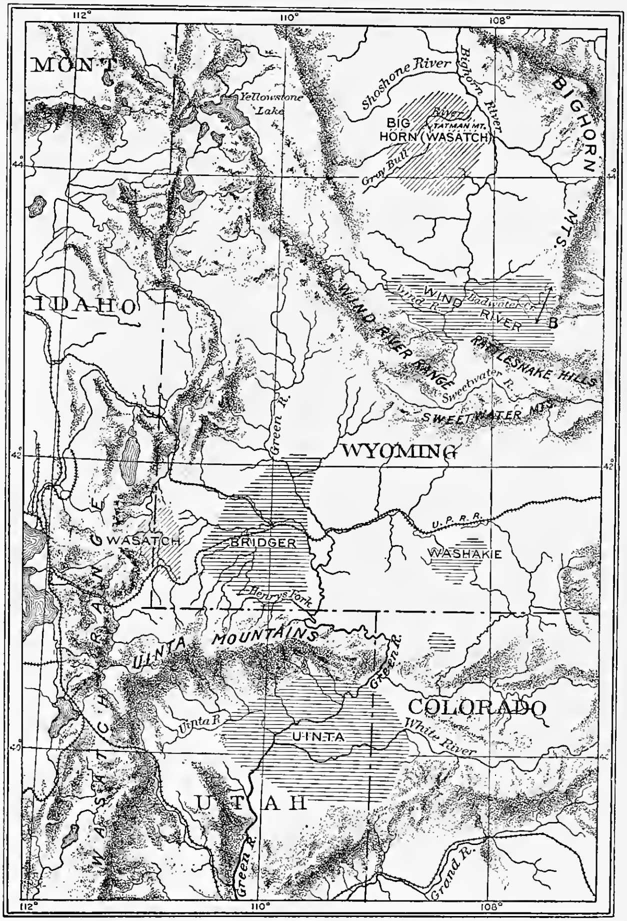


FIGURE 49.—Map showing cluster of lower, middle, and upper Eocene sedimentary basins in southwestern Wyoming and northern Utah, exhibiting parts of areas of the Wasatch, Wind River, Bridger, and Uinta formations

Extensive areas of the Wasatch are purposely omitted. After Osborn and Matthew (1909.321), U. S. Geol. Survey Bull. 361. Arrows show lines along which sections were taken.

Fluviatile and flood-plain deposition is indicated throughout Eocene time. The lignitic shales that cap the *Lambdotherium* zone of the Big Horn Basin, containing fresh-water mollusks (*Planorbis*) and crustaceans (Entomostraca), are certainly both fluviatile and palustrine.

TRANSITIONAL LOWER TO MIDDLE EOCENE DEPOSITS

HUERFANO FORMATION OF COLORADO (LOWER AND MIDDLE EOCENE)

While the lacustrine and flood-plain Green River and Wind River formations were being deposited in Wyoming there were accumulating in southeastern Colorado the lower fossiliferous beds of the Huerfano formation, described by Hills (1888.1), explored by Osborn and Wortman in 1896 and by Granger and Olsen in 1918, and now known as Huerfano A. The deposition of this formation apparently began near the end of Wasatch time and extended into early Bridger time. Among the mammals of the lower Huerfano, which corresponds with the upper Wind River (= "Lost Cabin"), are the rare *Coryphodon*, the small-limbed titanothere *Lambdotherium*, *Eohippus*, *Oxyaena*, *Didymictis*, and *Heptodon*, a purely upper Wind River (= "Lost Cabin") fauna.

The whole Huerfano formation is 3,500 feet thick, and a large part of it (see fig. 51) lies below horizon A. (Granger, 1918.) Huerfano B, although it lies immediately above Huerfano A, contains the genus *Palaeosyops*, a distinctive middle Eocene form. Consequently Huerfano B is placed at the base of the middle Eocene and is correlated with Bridger A, although part of its fauna is doubtless transitional from the summit of the underlying lower Eocene.

In the upper half of the Huerfano formation (Huerfano B) are found mammals that are also characteristic of the lower Bridger (A). The imperfectly known life of the upper level includes the tillodont *Trogosus* and two kinds of small titanotheres, one (*Eometarhinus*) resembling *Metarhinus* and the other *Palaeosyops fontinalis* of Bridger A; also a horse (*Orohippus?*) and animals resembling the Bridger genera *Hyrachyus*, *Hyopsodus*, *Microsyops*, as well as more ancient genera—the creodonts *Ambloctonus* and *Didymictis*—which suggest a fauna more ancient than that of Bridger B, corresponding perhaps with the still unknown fauna of Bridger A. It appears probable that the Huerfano will give us a complete faunistic transition between the end of Wasatch and the beginning of Bridger B (middle Eocene) time.

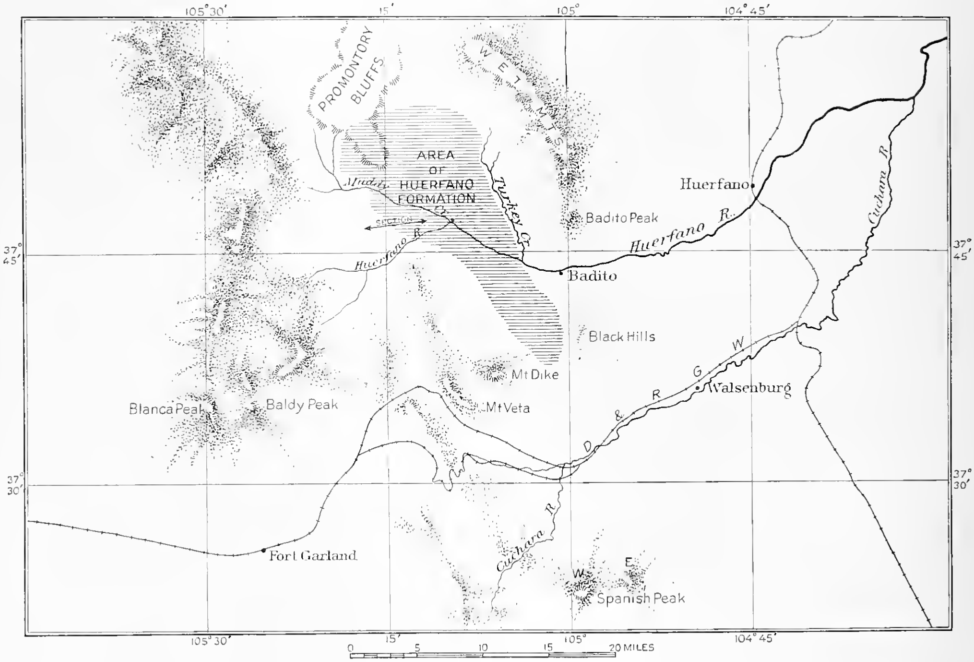


FIGURE 50.—Sketch map of the region of the Huerfano and Cuchara formations in southern Colorado

After Hayden (1880), Hills (1888.1), and Granger (1918).

WIND RIVER BEDS AND THEIR FAUNA

The discovery of the geologic section at Beaver Divide, between Wind River and Sweetwater River, is one of the most significant recently made in the study of Rocky Mountain basin geology. Here deposition without angular unconformity extends from the third

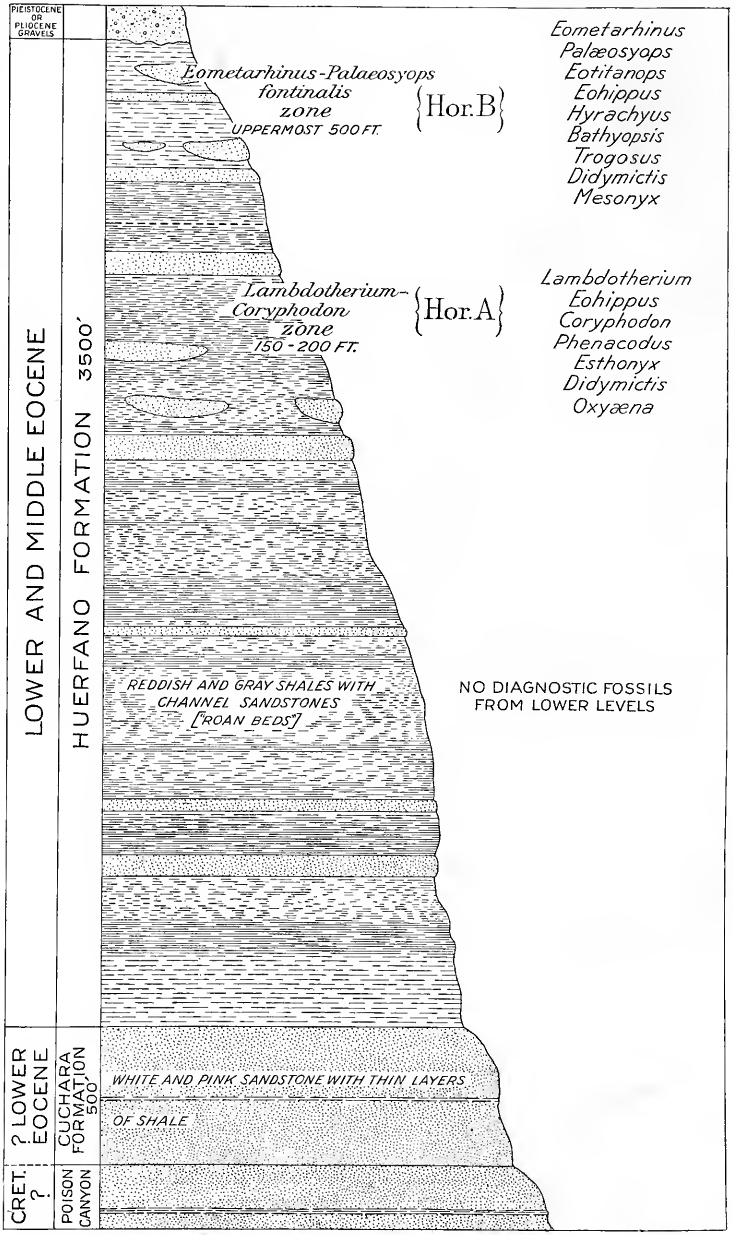


FIGURE 51.—Section of the Huerfano formation in southeastern Colorado as exposed west of Gardner, Huerfano Basin

Thickness 3,500 feet. Near the summit is a Wind River B fauna (*Lambdotherium* zone), and above that a Bridger A fauna (*Palaeosyops fontinalis* zone). After Granger (1918).

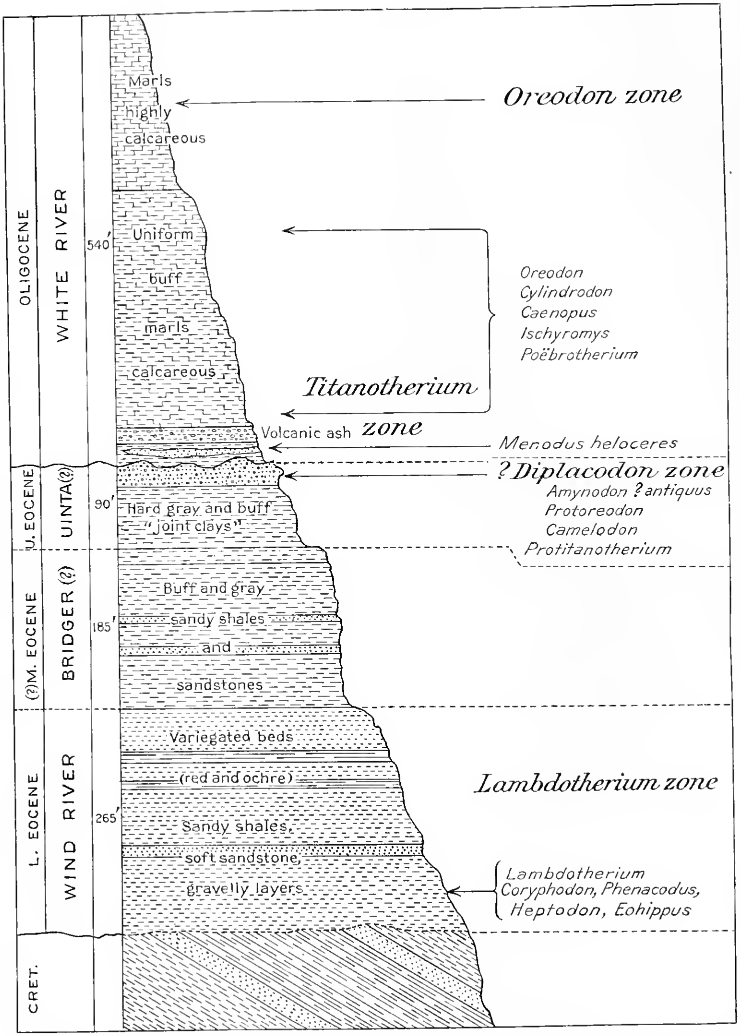


FIGURE 52.—Section of exposures from lower Eocene to lower Oligocene at Green Cove, on Beaver Divide, at the southwestern border of the Wind River Basin, Fremont County, Wyo.

Includes deposits in Wind River, Bridger (?), Uinta (?) and White River time. Chiefly after Granger (1910.1). This is a most significant section, for the base of the *Titanotherium* zone (Chadron A) unconformably overlies beds originally referred to Uinta C 1 (*Diplacodon* zone).

Wasatch *Heptodon-Coryphodon-Eohippus* zone through the Wind River *Lambdotherium-Eotitanops-Coryphodon* zone upward into the *Oreodon* zone of Oligocene time. This is the only undoubted Eocene-Oligocene sediment thus far determined in the Rocky Mountain basin region. Its total thickness is 1,080 feet, and it represents relatively slow sedimentation. There is a single period of erosional unconformity at the end of the upper Eocene.

The life of the Wind River beds of this section is distinctly of upper Wind River ("Lost Cabin") time, corresponding with Wind River B and Huerfano A, for it includes the titanothere *Lambdotherium popoagicum*, a *Coryphodon*, two species of Equidae (*Eohippus craspedotus* and *E. venticolus*), and two species of *Heptodon* (*H. calciculus* and *H. ventorum*), which are characteristic of closing Wasatch time. The presence of remains of garpikes and crocodiles in this fauna shows that these deposits were fluviatile and indicates that Wind River shales were of flood-plain origin, though they include many channel fillings of coarse arkose.

We thus have glimpses of a faunistic period broadly corresponding with the lower Ypresian of France, certainly extending from Wyoming to Colorado, and probably spreading much more widely in the Rocky Mountain and the adjacent Plains region. Though it includes surviving members of the older Wasatch life and incoming members of the succeeding Bridger life, the Wind River and Huerfano life stands directly intermediate between these; in fact, the representatives of archaic families destined to become extinct and those of modernized families destined to populate the earth are very nearly balanced, including 21 genera (30 species) of archaic mammals and 22 genera (36 species) of modernized mammals.

Simultaneously with the decline of the coryphodons the uintatheres reappeared in the genus *Bathyopsis*, ancestral to the giant *Uintatherium*, which characterizes Bridger C and D.

THIRD FAUNAL PHASE (MIDDLE AND UPPER EOCENE)

CORRELATION OF AMERICAN ZONES WITH EUROPEAN STAGES

There is strong evidence of uniform and favorable environment and persistent evolution throughout middle and upper Eocene time in the Rocky Mountain basin region. The changes show progressive modification and adaptation rather than breaks by migration or extinction. Both the archaic and the modernized families increased in size and variety. The surviving archaic mammals appear to have flourished and increased, especially in size and muscular power. Near the very end of Eocene time only two new families of quadrupeds appear, the ancestral camels (Camelidae) and the oreodonts (Oreodontidae), whereas in western Europe new families repeatedly appear from the south, east, and north. The general correlation of the European stages and the American zones is given on page 78.

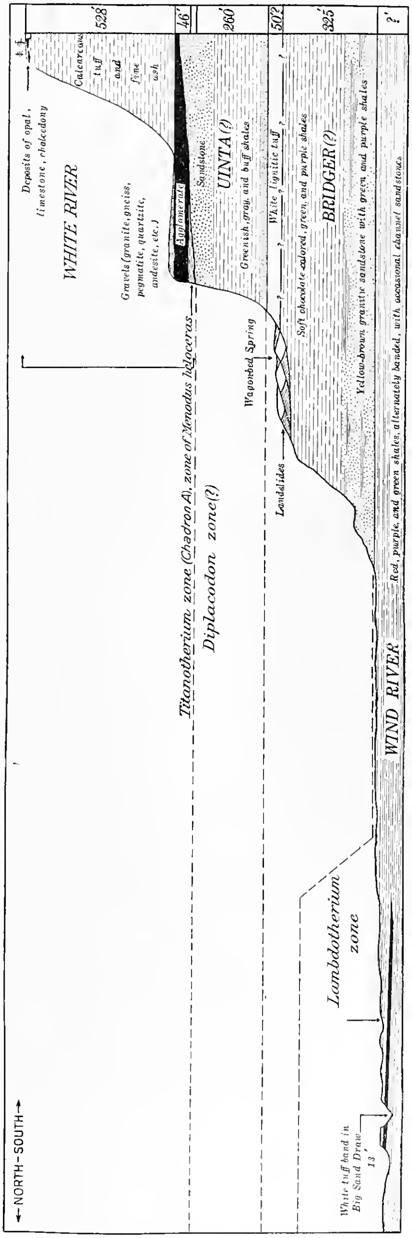


FIGURE 53.—Diagrammatic section across the Wind River Basin, Wyo., from Hudson to the top of the Beaver Divide at Wagonbed Spring

Section from top of Wind River formation to top of lignitic tuff measured half a mile north of Wagonbed Spring; section from top of tuff to top of White River measured half a mile south of spring. Chiefly after Sinclair and Granger (1911.1). Horizontal scale not accurate.

Correlation of middle Eocene and upper Eocene American life zones and European stages

Epoch	American life zone	Approximate European stage
Upper Eocene.	15. Diplacodon-Protitanotherium-Epihippus zone (Uinta C).	Ludian.
	14. Eobasileus-Dolichorhinus zone (Washakie B 2, Uinta B 2). 13. Metarhinus zone (Washakie B 1, Uinta B 1).	Bartonian.
Middle Eocene.	12. Uintatherium-Manteoceras-Mesatirhinus zone (Washakie A, Bridger C and D).	Lutetian.
	11. Palaeosyops paludosus-Orohippus zone (Bridger B). 10. Eometarhinus-Trogosus-Palaeosyops fontinalis zone (Bridger A, Huerfano B).	

TYPICAL BRIDGER FORMATION; MIDDLE EOCENE (LUTETIAN AND BARTONIAN OF EUROPE)

Character of sediments.—The Bridger formation, the most important and the most thoroughly explored of the Eocene Tertiary, occupies a great area north of the Uinta Mountains and east of the Wasatch. Unlike the Wasatch, the lower Bridger (horizon B) is unique; no contemporaneous fossiliferous deposition is known. At the base its sediments pass gently into the Green River shales, and the lower levels of Bridger A show gradual transition from lacustrine to flood-plain conditions. The Bridger formation attains its maximum thickness of 1,875 feet near the Uinta Mountains and thins out northward. Beyond the margins of the Green River lacustrine deposits the Bridger overlies upper members of the Wasatch group.

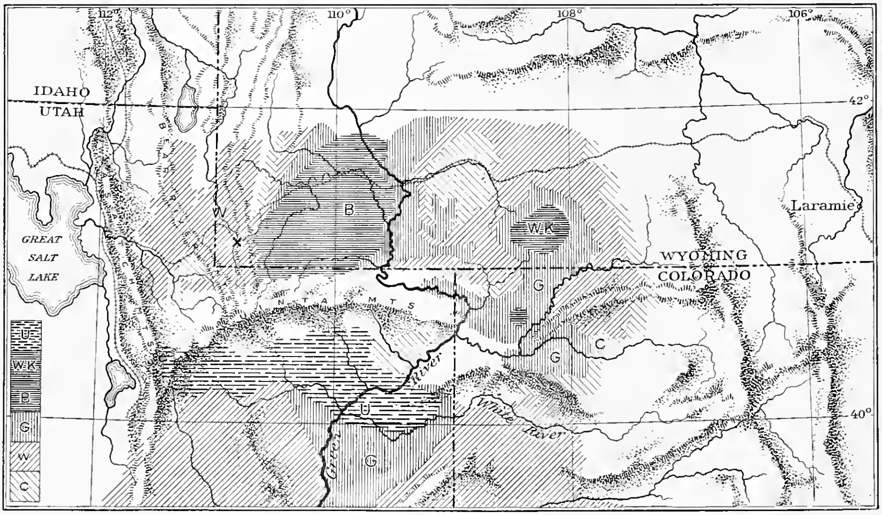


FIGURE 54.—Map showing the Eocene sediments encircling the Uinta Mountains of southwestern Wyoming and northern Utah

Modified after King (1876.1). U, Uinta Basin, typical Uinta formation of King and Marsh. (The area mapped includes older and possibly younger rocks than the true Uinta formation—*Diplacodon* zone.) B, Bridger Basin, typical Bridger formation of Hayden. WK, Washakie Basin, typical "Washakie" formation of Hayden. G, Green River formation. W, Typical Wasatch group of Hayden. X, Type locality of *Coryphodon* and associated Wasatch fossils. C, Cretaceous.

Unlike the lower Eocene Wasatch and Wind River sediments the Bridger is not composed chiefly of material derived by erosion from the adjacent mountains (Sinclair, 1906.1, p. 278) but consists of great series of deposits of volcanic ash and dust, solidified into tuffs, which weather into picturesque and in places highly colored "badlands." Apparently the greater part if not all of these tuffs were distributed from unknown eruptive volcanic centers by wind; but at four periods they were deposited in great shallow playa lakes and partly worked over by stream, delta, and flood-plain deposition. From the general absence of coarse materials such as would be transported by streams of high gradient, it is inferred that the Bridger formation accumulated in a relatively level area. (Sinclair, 1906.1, p. 279.)

Exploration of the Bridger formation.—The Bridger formation has been explored almost continuously by geologists and paleontologists, first by Hayden (1869–1871), next by King (1878), who regarded the Bridger as an ancient lake basin deposit, then by Osborn and Scott (1877–1878), and again by Endlich (1879). In 1902 the American Museum parties, guided by Matthew and Granger, under the direction of Osborn, undertook to determine whether the Bridger can be divided into a series of life zones. After four years of careful geologic field work by Granger and Matthew (1902–1905), who had at hand the level record of every specimen, the Bridger was subdivided lithologically and faunistically into five levels, A to E. Bridger A is relatively barren. Of these levels A and B were grouped into the lower Bridger (*Palaeosyops paludosus-Orohippus* zone), characterized by the absence of *Uintatherium*, and C and D, the upper Bridger (*Uintatherium-Manteoceras-Mesatirhinus* zone), distinguished by the appearance and great abundance of *Uintatherium*. Similar faunistic surveys in the Washakie Basin, east of the Bridger Basin, and in the Uinta Basin, south of the Uinta Mountains, have given very complete correlation of the local subdivisions of the section as follows:

Correlation of middle and upper (?) *Eocene sections of the Uinta, Washakie, and Bridger Basins*

Uinta Basin	Washakie Basin	Bridger Basin	Life zones
Uinta C.	Absent.	Absent.	Theoretic zone (No. 16); fauna unknown. 15. Diplacodon-Protitanotherium-Epihippus.
Uinta B.	Washakie B.	Bridger E (barren beds).	14. Eobasileus-Dolichorhinus. 13. Metarhinus.
Uinta A (barren).	Washakie A.	Bridger D. Bridger C.	12. Uintatherium-Manteoceras-Mesatirhinus.
Barren beds.	Barren beds.	Bridger B.	11. Palaeosyops paludosus-Orohippus.
		Bridger A.	10. Eometarhinus-Trogosus-Palaeosyops fontinalis.

Volcanic ash deposits.—The petrographic analysis of the rocks of the Bridger formation serves to support their correlation with the deposits of the Washakie Basin, to the east, and of the Uinta Basin, to the south. The recognition by Sinclair (1906.1, pp. 273–280) of the fact that the entire Bridger series was in large part originally volcanic dust and the later careful petrographic analysis by Johannsen (1914.1) led to the conclusion that the Bridger rocks are largely tuffs, perhaps modified in part by sufficient transportation to add the numerous grains of quartz they contain, and that these grains may be of sedimentary origin, although the material of the tuffs is mostly andesitic. Johannsen's analysis of the Bridger rocks is essentially as follows:

Bridger D. Irregular grains of quartzite, feldspar, hornblende, etc.: dacite tuff.
Bridger C. Fragments of quartz and hornblende; groundmass of glass tuff.
Bridger B. Smith's Fork; fragments of quartz, feldspar, hornblende: ?dacite tuff.
Bridger B. Church Buttes; fragments of quartz, feldspar, etc.: altered tuff, probably dacite tuff.
Bridger A. North of Church Buttes, fragments of quartz, feldspar, hornblende. No glass tuff seen.

Thus the Bridger is composed chiefly of dacite tuff, of altered dacite, and of glass tuff containing irregular grains of quartz, feldspar, and hornblende, which are at some places contained in a groundmass made up of entirely coarse angular particles of stringy glass full of bubbles. The Huerfano formation of Colorado, which is in large part older than the Bridger, is composed largely of glass tuff. The deposits in the Washakie Basin, east of the Bridger Basin, are composed chiefly of dacite and glass tuffs.

Playa lake deposits.—Conspicuous features of the Bridger formation are four hard "white layers," which were laid down at intervals in the series of beds.

Some of these "white layers" have been traced over many square miles. They are composed of tuffaceous shale and marl or of calcareous shale and are in places filled with fresh-water shells. They mark periods during which the deposition of volcanic dust was less rapid, when the Bridger Basin was temporarily baseleveled and the waters rose into wide, shallow playa lakes, in which sedimentation was slow. That these four relatively thin "white layers," which are variously known geographically as the "Cottonwood white layer," the "Burnt Fork white layer," the "Lone Tree white layer," and the "upper white layer," correspond with long periods of geologic time is shown by the marked faunal differences that separate them, which indicate that extensive migration occurred before and after the deposition of each of these layers, but especially the first, which separates the lower from the upper Bridger life zone.

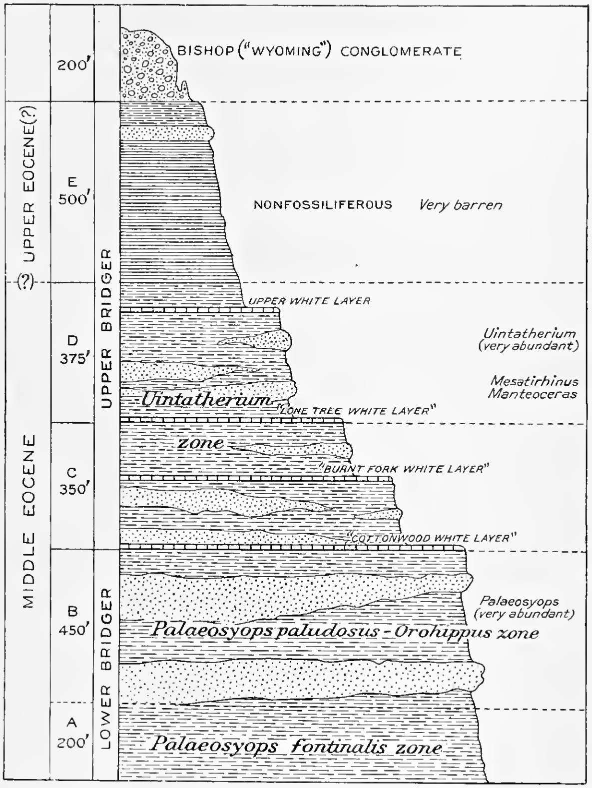


FIGURE 55.—Geologic section of the entire Bridger formation in the Bridger Basin, Wyo.

Shows the division by the four chief "white layers" and the main divisions by three principal life zones—A, *Palaeosyops fontinalis* zone; B, *Palaeosyops paludosus-Orohippus* zone; C and D, *Uintatherium* zone.

Life environment in Bridger time.—From observations made by Hay (1905.1, pp. 327–329) while he was collecting fossil turtles in the Bridger in 1903, he concluded that the Bridger deposits were almost solely the result of fluviatile and flood-plain action, that this basin was a nearly level country, which was probably covered with vegetation and well forested. The distribution of fossil remains in all parts of the Bridger area indicates that the animals lived near the places where they became buried and that they were chiefly such as may inhabit well-wooded regions. The river-channel beds, which are composed of coarse materials, show that streams with rapid currents traversed the basin. These streams were bordered by swamps in which were formed beds of impure lignite, or by fresh-water bays in which the shells of fresh-water mussels accumulated. The finer deposits indicate shallow, muddy bays, in which the remains of the larger quadrupeds are occasionally found in positions indicating that they had been mired in a standing posture. The old stream channels have yielded remains of several species of bowfins (Amiidae), garpikes (*Lepidosteus*), and siluroids. Crocodiles were numerous and diversified. The reptiles suggest that the climate was Floridian, or south temperate, and we may picture a partly open, partly forested country, somewhat similar to the existing bayou region of the Mississippi Delta of Louisiana. Analysis of the Testudinata by Hay (1908.1) has also afforded a clear idea of the physiographic conditions in Bridger time. The soft-shelled river turtles (Trionychoidea) were represented by at least 25 species, and there are now in the world only 26; the Bridger rivers and brooks fairly swarmed with these creatures, some of them equal in size to the largest existing Asiatic species. There are indications of 4 species of the family Emydidae (order Cryptodira), as compared with the 12 species now living in the Mississippi Valley. The genus *Baptemys*, of the same order, has its nearest relatives at present in Central America, and a third genus (*Anosteira*) is reported by Lydekker in the upper Eocene of England. The presence of extensive stretches of land is indicated by the true land tortoises (Testudinidae) of the genus *Hadrianus*, including giant tortoises nearly 3 feet long, which probably lived on dry lands bordering the sluggish Bridger streams. The ancient Lower Cretaceous order Amphichelydia is also represented here by four species belonging to two genera.

The environmental adaptations of the animals of the Bridger Basin were classified by Matthew (1901.1, pp. 309, 310) as follows:

Land animals:

1. Aerial: Remains of birds rare and fragmentary, as in nearly all geologic formations.

2. Arboreal: Primates, many Carnivora, and some Insectivora and Rodentia. Out of 1,007 specimens, belonging to 46 genera, 13 genera (184 specimens) were certainly arboreal and 11 genera (485 specimens) were probably arboreal.
3. Terrestrial (cursorial and ambulatory): Some of the carnivores and all the ungulates (17 genera, 314 specimens). Also some lizards and chelonians.
4. Fossorial: Certainly fossorial, 3 genera (8 specimens). Some of the insectivores may also have been fossorial.
5. Amphibious: One insectivore (*Pantolestes*) (1 genus). Probably certain carnivores.

Water animals:

6. Fresh-water: Numerous crocodiles, aquatic turtles, fish, and fresh-water mollusks.
7. Marine: No marine animals. Contrast this lack of types with the types of fish in the preceding Green River formation.

The Bridger life thus included many arboreal, terrestrial, and aquatic forms, the last mostly reptiles, fishes, and invertebrates. The slow-moving, ambulatory quadrupeds form a relatively large proportion of the mammals, but the cursorial types, such as the Equidae (*Orohippus*), are relatively rare; also the fossorial types. The Bridger life seems to be that of a partly forested flood plain. The remains of large mammals are so numerous as to indicate abundant open, gladed areas, comparable to the partly forested and partly open delta regions along certain rivers of modern time.

The foot structure of the Bridger quadrupeds gives less certain evidence of an open plains country, favorable to cursorial types, than that of the Wasatch (lower Eocene) quadrupeds of the same region.

No impressions of leaves from the Bridger forests have been discovered. It is probable that the forests of Green River type, described on pages 72–73, persisted into Bridger time and that the climate then was warm-temperate, almost subtropical.

The faunal history of the Bridger as a whole shows a gradual reduction in the number of archaic mammals of Mesozoic stock and a steady increase in the number of their competitors among the modernized mammals, the numerical relations between these two groups in upper Bridger time being as follows:

	Genera	Species
Archaic mammals	15	35
Modernized mammals	57	146
	72	181

Duration of the Bridger epoch.—Matthew (1909.1), following the earlier geologists, believes that the lacustrine conditions in Green River time arose from the uplift of the Uinta Mountain range, which blocked the basin and caused the formation of the great lake in which the material that formed Green River shale was laid down. As the river gradually cut its way through the east end of the Uinta Range the lake gave way to the broad Bridger flood plain, in which was deposited the volcanic ash washed down from the slopes of the Uinta Mountains to the south, and the deposit was worked over and sorted by the streams that flowed across the plain. The Bridger Basin was subject to intermittent overflow, which gave rise to large but shallow lakes of clear water. If we should assume that the Bridger formation occupied one-tenth of total estimated Eocene time—90,000 to 100,000 years—the fossiliferous beds, which are 1,100 feet thick, have accumulated at an average rate of 12 inches per century. This estimate would allow 110,000 years for the deposition of the Bridger formation exclusive of the "white layers" formed at intervals when deposition was arrested. The titanothere remains of the Bridger indicate a long period of evolution, but not so long as that of the Chadron (lower Oligocene).

Chief localities and exposures of the Bridger formation in the Bridger Basin

		Level
Bridger E:		
Uppermost exposures:		
Sage Creek Mountain.		
Henrys Fork Table.		
Twin Buttes.		
Bridger D:		
Upper exposures:		
Twin Buttes		D 1–5
Spanish John's Meadow		D 1–5
Cat Tail Spring		D 1–5
Henrys Fork, Burnt Fork post office		D 1–5
Henrys Fork, Lone Tree post office		D 1–5
Summers Dry Creek		D 1–5
Henrys Fork Hill		D 1–5
Sage Creek Spring		D 1–5
Lane Meadow		D 1–5
Bridger C:		
Lower exposures:		
Henrys Fork, Lone Tree post office		C 4–5
Lane Meadow		C 3–5
Spanish John's Meadow		C 3–5
Henrys Fork Hill		C 3–5
Twin Buttes		C 1–5
Dry Creek		C 1–5
Henrys Fork, Burnt Fork post office		C 1–5
Church Buttes, third bench		C 1–3
Bridger B:		
Upper exposures:		
Cottonwood Creek	Typical	B 4–5
Millersville, 6 miles southeast of		B 4–5
Cottonwood Creek, middle of		B 3
Grizzly Buttes		B 3
Church Buttes		B 2–3
Lower exposures:		
Cottonwood Creek		B 2
Grizzly Buttes	Typical	B 2
Exposure B, 5 miles south of Granger		B 2
Millersville		B 1–2
Cottonwood Corral, Blacks Fork		B 1–3
Exposure A, 5 miles south of Granger		B 1
Church Buttes		B 1
Bridger A:		
Hams Fork Bluff; Granger to Opal, 25 miles.		
Mouth of Big Sandy Creek (?*Palaeosyops fontinalis* zone).		
Big Muddy exposures between Carter and Granger.		
Blacks Fork Bluffs, east of Granger.		

ZONE 10: EOMETARHINUS-TROGOSUS-PALAEOSYOPS FONTINALIS ZONE

[Bridger A and Huerfano B; lower Lutetian of Europe]

The lower Bridger (Bridger A and B) corresponds with the "calcaire grossier supérieur" of the Paris Basin. The correlation of Bridger A with Huerfano B has recently been established through the discovery in each of the mammalian species *Palaeosyops* (*Limnohyops*) *fontinalis* Cope. (Osborn, 1919.494.) In these beds vertebrate fossils are rare and include, besides the titanothere above mentioned, remains of crocodiles, turtles, and fishes only. Bridger A consists of some 200 feet of calcareous shale alternating with tuff (Matthew, 1909.1), which are exposed principally around the eastern, northern, and western margins of the Bridger Basin. It is therefore supposed that Bridger A, which passes down into the lacustrine Green River shales, is partly of lacustrine, partly of fluviatile origin and is transitional both geologically and in its fauna between Green River (upper Wind River) and Bridger B time. Sinclair describes this horizon as consisting of "buff and pale-green tuffaceous shales and sandstones, often containing in enormous numbers shells of *Paludina* and *Unio*."

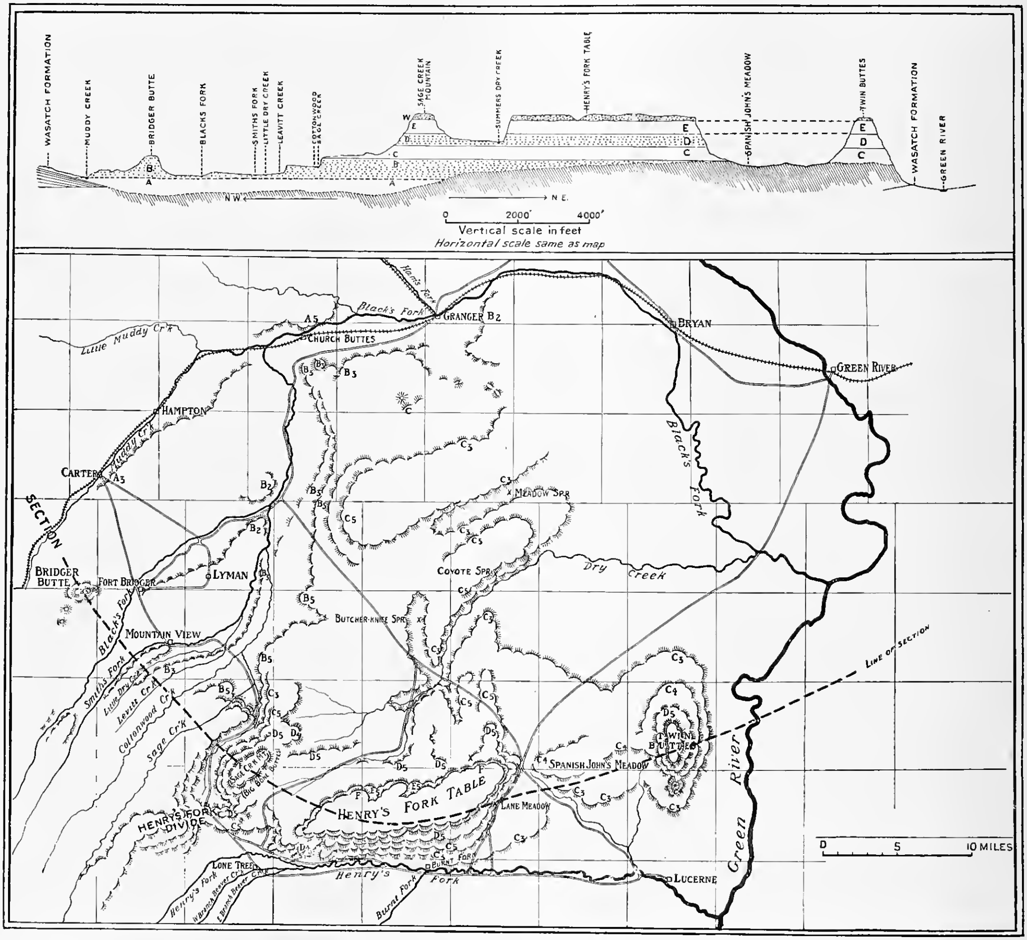


FIGURE 56.—Map of the Bridger Basin, Wyo. (No. 8, fig. 35)

Showing the principal topographic features, Twin Buttes and Henrys Fork Table, and a diagrammatic section of the Bridger formation (A, B, C, D, and E) capped by the Bishop ("Wyoming") conglomerate (W). After Matthew and Granger, 1902, 1909.

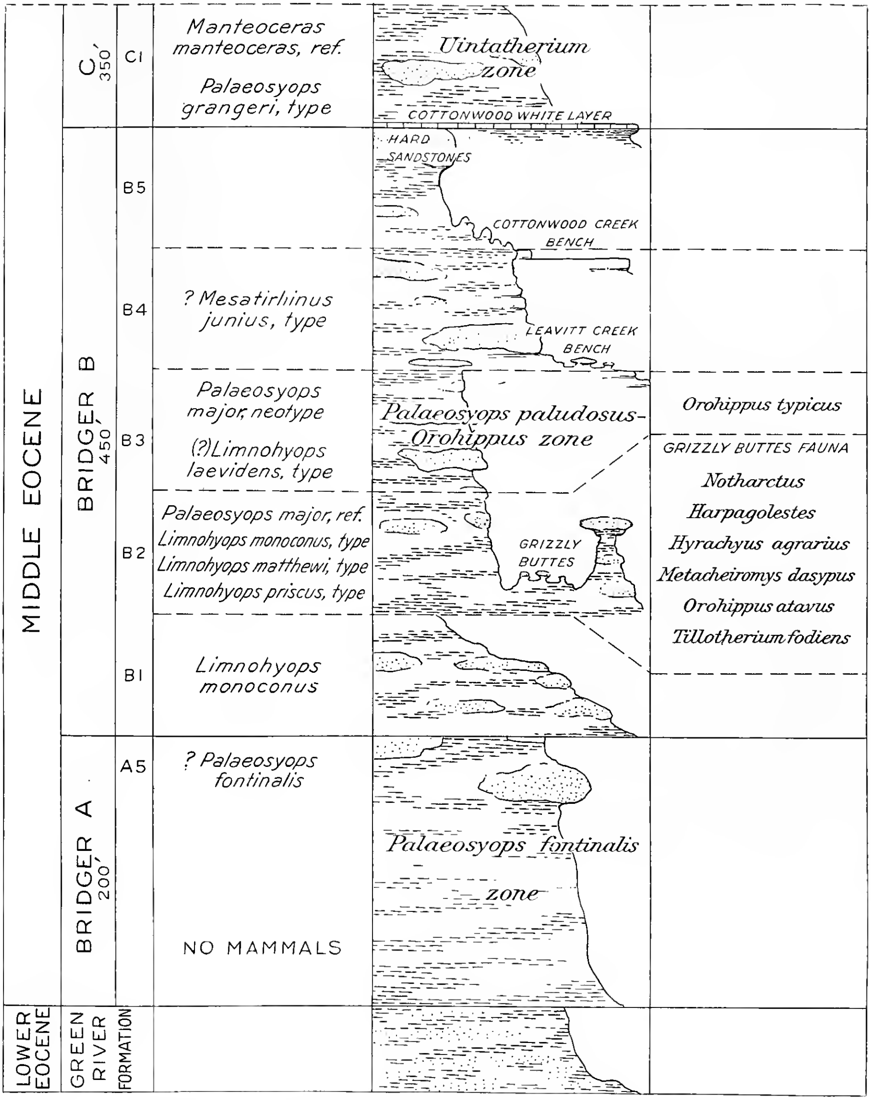


FIGURE 57.—Section of the lower part of the Bridger formation in the Bridger Basin, Wyo. (No. 8, fig. 35), showing the succession of the species of titanotheres and other mammals

The section is 650 feet thick. The principal geologic features are represented in the center. After the studies of Osborn, Granger, and Matthew.

ZONE 11: PALEOSYOPS PALUDOSUS-OROHIPPUS ZONE

[Bridger B; upper Lutetian of Europe]

The richly fossiliferous deposits belonging to the *Paleosyops paludosus-Orohippus* zone (Bridger B) are exposed chiefly in the northern area of the Bridger formation, near Fort Bridger, along Blacks Fork and its tributaries. They represent a very long period and consist of 450 feet of tuffs and sandstones (fig. 4) divided into two principal escarpments, which are separated by Cottonwood Creek valley.

In this zone the titanotheres and other mammals undergo notable progressive evolution, and there is a marked succession of species. (See fig. 57.)

The succession of the species of titanotheres in Bridger B, in descending geologic order, is as follows:

?Mesatirhinus junius Leidy.
Palaeosyops major Leidy, hypotype.
Limnohyops laevidens Cope, type.
Palaeosyops major Leidy, referred.
Limnohyops monoconus Osborn, referred.
Limnohyops monoconus Osborn, type.
Limnohyops matthewi Osborn, type.
Palaeosyops paludosus Leidy.
Palaeosyops paludosus, referred.
Palaeosyops paludosus, type.

The species of titanotheres found in Bridger B belong exclusively to the subfamily Palaeosyopinae and represent the two generic branches *Palaeosyops* and *Limnohyops*, closely related animals with broad spreading feet and heavy limbs, slow in gait. The reference to *Mesatirhinus* of the species *P. junius* Leidy is somewhat doubtful. The lower half of Bridger B at Grizzly Buttes (Pl. VII, *B*), an escarpment along Smiths Fork, is by far the richest collecting ground in the Bridger Basin; thousands of specimens have been taken from it, including many more or less complete skulls and skeletons, all recorded from Bridger B 2. Beds at a slightly higher level, in Bridger B 2 and in Bridger B 3, on the escarpment along Cottonwood Creek, have yielded a number of complete skeletons, including those of several species of Equidae (*Orohippus*), a variety of catlike and doglike creodonts (*Limnocyon*, *Harpagolestes*), abundant small civet-like creodonts (*Viverravus*, *Sinopa*), ancestral canids (*Miacis*, *Uintacyon*), a surviving (?) condylarth (*Hyopsodus*); also ancestral Edentata (*Metacheiromys*, armadillo-like) and the rodent-like tillodonts (*Tillotherium fodiens*, *Trogosus*). They have also yielded many rodents (*Paramys*, *Sciuravus*), as well as a rich primate fauna of lemuroids (*Notharctus*). The entire fauna has been very carefully reviewed and analyzed by Matthew (1909.1, pp. 298–302).

Rich as is the fossil life of the lower Bridger, many mammalian subfamilies and many genera and species are lacking which occur abundantly in the upper Bridger. Noticeable is the absence of uintatheres (*Uintatherium*) and of three important genera of titanotheres (*Manteoceras*, *Telmatherium*, *Mesatirhinus*), which appear abundantly in the upper Bridger.

The "Cottonwood Creek white layer," marking the summit of Bridger B, indicates a long period of shallow lake flooding of the Bridger Basin during which the large amblypod uintatheres and the more advanced titanotheres entered the basin. *Uintatherium* is not found in Bridger B, but it occurs at the very base of Bridger C, the lowest level of the upper Bridger.

ZONE 12: UINTATHERIUM-MANTEOCERAS-MESATIRHINUS ZONE

[Bridger C and D, Washakie A, and Uinta A; part of Bartonian of Europe]

The fauna of zone 12 in the Bridger Basin, which includes deposits 725 feet thick (Bridger D, 375 feet; Bridger C, 350 feet; see fig. 58), may be clearly distinguished from that of zone 11 (lower Bridger = Bridger B and A) by its content of the remains of the animals listed below:

Titanotheres:
    Palaeosyops robustus Leidy.
    Palaeosyops copei, type.
    ?Telmatherium validum, type.
    Manteoceras manteoceras.
    Mesatirhinus petersoni, type.
    Palaeosyops leidyi, type.
    Limnohyops laticeps, type.
    Mesatirhinus megarhinus, type.
    ?Telmatherium cultridens.
Other mammals:
    Hyrachyus princeps (cursorial rhinoceros).
    Patriofelis ferox (catlike creodont).
    Isectolophus latidens (tapir).
    Uintatherium robustum (four-horned amblypod).
    Notharctus crassus (large lemuroid).
    Pantolestes natans (aquatic insectivore).
    Homacodon vagans (primitive artiodactyl).
    Uintatherium mirabile (amblypod uintathere).
    Orohippus sylvaticus (primitive equine).

Bridger C.—The lowest beds of the horizon known as Bridger C are exposed at the foot of Sage Creek Mountain, along the southern slope of Henrys Fork Table; also at the foot of Twin Buttes and along the slopes north of Twin Buttes. They consist of 350 feet of gray and greenish-gray tuffs, divided into a lower and an upper half by the "Burnt Fork white layer" and bounded above by the "Lone Tree white layer." After careful analysis of the fauna of Bridger C, Matthew concluded (1909.1, p. 304) that its marked distinction from the fauna of Bridger B was due to the immigration of several new genera into the Bridger Basin. Among these especially are the titanothere genera *Manteoceras*, *Telmatherium*, and *Mesatirhinus*, which appear to be really newcomers and not in any sense descendants of the lower Bridger genera *Palaeosyops* and *Limnohyops*. The two genera last named, however, are represented in Bridger C by distinctly new specific forms, much more progressive than those in Bridger B. Thus Bridger C is characterized both by marked evolutionary changes in mammals that pass over from the lower levels and by the introduction of a fauna that is more or less new. Of this new fauna

Uintatherium is closely related to the ancestral *Bathyopsis*, which is found in the Wind River *Lambdotherium* zone and in the long antecedent first Wasatch zone. The pseudotapir *Isectolophus* is related in tooth structure to *Systemodon*, which is characteristic of the third Wasatch zone. We are therefore disposed to regard the life of the upper Bridger (*Uintatherium*) zone as the result of a local immigration from the adjacent Rocky Mountain or Plains region into the Bridger Basin, and not as the result of a continental immigration such as is made manifest in the lower Eocene.

Bridger D.—Upon the "Lone Tree white layer" lie the 375 feet of strata that form Bridger D, in which are found five faunistic levels, D 1 to D 5. The fossiliferous sediments of this closing period of the Bridger consist of 350 feet of "gray and greenish-gray sandy and clayey tuffs, with one or more ash beds," including the upper "white layer," which lies about 75 feet below the top of the formation. Among the titanotheres of this zone are descendants of species of *Palaeosyops*, *Limnohyops*, *Manteoceras*, and *Telmatherium*, which continue to increase in size and which represent advancing mutations that are exhibited in the comparative measurements shown in the tables on pages 304, 313, 341, 364. It is noteworthy that there is no very marked faunistic change in the species of titanotheres that persisted from Bridger C to Bridger D. For example, *Manteoceras manteoceras* persists from the lower to the higher levels, and *Mesatirhinus petersoni* is recorded in both C 2 and D 3. Exceptions to this slow evolution are seen in two species—*Palaeosyops copei*, which represents in certain characters an advanced stage of evolution allied to a stage found in the lower sediments of the Washakie Basin, and *Telmatherium validum*, assigned to Bridger D, which shows a distinct advance upon *Telmatherium cultridens*, assigned to Bridger C 5.

Bridger E.—Bridger E is theoretically correlated with Washakie B and Uinta B (upper Eocene). The topmost beds of the Bridger formation, 500 feet thick, include sediments that are almost barren of fossils, but the few fragments of mammals they have yielded are of undoubted Bridger age. The 500 feet of soft banded tuff containing at intervals thick layers of volcanic ash indicate increasingly active volcanism. The layers of gypsum found at this horizon were probably deposited in playa lakes (Sinclair, 1906.1), like those in the Humboldt Basin of the present time. The dark-red bands in Bridger E may indicate an arid climate. The correlation of Bridger E with Washakie B, to the east, is purely conjectural, for neither contains determinable remains of mammals. Matthew (1909.1, p. 306) attributes the paucity of life in this zone to violent volcanic eruptions, observing that the thick and generally unsorted beds of ash indicate great volcanic activity and that the large amount of gypsum and the absence of fossils might be due to the consequent destruction of vegetal and animal life, which converted the region into a barren plain that was alternately submerged and desiccated.

The *Uintatherium* zone in the Washakie Basin (Washakie A) is described on pages 85, 87, in the description of the deposits of that basin. The barren deposits in the Uinta Basin (Uinta A) that correspond to the *Uintatherium* zone are described on pages 91–92, in the description of the Uinta Basin.

WASHAKIE BASIN, WYO.

STRATIGRAPHY OF THE BASIN

Deposits and faunal zones.—The Washakie Basin lies about 50 miles east of the Bridger Basin, and the two contain similar volcanic sediments. The basin was described by Hayden in 1869–70 (1871.2, p. 73), and more fully by Cope in 1873 (1873.4). Its faunistic levels were studied by the Princeton expedition (Osborn and McMaster, 1881.8) and by expeditions of the American Museum of Natural History, under Wortman (1893, 1895) and Granger (1906). Granger (1909.1, pp. 13–32) gave the first complete and accurate description of the geology of the Washakie Basin in his "Faunal horizons of the Washakie formation of southern Wyoming" (1909.1, pp. 13–32). King treated the deposits of the Washakie Basin as of Bridger age and of lacustrine origin. Osborn (Osborn and McMaster, 1881.8) favored the theory of separate deposition, and Scott (1899.1) showed that where the fauna of the Washakie Basin departs from that of the Bridger it approaches that of the Uinta. The discovery of the true upper Bridger fauna in horizon A of the Washakie Basin was due to the American Museum expeditions of 1893, 1895, under Wortman.

The Washakie Basin, with its vivid coloring and its alternation of hard and soft layers of tuff and sandstone, affords the most picturesque geologic views to be found in the Rocky Mountain Eocene basins. Haystack Mountain ("Mammoth Buttes" of Cope), a long ridge of badlands near the north end of the basin, which in places rises 400 feet above the plain, forms the northern border of an extensive semicircular "central basin" that has the appearance of a gigantic crater. The floor of this basin is rather level and regular, being broken only by a few low tables and buttes, which have long been preserved from erosion by their capping of hard sandstone, though their sides are trenched by innumerable deep, vertical-walled canyons, which present a great variety of architectural forms that are illuminated by brilliant coloring.

Washakie A (*Uintatherium zone, middle Eocene*).—The "lower brown sandstone" of the Washakie Basin, known as Washakie A (fig. 60), contains the fauna of the *Uintatherium-Manteoceras-Mesatirhinus* zone. It was deposited contemporaneously with the upper Bridger (Bridger D), to the west, and probably with the non-

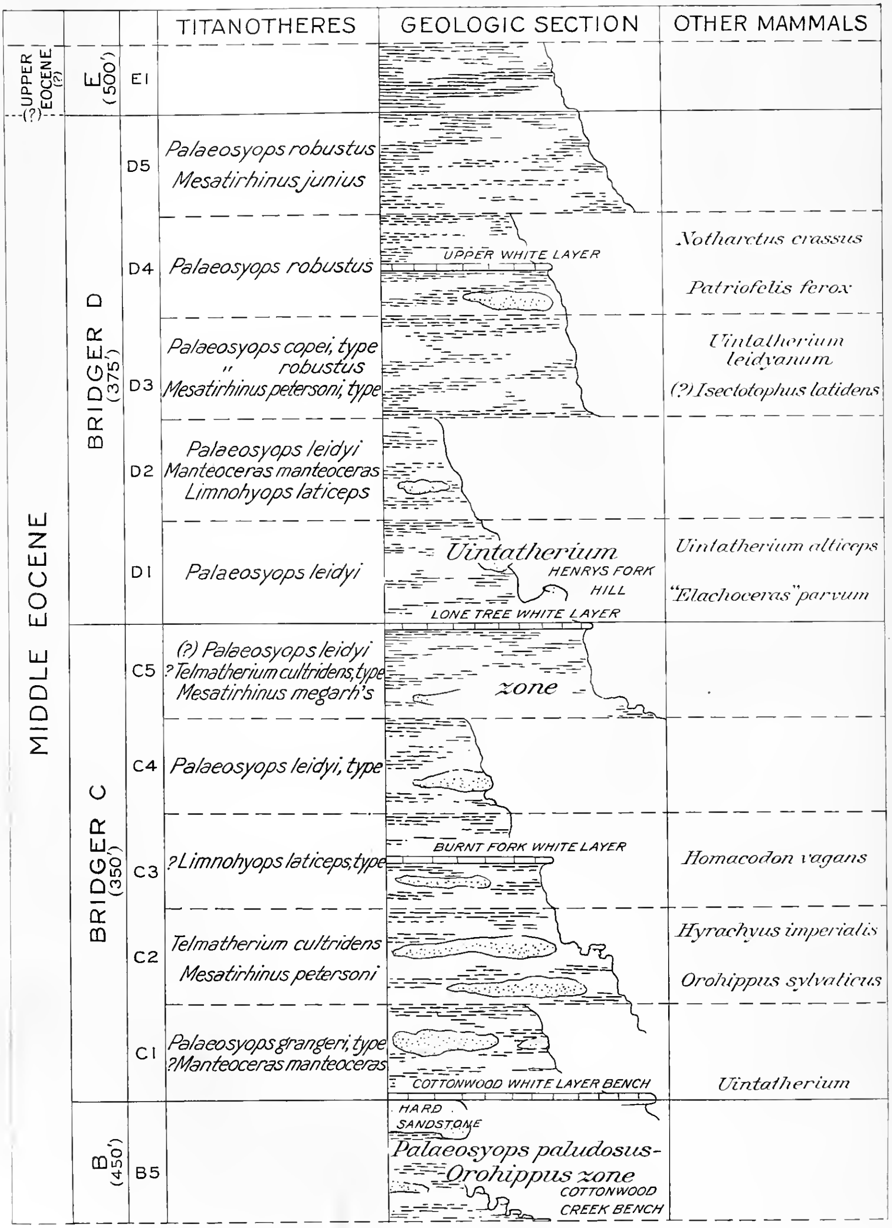


FIGURE 58.—Section of the upper part of the Bridger formation in the Bridger Basin, Wyo.

Shows the vertical distribution of the titanothere species on the left, the principal geologic features in the center, and the distribution of the other species of mammals on the right. Principally after Osborn, Granger, and Matthew.

fossiliferous Uinta A, to the south. Its contemporaneity with Bridger D is established through the common presence of the following species:

Uintatherium robustum.
Uintatherium mirabile.
Manteoceras manteoceras.
Notharctus tenebrosus Leidy.
Hyrachyus princeps Leidy.
Sinopa.
Palaeosyops copei Osborn.
Mesatirhinus megarhinus.
Mesatirhinus petersoni.
Hyopsodus.
Paramys.

This fauna of the *Uintatherium* zone occurs in 260 feet of Washakie A, which is composed largely of altered eruptive rocks, probably dacite tuffs, of calcareous and siliceous shales, and of glass tuffs mingled with grains of quartz, hornblende, feldspar, according to the analysis of Johannsen (1914.1, p. 214).

The "lower brown sandstone" layer yields a rich fauna of uintatheres. This layer forms a persistent bench, which constitutes the lower rim of the basin on its northern border. This "lower brown sandstone" passes at a low angle southward beneath the floor of the basin. Below it, and apparently conformable with it, lie gray sandy shales, which are provisionally referred to the Green River but which were probably laid down in lower Bridger time (Bridger A and perhaps Bridger B). As these deposits show no marked evidence of erosion it seems probable that the Washakie Basin was filled with a lake in Green River time while Bridger A was being deposited to the west.

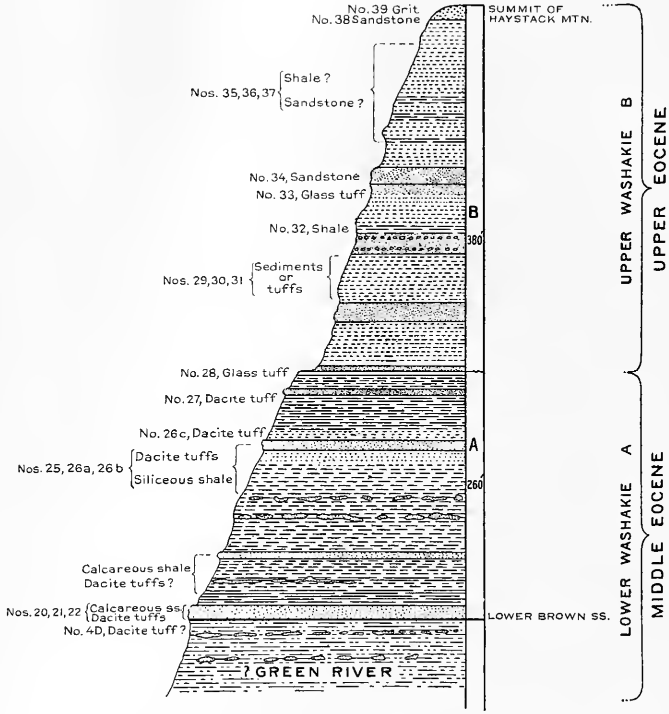


FIGURE 59.—Diagrammatic vertical section of deposits near Barrel Springs, Washakie Basin, southern Wyoming

Shows the alternation of tuffs, siliceous, calcareous, and sandstone materials. Johannsen (1914.1), after Granger, with modifications. The numbers refer to lithologic specimens examined by Johannsen.

Washakie B (*Metarhinus and Eobasileus-Dolichorhinus zones, upper Eocene*).—The upper Eocene Washakie B horizon is described on pages 89–90, in the description of upper Eocene faunal zones 13 and 14, to which it belongs.

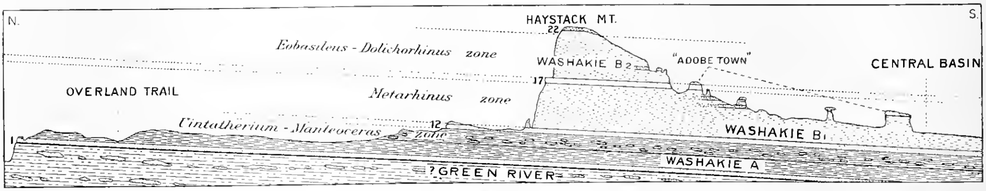


FIGURE 60.—Diagrammatic horizontal section of the Washakie Basin, southern Wyoming, from north to south

After Granger (1909.1). This section shows the *Uintatherium-Manteoceras* zone (Washakie A, lower brown sandstones), discovered by the American Museum in 1893; *Metarhinus* zone (Washakie B 1), base of the original "Washakie" formation of Hayden and Cope; *Dolichorhinus-Eobasileus* zone (Washakie B 2), summit of the original "Washakie" formation of Hayden and Cope; "Adobe Town," roughly eroded area in which *Amynodon antiquus*, *Achaenodon*, etc., were discovered by the Princeton expedition of 1878. The numbers show locations of lithologic specimens studied by Johannsen.

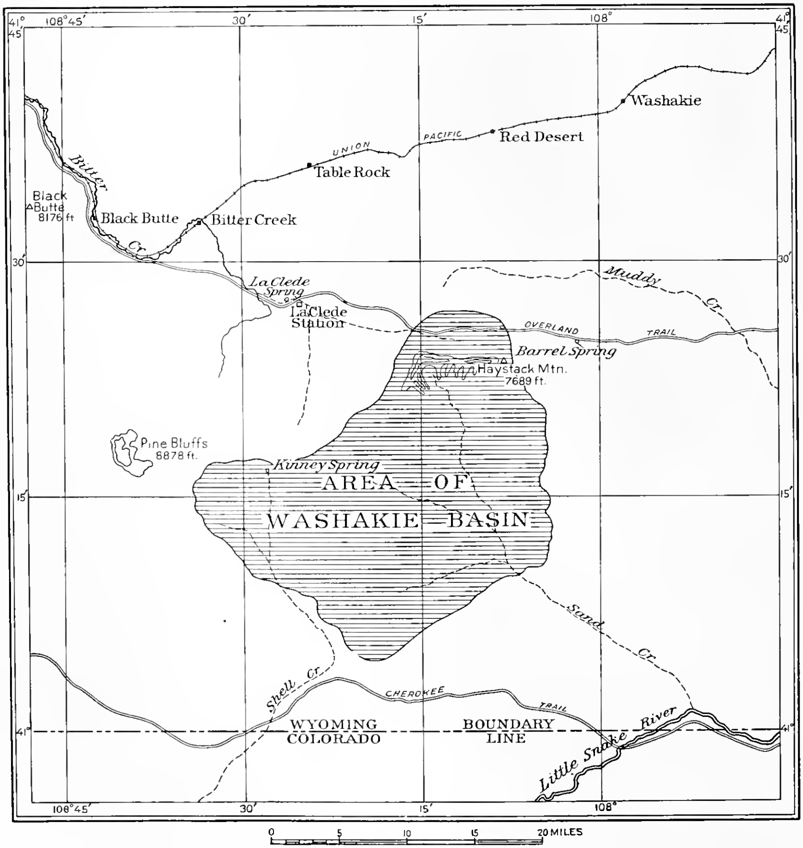


FIGURE 61.—Sketch map of the Washakie Basin region, in southern Wyoming

After Granger (1909.1) from Clarence King (1876.1). The shaded area is the "Washakie" formation of Hayden, mapped by King and the United States Geological Survey as the Bridger formation.

Mammalian life of the Washakie Basin

	Washakie A (Uintatherium-Manteoceras-Mesatirhinus zone). These forms are found also in Bridger C and D, to the west	Washakie B 1 and B 2 (Eobasileus-Dolichorhinus zone and Metarhinus zone). These forms are found also in Uinta A and B, south of the Uinta Range.
Primates:		
Lemuroids	Notharctus sp. Hemiaeodon sp.	
Rodents	Paramys cf. P. delicatus.	Paramys leptodus, type. Paramys grangeri.
Carnivores:		
Creodonts	Thinocyon cledensis, type. Patriofelis ferox. Sinopa rapax var. lania, type. Synoplotherium lanius, type.	Harpagolestes immanis. (Giant creodont of the family Mesonychidae.)
Miacids (doglike carnivores).	Miacis washakius, type. Miacis medius. Oodectes? pugnax, type.	Limnocyon potens. (An oxyaenid creodont.)
Condylarths	Hyopsodus cf. H. despiciens.	
Amblypods	Uintatherium grande, type. Uintatherium speirianum, type.	Eobasileus cornutus, type. (Giant amblypod with the front horn directly above the eyes; first appearance.) Eobasileus galeatus, type. Eobasileus furcatus, type. Eobasileus pressicornis, type.
Artiodactyls	Homacodon sp.	Achaenodon insolens, type. (First of the elotheres.) Achaenodon robustus, type. ?Protylopus sp. (A cameloid form.)
Perissodactyls:		
Titanotheres	Palaeosyops copei? (Last of Palaeosyops. Palaeosyops sp. Manteoceras manteoceras, type. ("Prophet-horn" titanotheres.) Manteoceras washakiensis, type. Mesatirhinus megarhinus, type. (Ancestor of Dolichorhinus.) Mesatirhinus petersoni.	Metarhinus earlei, type. (Fluviatile type.) Dolichorhinus hyognathus, type. (Dolichorhinus cornutus stage.) Dolichorhinus vallidens, type.
Rhinoceroses and rhinoceratoids.	Hyrachyus sp. (Cursorial rhinoceros.) Triplopus cubitalis.	Hyrachyus sp. (Cursorial rhinoceros of Bridge type.) Triplopus sp. Amynodon antiquus, type. (First of the amynodonts (aquatic rhinoceroses).)
Chalicotheroids	Eomoropus amarorum, type. (Forest-living ancestral chalicothere; ancestor of Moropus.)	
Lophiodonts	Helaletes sp. Desmatotherium guyoti, type. Dilophodon minusculus, type. Dilophodon minusculus?	

ZONES 13 AND 14: METARHINUS ZONE AND EOBASILEUS-DOLICHORHINUS ZONE

[Uinta B 1 and Washakie B 1; Uinta B 2]

The great life division known as Washakie B, 380 feet in thickness, contains a new and dominant fauna, which is not represented at all in Bridger D or Washakie A. It is significant that this unit is divided into two zones by its fauna, exactly as Uinta B is divided into two zones, the *Eobasileus-Dolichorhinus* zone (Washakie B 2 = Uinta B 2), and the *Metarhinus* zone (Washakie B 1 = Uinta B 1 = (in part) Bartonian of Europe). Certain of the older mammalian families and genera (as *Uintatherium*) begin to disappear and new generic and specific forms replace them. Conspicuous among these is the amblypod *Eobasileus*, first described from this region by Cope, which replaces *Uintatherium*. A full list of this fauna is given above. Among the distinctive forms are the following:

Eobasileus cornutus Cope, type.
Dolichorhinus hyognathus Scott and Osborn, type.
Uintatherium speirianum Osborn, type.
Triplopus cubitalis Cope, type.
Eomoropus amarorum Cope, type.
Amynodon antiquus Scott and Osborn.
Achaenodon insolens Cope.
Metarhinus earlei Osborn, type.

Washakie A is characterized by "rusty brown nodular sandstones," and Washakie B by "coarse white, pink, and salmon-colored sandstones" and by "the extremely coarse green sandstones or feldspar conglomerates. The rocks first recognized as sandstones prove to be interspersed with dacite and glass tuffs." (Johannsen, 1914.1, p. 215.) The sandstones, which were derived from granite by erosion, consist of grains of quartz, hornblende, and feldspar embedded in a slightly devitrified groundmass. (See Pl. IX.)

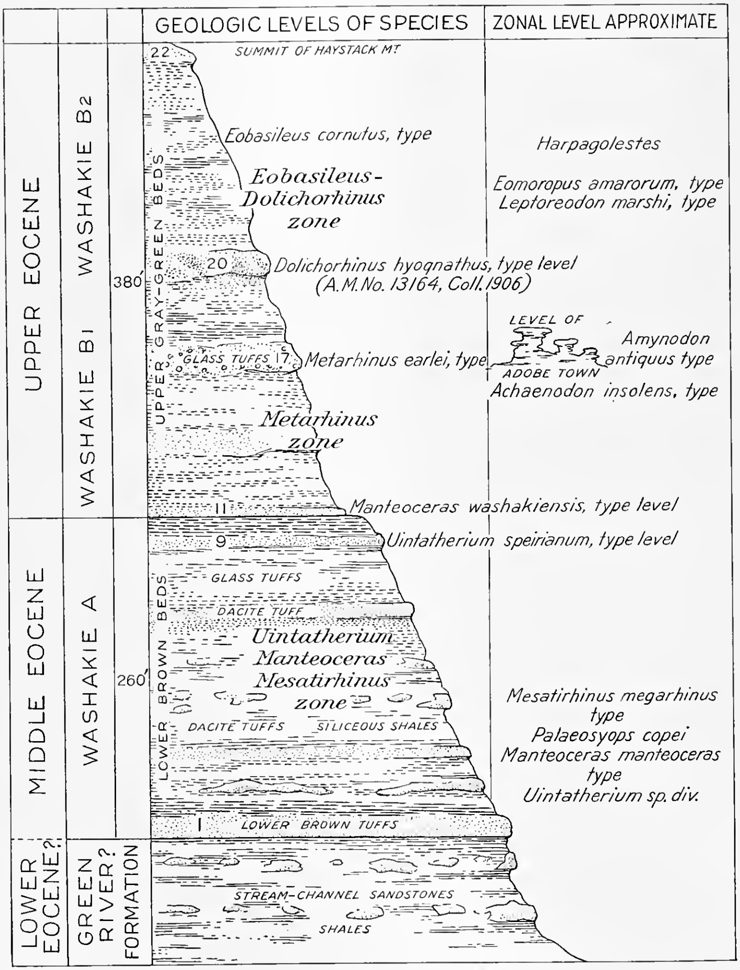


FIGURE 62.—Columnar section of the Washakie Basin, Wyo. (No. 9, fig. 35), showing life zones

Shows the principal genera of the lower and upper life zones and the actual level of certain characteristic species. Chiefly after Granger (1909.1). This section includes the *Uintatherium* zone (Washakie A), lower brown sandstones; *Metarhinus* zone (Washakie B 1); and *Eobasileus-Dolichorhinus* zone (Washakie B 2), upper gray-green beds. Numbers in column show position of lithologic specimens examined by Johannsen.

The composition of these sediments indicates the presence in this region of active volcanoes, which were discharging great clouds of dust. Unlike the sediments of the Bridger Basin the sediments of the Washakie Basin were deposited in rather turbulent water and contain none of the "white layers" that indicate the still water that prevailed in the upper Bridger. Turbulent water is not favorable to the preservation of the remains of small mammals. Only one of the smaller perissodactyl ungulates (*Triplopus*) has been found, and no remains of Equidae. The first aquatic rhinoceroses (*Amynodon*) belong to a river-frequenting type; the first of the entelodonts (*Achaenodon*) is also a river-frequenting form; the first of the forest-dwelling chalicotheres (*Eomoropus*) also occurs. Thus the Washakie Basin has preserved for us mainly the larger swamp and river-border fauna but has yielded little record of either the arboreal or plains-living cursorial fauna of the time.

In the fauna of the Washakie Basin (a list of which is given in the table on p. 89) the large hoofed animals predominate, especially those adapted to stream borders, swampy land, rivers, and streams. A small fauna of insectivores, lemuroids, carnivores, and ancestral artiodactyls doubtless abounded, but the environment was unfavorable to the preservation of such remains, and the microfauna has been found only rarely. The small titanothere *Metarhinus* is highly distinctive of this Washakie B 1 life zone. (Riggs, 1912.1.)

Uinta B.—Exactly the same physiographic conditions prevailed at the same time in the great basin south of the Uinta Mountains while the sediments known as Uinta B were being deposited. These sediments, which have a combined thickness of 800 feet, contain exactly the same riparian fauna, including a large number of identical species, and therefore constitute an extension of the *Eobasileus-Dolichorhinus* and *Metarhinus* life zones to the south. The fauna and deposits of Uinta B are more fully described on pages 91–99, in the description of the Uinta Basin.

UINTA BASIN, UTAH

PHYSIOGRAPHIC, CLIMATIC, AND VOLCANIC CONDITIONS IN THE UINTA BASIN DURING MIDDLE (?) AND LATER EOCENE TIME

It is a striking fact that the later Eocene sediments in the Uinta Basin are composed mainly of altered eruptives, probably dacite tuffs, as indicated by analyses of nine samples by Johannsen (1914.1, pp. 212–214). The rocks of the lower levels, described as "brown sandstones" comparable in lithologic appearance to Washakie A, contain a large element of tuff and consist microscopically of irregularly broken and rounded fragments of quartz, lime-soda feldspar, hornblende, biotite, and fragments of andesite or basalt in a brown groundmass, which is chiefly chlorite but contains some calcite. On the lower levels (in Uinta A) brown is the prevailing color, as in Washakie A. In Uinta B sediments of this color pass into pinkish-brown and reddish-brown sediments, and in Uinta C into pale-green and gray fine-grained rocks containing considerable glass. Many rocks that look like sandstones prove under the microscope to resemble flow breccias.

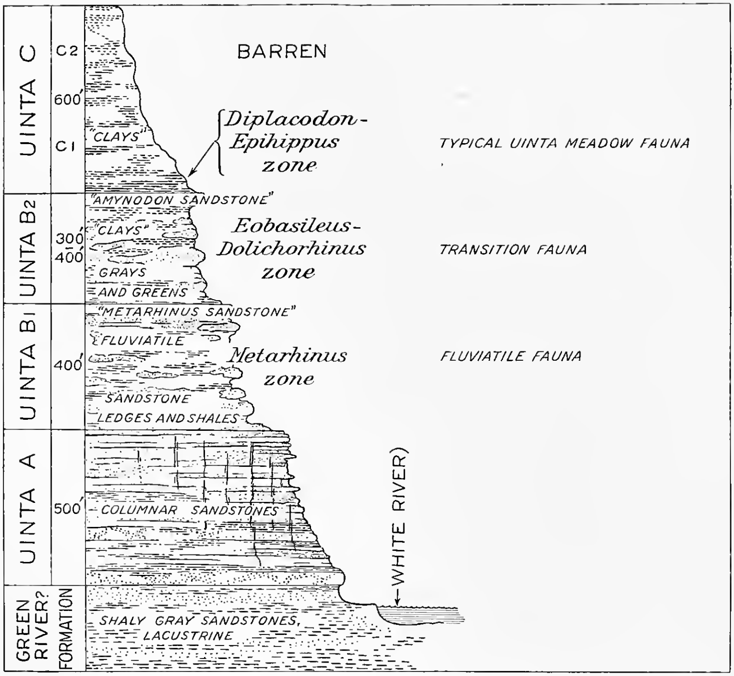


FIGURE 63.—Diagrammatic section of the Uinta formation exposed in the north wall of White River Canyon 3 miles below mouth of Evacuation Creek, Utah

After observations of Peterson, Douglass, and Riggs. Uinta A, columnar sandstones, unfossiliferous; Uinta B 1, *Metarhinus* zone capped by "*Metarhinus* sandstone," containing a fluviatile fauna; Uinta B 2, *Eobasileus-Dolichorhinus* zone, capped by "*Amynodon* sandstone," containing a transition fauna; Uinta C, *Diplacodon-Epihippus* zone, containing the typical Uinta fauna of Marsh 100 feet above "*Amynodon* sandstone."

GEOLOGIC HORIZONS IN THE UINTA BASIN

The deposits of horizons A and B of the Uinta Basin are not those of the typical Uinta formation of Marsh (1871.3), of King (1878), or of Scott and Osborn (1891.1), all of which belong to Uinta C, the *Diplacodon* zone; they form the lower part of the section (Uinta A and Uinta B), determined by the American Museum expedition of 1894 under Peterson (Osborn, 1895.98) and successively explored with remarkable results by Peterson, Douglass, and Riggs, whose observations and exact records of the vertical distribution of genera and species have firmly established the stratigraphy of the Uinta Basin section as presented in Figure 65. (See Pl. IX.)

Uinta A as now defined is entirely unfossiliferous but is here correlated with the middle Eocene fossiliferous horizon A of the Washakie Basin (*Uintatherium* zone).

Uinta B 1 (in some previous reports included in Uinta A) contains a rich river-border fauna, like that of Washakie B 1.

Uinta B 2 (formerly constituting all of Uinta B) contains a larger land and river-border fauna, like that of Washakie B 2.

Uinta C contains the typical Uinta (*Diplacodon*) fauna.

The sediments in the Uinta Basin between the *Diplacodon* zone and the Green River formation were classified by White (1878.1, p. 37) as Bridger, although no fossils were found in it, and were treated as contemporaneous with the Bridger deposits. We now know that the sediments that form Uinta B were certainly laid down after Bridger C and D had been deposited, but they may have been contemporaneous with the unfossiliferous Bridger E. During the American Museum explorations of 1893–94 Peterson discovered 150 fossil mammals in the lower series, which were first correlated by Osborn (1895.98, p. 72) with the typical "upper Washakie," now known as Washakie B. The determination of the stratigraphy as well as the faunistic succession has been modified by the subsequent explorations and publications of Douglass (1909.1) and Riggs (1912.1). The stratigraphic order of the later Eocene deposits of the Uinta Basin and the correlated fauna may be presented as follows:

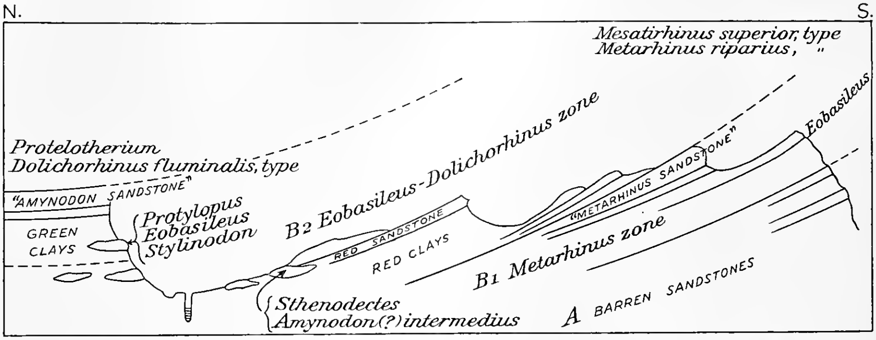


FIGURE 64.—Section of the Uinta formation (No. 10, fig. 35) from Kennedy's Basin to White River Canyon, Utah

This section includes Uinta A, the barren sandstones; Uinta B 1, the *Metarhinus* zone capped by prominent bluffs of "*Metarhinus* sandstone"; above this Uinta B 2, the *Eobasileus-Dolichorhinus* zone, capped by the "*Amynodon* sandstone." After E. S. Riggs (1912.1); see also F. B. Weeks (1907.1).

Later Eocene deposits and fauna in the Uinta Basin, Utah

Formation and nature of deposits	Geographic conditions and mammalian fauna
Uinta of King, Marsh, and White: Diplacodon elatus beds of Marsh; horizon C of Peterson, Douglass, and Riggs. Dacite tuffs and sandstones, grayish and greenish. Ferruginous. Thickness, about 600 feet.	Meadow, forest, and river fauna. Large titanotheres: Diplacodon elatus, Protitanotherium emarginatum, etc. Artiodactyla: Protoreodon, Leptotragulus, primitive camels. Small equines (Epihippus uintensis). Other large and small members of the true Uinta fauna. No traces of Amblypoda.
Uinta B 2 of Peterson and Osborn: Dolichorhinus cornutus zone of Osborn (1895.98). Amynodon beds of Riggs (1912.1, p. 22). Coarse brownish dacite tuffs and sandstones, capped at the summit by the "Amynodon sandstone," immediately underlying Uinta C. Thickness, 285 feet.	Fauna chiefly stream border and fluviatile and some small forms. Last uintathere (Eobasileus). Aquatic rhinoceros (Amynodon intermedius) abundant. Entelodonts (Protelotherium uintense). Rare cameloids (Protylopus). Rare edentates (Stylinodon). Numerous long-headed titanotheres (Dolichorhinus cornutus, D. fluminalis, Sthenodectes). In the upper levels, first long-horned titanothere (Eotitanotherium of Peterson); ancestral Symborodon-like titanotheres (Rhadinorhinus). Titanotheres extinct at this level or not recorded from it are Mesatirhinus and Metarhinus.
Uinta A of Peterson and Osborn, in part [Telmatotherium megarhinum beds of Osborn = Metarhinus fluviatilis zone, Osborn, upper Metarhinus zone of Riggs]: Capped by the "Metarhinus sandstones" of Riggs, with underlying coarse-grained brownish dacite tuffs and sandstone ledges; channel beds, varying in thickness from 5 to 30 feet, containing abundant remains of Metarhinus. Thickness, 266 feet.	Abundant fluviatile and forest fauna, of small variety. Titanotheres: Small lowland varieties of Metarhinus very abundant, including several distinct specific forms; also the long-headed Dolichorhinus superior, the short-headed Sphenocoelus, Metarhinus earlei, M. riparius, M. fluviatilis, Rhadinorhinus, Dolichorhinus longiceps, an ancestral form of Dolichorhinus cornutus. The amblypods Eobasileus or Uintatherium. The large creodont Mesonyx obtusidens.
Uinta A of Peterson and Osborn, lower levels (lower Metarhinus zone of Riggs): Capping of columnar sandstones, underlain by friable sandy shales, interspersed with ledges. Thickness, 585 feet (Douglass, 1913). Unfossiliferous. Underlain by Green River formation.	No fossil mammals certainly recorded by Peterson, Douglass, or Riggs from this level.

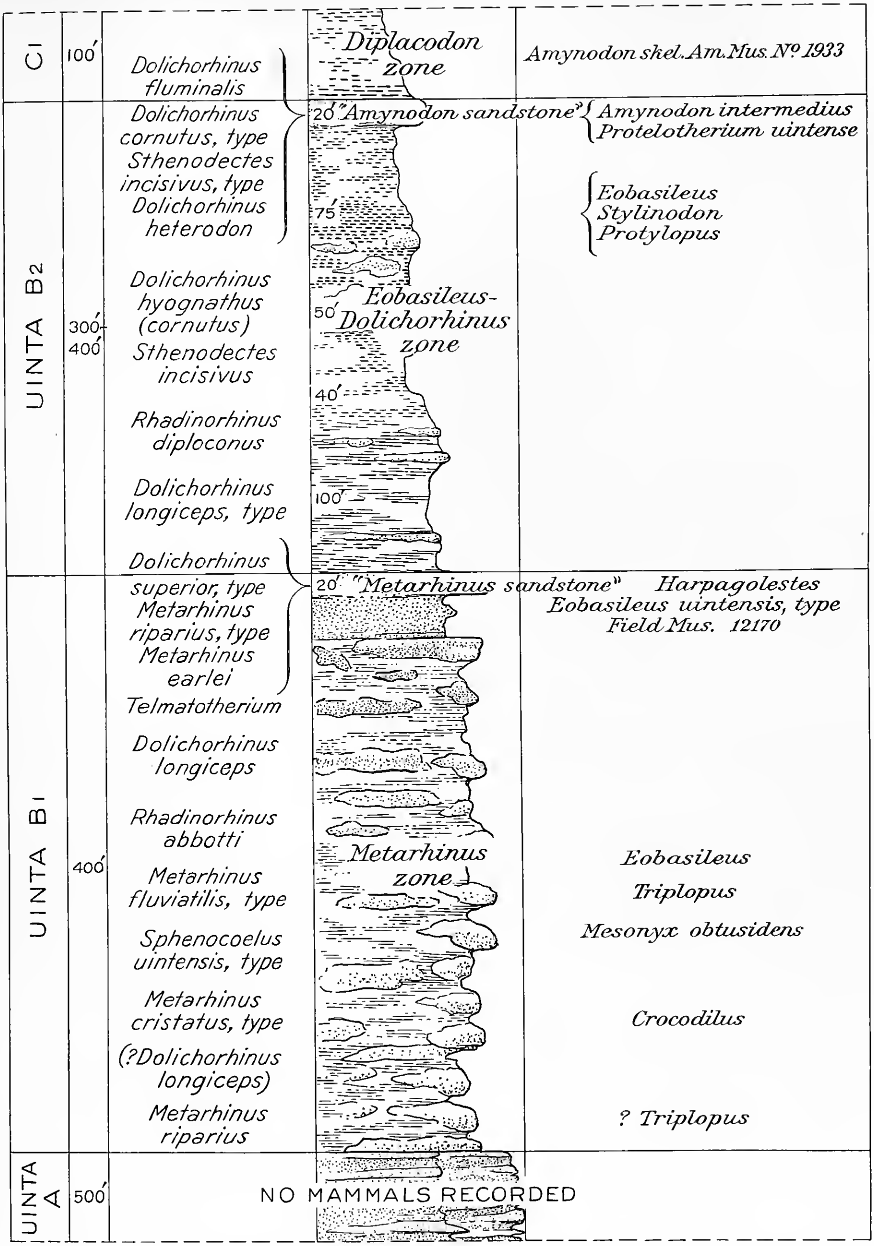


FIGURE 65.—Section of the *Eobasileus-Dolichorhinus* and *Metarhinus* zones in the Uinta Basin, Utah, showing stratigraphic distribution of species of titanotheres

The species of titanotheres are shown in the left-hand column, the geologic strata in the middle column, other characteristic mammals in the right-hand column. After observations made by Peterson, Douglass, Riggs, and Osborn.

The researches of Peterson, Douglass, Riggs, and Osborn prove that Washakie B and Uinta B comprise two distinct faunal divisions—a lower, Uinta B 1 (*Metarhinus fluviatilis*, *M. earlei* zone), probably corresponding with the lower levels (B 1) of Washakie B, and an upper, Uinta B 2 (*Eobasileus-Dolichorhinus* (*cornutus*) *hyognathus* zone), probably corresponding with the upper levels (B 2) of Washakie B.

UINTA B 1 (METARHINUS ZONE=ZONE 13)

Riparian fauna.—The fauna of the *Metarhinus* zone was evidently that of a riparian lowland and was in part fluviatile or aquatic, as is indicated by its adaptations to aquatic and lowland life, which are independently developed in members of several different families. These adaptations are indicated by some of the specific names, such as *Metarhinus riparius*, *M. fluviatilis*, two diminutive titanotheres, and *Dolichorhinus fluminalis*. The animal last named is a short-limbed swamp-dwelling form, a fit companion of the river-seeking rhinoceros *Amynodon intermedius*, which begins to show aquatic adaptations in the structure of the orbit. The generic aspect of this fauna is almost identical with that of Washakie B, with the single exception that near the summit of Uinta B the entelodont *Protelotherium* replaces *Achaenodon* of Washakie B. The fauna contains a single new titanothere, *Rhadinorhinus*, which is closely related to *Metarhinus*. Some of the specific forms are identical with those of Washakie B and some exhibit more recent phases of evolution, which may be represented in the unfossiliferous upper levels of Washakie B. We consequently reach the broad generalization that Washakie B 1 and Uinta B 1 were not only contemporaneous sediments but that they indicate the prevalence of similar physiographic and climatic conditions at this time on the north and the south sides of the Uinta Range.

River-channel fauna.—Remains of the small titanothere *Metarhinus* have been found in ancient river channels, as determined by Riggs. This genus is by far the most distinctive fossil of this life zone and is apparently confined to it, although at certain levels primitive species of *Dolichorhinus* (*D. longiceps*) are found in equal abundance (Riggs, 1912.1, p. 20). This life zone, which is 400 feet thick, is composed chiefly of massive ledges of sandstone alternating with layers of sandy shales or indurated clays. In all the ledges there are traces of cross-bedding, and at many places there are beds of coarser river sand containing pebbles of quartzose material, sandstone, and clay shale. In these beds are found disarticulated bones of mammals, as well as the branches and at some places the trunks of trees, all pointing to the action of swiftly flowing streams that swept through a flood plain. Many skulls are found embedded in gravel, with their narial or orbital cavities filled with pebbles such as could be carried only by rapidly flowing water. Another evidence of stream action lies in the dissociation of the parts of single skeletons. Whole skeletons have exceptionally been found but little disturbed, lying in a fine-grained homogeneous sandstone, apparently deposited in quieter water, such as deep pools or eddies. Remains of the long-headed titanothere *Dolichorhinus* are found only in the heavy sandstones, so that this animal was apparently confined to the vicinity of streams. Supposed river-frequenting species of *Metarhinus*, always found in sandstone, include *M. fluviatilis*, *M. riparius*, and *M. earlei*. The species last named is found also in the lower levels of Washakie B, north of the Uinta Mountains. As we ascend in this *Metarhinus* zone we find, according to Riggs (1912, p. 24), increasing numbers of upland forms. The "*Metarhinus* sandstone" ledge that caps this zone has yielded the type specimens of *Dolichorhinus superior*, *Metarhinus riparius*, and *M. earlei*, the last-recorded appearance of these animals in the Uinta Basin.

UINTA B 2 (EOBASILEUS-DOLICHORHINUS ZONE=ZONE 14)

In the beds of the *Eobasileus-Dolichorhinus* zone the river sandstones and channel deposits gradually give place to shales and clays, indicating physiographic changes in this part of the Uinta Basin. In the lower 100 feet of bluish or grayish shales, which are overlain by 40 feet or more of fine red clays, little evidence of mammal life is found, but certain thin beds contain fragments of *Eobasileus*. As we rise in the formation the gray "clays" begin to yield a mixed fauna of lowland and plains forms, including *Protylopus* and *Stylinodon*, together with remains of *Dolichorhinus* (*cornutus*) *hyognathus* and *Amynodon intermedius*. The massive "*Amynodon* sandstone," which forms the summit of this life zone, yields the type specimen of the long-headed titanotheres *Dolichorhinus* (*cornutus*) *hyognathus*, *D. fluminalis;* also of *Sthenodectes incisivus*. This is the last appearance of the genus *Dolichorhinus* in the Uinta Basin. Doubtless the massive "*Amynodon* sandstone" terminated the active period of fluviatile and flood-plain deposition in this locality. The *D.* (*cornutus*) *hyognathus* zone yields the large enteledont *Protelotherium uintense*, which is intermediate between *Achaenodon insolens* of Washakie B and *Elotherium* of the White River group. This sandstone contains also the lophiodont *Desmatotherium guyoti*, which is a forerunner of *Colodon* of the White River (Oligocene) group.

ZONE 15: DIPLACODON-PROTITANOTHERIUM-EPIHIPPUS ZONE

[Uinta C 1; Ludian of Europe]

To zone 15 belong the Uinta of King and Marsh, the "Brown's Park beds" of Powell, and the Uinta(?) of the Beaver Divide, Wind River Basin. This zone (Uinta C 1) is correlated with the European stage that was named Ludian, after the "marnes de Ludes" in the Paris Basin, a stage typified by the "gypse de Montmartre," made famous by the classic researches of Cuvier. The lower Ludian yielded the type specimen of the equine *Lophiotherium,* a horse in the same stage of evolution as the diminutive American *Epihippus* of the Uinta. The American beds contain a rich titanothere fauna. They include the "*Diplacodon* beds" of Marsh (1877.1, p. 354) and contain the robust titanothere *Protitanotherium,* which is intermediate between the "prophet-horn" *Manteoceras* and the horned titanotheres of the lower Oligocene; also the type of *Protitanotherium superbum,* an animal greatly exceeding in size the earlier Oligocene titanotheres. Of great interest is the survival of the ancestral genus *Manteoceras* in the species *M. uintensis,* a genus first occurring in the upper Bridger, and the Bridger genus *Telmatherium* in the species *T. ultimum.*

The amphibious rhinoceros *Amynodon* occurs in the species *A. antiquus.* It should be noted that the remains of all these large mammals were found not far above the base of Uinta C, and that all the specimens in the chief collections of small Artiodactyla (*Protoreodon, Leptotragulus*) and of Perissodactyla (*Triplopus, Lophiodon, Isectolophus,* a tapiroid, *Epihippus*) (Peterson) were obtained from the lower levels of Uinta C. With *Epihippus* were found the only primate that has been discovered in the Uinta Basin, *Notharctus? uintensis,* a lemuroid, and the supposed condylarth or insectivore *Hyopsodus.* The few surviving ancient creodonts are represented by *Oxyaenodon* and by the giant *Harpagolestes uintensis.* Especially important is our first knowledge of the plains fauna (Hypertragulidae and Camelidae) represented respectively by genera believed to be ancestral to the tragulids (*Leptotragulus*) and to the camels (*Protylopus, Camelomeryx);* also members of the oreodonts (*Protoreodon*), and the agriochoerids (*Agriochoerus*). The diminutive tylopod *Protylopus* has been selected as the possible ancestor of the great family of American camels.

The fauna found near the base of the true Uinta thus includes a considerable light-limbed meadow and plains element, transitional to the plains fauna of the lowest Oligocene of the White River group. The occurrence of this fauna near the base of Uinta C indicates that the Uinta formation probably passes up into lower Oligocene time. The beds represent a considerable change in local physiographic conditions from those of Uinta B. The fine-grained soft material, composed of altered eruptives, probably dacite tuffs, is of much the same texture as the characteristic "*Titanotherium* beds" (Chadron formation) of South Dakota, except as to its color, which is brick-red; in fact, a reddish tinge prevails throughout the sediments of Uinta C.

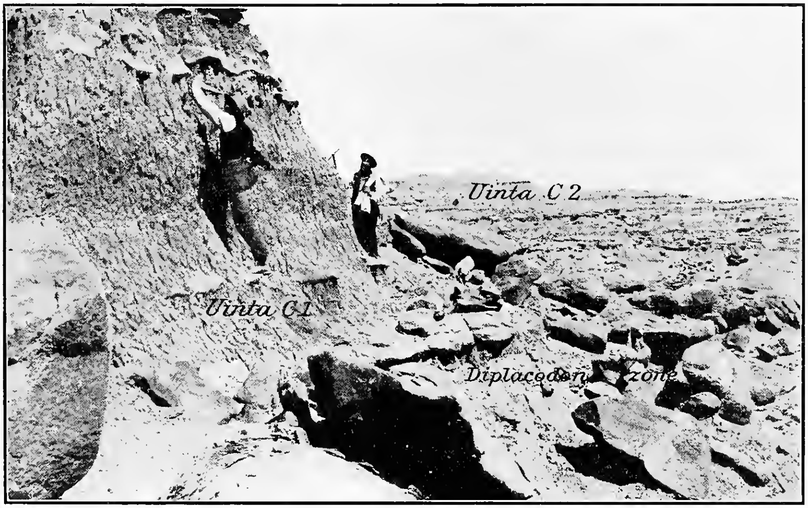


FIGURE 66.—Badlands near the mouth of White River, Uinta Basin, Utah (No. 10, fig. 35)

Wortman and Peterson collecting. This view shows the typical Uinta formation (Uinta C 1) and the *Diplacodon* zone in the foreground, with Uinta C 2 (unfossiliferous) in the distance. After Osborn (1910.346). Am. Mus. negative 17663. Compare Plate XII, *B.*

During this latest part of the Eocene epoch the titanotheres of the Rocky Mountain basin south of the Uinta Mountains distinctly approach in character the titanotheres of the Great Plains. The appearance in this layer and near the summit of Uinta B of two or three entirely new forms of titanotheres (*Eotitanotherium, Diplacodon, Protitanotherium*) is less indicative of new migrations into the Rocky Mountain region than of new physiographic conditions favorable to the fossilization of some of the upland and meadow Herbivora that had been evolving in the adjacent Plains region but had not mingled with the fluviatile, swamp, and forest-border fauna that inhabited the Uinta Basin in Uinta B time.

The following summary of the later Eocene faunas of the Uinta Basin should be examined in connection with Figures 63–66.

Composite section of mammalian faunas of the later Eocene sediments of the Uinta Basin

[After Peterson, Osborn, Riggs, and Douglass]

Section	Titanotheres	Other forms of life
Uinta C (true Uinta formation = Diplacodon zone); 600 feet. Badlands like those of South Dakota, but of brick-red color. Brownish and reddish ferruginous sandstones and clays (Peterson).	Diplacodon elatus, type. Protitanotherium emarginatum. Protitanotherium superbum, type. Telmatherium ultimum, type. Manteoceras uintensis, type.	First oreodonts. Cameloids. Dichobunids. Aquatic rhinoceros (Amynodon). Small perissodactyls (tapiroids, lophiodonts, Epihippus). Last creodonts, Mesonychidae and Oxyaenidae. No amblypods found.
Uinta B 2 (Eobasileus-Dolichorhinus zone); 300–400 feet. Section along gilsonite vein No. 2 (Riggs). Includes "Amynodon sandstone," gray and greenish clays, ferruginous sandstones, bluish and greenish shales. Two red layers with fossiliferous sandstone between (Douglass). Supposed base of horizon B 2.	Eotitanotherium osborni, type. Dolichorhinus cornutus (=hyognathus), type. Dolichorhinus fluminalis, type. Dolichorhinus heterodon, type. Sthenodectes incisivus, type. ?Rhadinorhinus diploconus, type. Dolichorhinus longiceps, type (near base).	Last amblypod (Eobasileus). First cameloid (Protylopus). Last taeniodonts (Stylinodon). Aquatic rhinoceros (Amynodon). Primitive entelodont (Protelotherium uintense). Remains of plants and fishes; occasionally plentiful in sandstone ledges (Peterson). Last primates ("Notharctus"). Giant creodonts, Mesonychidae (Harpagolestes).
Uinta B 1 (Metarhinus zone = upper Metarhinus zone of Riggs); 400 feet. Section on divide between White River Canyon and Coyote Basin (Riggs). Also section 3 miles below mouth of Evacuation Creek (Riggs): "Metarhinus sandstone." "Eobasileus sandstone" = massive ledges of reddish sandstone, alternating with layers of sandy shales. Indurated clays.	Dolichorhinus superior, type. Metarhinus riparius, type. Metarhinus earlei. "Telmatherium," large jaw. Dolichorhinus longiceps. Rhadinorhinus abbotti, type. Metarhinus fluviatilis, type. Dolichorhinus longiceps, skeleton. Metarhinus riparius (from base). Sphenocoelus. Heterotitanops parvus. (=?Metarhinus), from base of B 1.	Giant creodont (Harpagolestes). Crocodiles. Turtles. Giant amblypod (Eobasileus). Light-limbed perissodactyl (Triplopus). Creodonts, Mesonychidae (Mesonyx).
Uinta A (lower A of Peterson, lower Metarhinus zone of Riggs); 500 feet (Riggs); 585 feet (Douglass). Section in north wall of White River Canyon (Riggs): "Columnar sandstones, about 300 feet thick, weathering as bold cliffs, or buttresses along the canyon of White River. Color slightly more grayish than the underlying shales, but brown predominates (Riggs). "Two hundred feet friable sandy shales, weathering in steep slopes, with horizontal outcroppings of nodular or sandy layers, or by massive ledges of limited extent" (Riggs).	None.	No mammals (Peterson, Riggs). Fragments of turtles. Unios. Remains of plants and occasionally large tree trunks in sandstone ledges (Peterson).
Green River (?) formation. Shaly gray sandstone of lacustrine origin.	None.	Remains of plants, fishes, and insects in the shales (Peterson).

SUMMARY OF FAUNAS OF UINTA B AND C

Though the whole later Eocene section of the Uinta is 1,900 feet thick it includes 500 feet of unfossiliferous beds both at its base and at its summit, so that the fossiliferous beds cover only about 900 feet. The stages of evolution are best measured in the successive species of *Dolichorhinus,* which are found both at low and at high levels in the fossiliferous part of the section.

The archaic mammals that play so large a part through lower and middle Eocene time diminish in number and approach extinction at the end of Eocene time. The numerical inferiority of the waning archaic mammals and the rapid increase in the numbers of modernized mammals are indicated in the following table, prepared in 1910:

Transition in mammalian life at end of Eocene time

	Genera	Species
Archaic mammals:		
Amblypoda	2	6
Condylarthra (Hyopsodontidae)	1	2
Creodonta	5	5
	8	13
Modernized mammals:		
Primates	2	?3
Rodentia	1	3
Carnivora (Miacidae)	3	4
Artiodactyla	3	4
Perissodactyla	9	16
	18	30

The Amblypoda culminate in the gigantic *Eobasileus,* which disappears at the end of Uinta B, when the gigantic creodont Mesonychidae and the catlike Oxyaenidae appear for the last time. It is noteworthy that these animals attain their largest size in this, their waning period. The lemuroid primates are found in greatly diminished numbers as compared with those in the Bridger, possibly because the conditions were unfavorable to the fossilization of remains of arboreal animals; in fact, we know nothing of the forest or the arboreal fauna during the entire period of Washakie B and Uinta B because of prevailing fluviatile conditions of deposition.

ADAPTIVE RADIATION OF THE TITANOTHERES IN THE UINTA BASIN

GENERA AND SPECIES REPRESENTED

Through these 650 feet of fossiliferous sediments the titanothere fauna of the Uinta Basin is revealed as extraordinarily large and varied, no less than 11 genera and 22 species having been described. The animals range in size from the small *Metarhinus fluviatilis,* some of which were not so large as a tapir, to the huge *Protitanotherium superbum.*

The titanothere *Metarhinus* is abundant and characteristic in Uinta B 1, ranging from the base to the summit but not extending into Uinta B 2 as here defined. (In previous reports horizon B 2 has been included in Uinta A.) According to Riggs (1912.1, p. 27) the genus includes two phyla—the first comprising the small *Metarhinus fluviatilis* Osborn and *M. riparius* Riggs, with long, narrow skull; the second including the broad-skulled forms *M. earlei* Osborn (which is also found in Washakie B) and *M. cristatus* Riggs. *Metarhinus* was a companion of its long-skulled relative *Dolichorhinus* in and near the rapidly flowing streams, its remains being usually found in coarse and semigravelly sandstones. (Riggs, op. cit., p. 24.) In Uinta B 2 rapid streams, apparently the favorite haunt of *Metarhinus,* were less abundant than in Uinta B 1 (Riggs, op. cit., p. 25), which partly accounts for the apparently sudden disappearance of these animals from the sediments.

Sphenocoelus uintensis, which is also probably from the *Metarhinus* zone (Uinta B 1), is known only from the hinder half of a skull. This strange animal is clearly a member of the *Metarhinus-Dolichorhinus* group and may be closely related to the long-skulled *Metarhinus riparius.* The *Metarhinus* series as a whole is clearly related to the older and more primitive *Mesatirhinus megarhinus* of Washakie A and Bridger C and D, which is also structurally ancestral to *Dolichorhinus.*

The name *Heterotitanops parvus* Peterson has been applied to the skeleton of a very young animal from Uinta B 1. It was found, articulated, in a hard sandstone concretion and lower down in Uinta B 1 than any mammalian remains heretofore described from that horizon. (Peterson, 1914.2.) In the opinion of Gregory the characters of the deciduous dentition and of the facial region of the skull of this animal indicate that it probably represents the newly born young of some of the *Metarhinus-Rhadinorhinus* group.

Rhadinorhinus is distinguished from *Metarhinus* by its tapering nasals and by the reduced infraorbital process of the malar bones. One species, *R. abbotti* Riggs, is found in Uinta B 1, and another, *R. diploconus* Osborn, is recorded from Uinta B 2. Riggs suggests that *Rhadinorhinus* was an upland rather than semiaquatic form. Gregory noted in 1902 that it foreshadows the long-horned titanothere *Megacerops* (*Symborodon*) of the lower Oligocene in the abbreviation of the face and in the characters of the dentition.

The long-skulled *Dolichorhinus* is represented by two species in Uinta B 1 (one of which, *D. longiceps* Douglass, extends into the base of Uinta B 2) and by four species in Uinta B 2. The most primitive species, *D. superior,* is in general intermediate in structure between the ancestral *Mesatirhinus* and the later species of *Dolichorhinus.* The most advanced species, *D. fluminalis* Riggs, is from the upper levels of Uinta

B 2. The allied *D. cornutus* is believed to be specifically identical with *D. hyognathus* of Washakie B. In Uinta B 1 remains of *Dolichorhinus*, as noted by Riggs, are frequently found associated with those of *Metarhinus* in coarse pebbly sandstone laid down in rapid streams; but in Uinta B 2 they are frequently found in lenticular sandstones, which were apparently deposited in quiet water, for they show little evidence of water currents, and which yield skulls associated with mandibles and parts of skeletons. Riggs accordingly infers that *Dolichorhinus* inhabited the low grounds near quiet waters rather than the swift currents preferred by *Metarhinus*.

Contrasting with the elongate and straight-sided skull of *Dolichorhinus* is the broad, robust skull of *Sthenodectes incisivus* (Douglass), a titanothere with exceptionally massive incisor and canine teeth and broad, low-crowned upper molars. The type skull was found by Douglass in a thick deposit of sandstone and small gravel, evidently of stream origin, near the middle of Uinta B 2, whereas Riggs's specimen was found in lenticular sandstones at about the same level. *Sthenodectes* shares many characters in common with the Bridger genera *Manteoceras* and *Telmatherium* and appears to be an advanced member of that macrodont group.

With the possible exception of *Rhadinorhinus* all the titanotheres so far noted from Uinta B 1 and B 2 belonged to aberrantly specialized side lines, which are not found in later formations and apparently became extinct.

One titanothere recorded from near the summit of Uinta B 2, namely, *Eotitanotherium osborni* Peterson (1914.1; 1914.4), is highly progressive toward the giant plains-living types of the uppermost Eocene (Uinta C) and of the lower Oligocene. This animal, represented by parts of two skeletons in the Carnegie Museum, surpasses even *Protitanotherium* of Uinta C in the development of a pair of large oval bony protuberances above the eyes. One of the most remarkable features of *Eotitanotherium* is the progressive submolariform character of its third and fourth upper molars, which are, indeed, slightly more advanced in type than those of certain lower Oligocene titanotheres. The animal was about as large as a rhinoceros, and throughout the skeleton are mingled the earlier characters of its Eocene predecessors with progressive, plains-living adaptations prophetic of some of the Oligocene titanotheres, especially those of the menodontine group.

The titanothere fauna of the true Uinta (Uinta C), though less extensive in genera and species than that of Uinta B 1 and B 2, is none the less of prime importance to the historian of the family. Thus the titanotheres of the true Uinta include, first, certain conservative phyla (*Manteoceras*, *Telmatherium*), which represent the little-altered descendants of genera either of Uinta B 1 and B 2 or of Washakie and Bridger types; second, two very progressive and different phyla, *Diplacodon* and *Protitanotherium*, of uncertain relationships, which appear to be immigrants from other localities.

ADAPTIVE RADIATION OF PHYLA

There seem to be at least four contemporary phyla, representing wide local adaptive radiation:

First, the robust, short-limbed forms, one of which, *Manteoceras uintensis* Douglass, found in gray sandstone in the red beds of the lower portion of Uinta C, is considerably larger than the more primitive species of *Manteoceras* in the upper Bridger and Washakie A but is little modified otherwise. Its horn swellings, if developed at all, were not large, and it is strongly macrodont in type, like *Telmatherium* and *Sthenodectes*.

Second, the long-limbed, long-headed, relatively hornless *Telmatherium*, which is distinguished especially by its deep malar bones and the high sagittal crest and is represented in Uinta C by the great *Telmatherium ultimum* and the gigantic *T. altidens*. *T. ultimum* is practically hornless, having only the slightest rugosity at the naso-frontal junction in the type skull. Accordingly the species *Manteoceras uintensis* and *Telmatherium ultimum* and the genus *Sthenodectes*, while advancing in the direction of the Oligocene type in various characters, are apparently excluded from direct ancestry to the later types by certain specializations, such as marked enlargement of the incisors and canines, and by the lack of development of effective horn swellings.

Third, *Diplacodon elatus* Marsh of Uinta C, a progressive titanothere, which is known chiefly from the upper dentition and takes its generic name from its submolariform third and fourth premolars. The precise relations of this animal are still in doubt. The premolars and molars may have been derived from the type represented by *Rhadinorhinus diploconus* of Uinta B 2, which is the only one of the older titanotheres that has the dentition and skull at all like those of *Diplacodon*. In other respects the *Diplacodon* dentition suggests that of the lower Oligocene titanothere *Menodus trigonoceras*, and in still another respect it resembles that of *Eotitanotherium* of Uinta B 2, though it differs from that genus in the more molariform condition of the third upper molar.

Fourth, *Protitanotherium emarginatum* Hatcher, which is known from the facial part of the skull and the lower jaw of the type specimen. It is a large animal, which, so far as known, approaches the Oligocene type of *Brontops*. It has oval horn swellings which are less protruding than those of the type of *Eotitanotherium*; its nasals are wide distally, in contrast to the tapering nasals of *Eotitanotherium*; its canines are very stout and acutely conical; its stout upper incisors form a flattened arch. Altogether it seems to represent a phylum distinct from *Eotitano-*

therium and of doubtful relationship both to earlier or to later titanotheres, although it was possibly derived from *Manteoceras*. Of the same phylum is *Protitanotherium superbum*, a gigantic animal, with a jaw 24 inches long and premolars and molars of very progressive type. It is much larger than the smaller titanotheres of the lower Oligocene.

Another titanothere of uncertain relationship is *Brachydiastematherium* from Transylvania, eastern Hungary (now Rumania). The geologic age of this animal is not certain, but it is in an upper Eocene stage of evolution as compared with the titanotheres of America.

FAUNA UNREPRESENTED

The sequence of titanothere species in the Uinta Basin illustrates the vagaries of the fossil records of the Rocky Mountain basin region caused by local physiographic changes; each kind of sedimentation exhibits only a part of the fauna. For the entire period covered by the lower sediments of the Uinta Basin little or no knowledge of the small terrestrial fauna has come to light, none of the arboreal fauna, and none of the plains and upland fauna, in contrast with the surprisingly extensive knowledge of the fluviatile and the swamp-dwelling fauna. Gradually conditions changed, and Uinta B 2, as we ascend, affords an increasing knowledge of the cursorial meadow fauna; but it is not until Uinta C (true Uinta) that local conditions became favorable to the preservation and fossilization of the small cursorial mammals of the artiodactyl and perissodactyl divisions of the ungulates. The sudden appearance of these animals might be attributed to immigration, but it is equally probable that they were all evolving in the same region or in the adjacent Plains region. Thus the data do not necessarily suggest immigration or migration; these animals may have been brought into the field of observation by changing conditions of fossilization. The manner in which these numerous phyla of titanotheres enter this field is shown in the following table:

Geologic and geographic range of phyla (here "subfamilies" and certain genera) of titanotheres

[Showing their successive immigration from the north and their evolution in their new habitat. The earliest immigrants are those named at the bottom of the first column; the later immigrants are named in order from bottom to top. The difference in the length of the black bars has no significance]

Phylum	Wind River B[a] ("Lost Cabin") (middle Eocene)	Bridger (upper middle Eocene)					Washakie (upper Eocene)		Uinta (uppermost Eocene)			Chadron (Oligocene)		
		A[b]	B	C[c]	D[c]	E	A[d]	B	A	B[e]	C	A	B	C
Brontotheriinae												■	■	■
Megaceropinae													■	■
Menodontinae												■	■	■
Allops												■	■	■
Diploclonus												■	■	■
Brontopinae												■	■	■
Diplacodontinae[f]										■	■			
Sthenodectes										■				
Rhadinorhininae										■				
Metarhinus								■		■				
Dolichorhininae				■	■		■	■		■				
Manteoceratinae				■	■		■				■			
Telmatheriinae				■	■		■				■			
Palaeosyopinae			■	■	■		■							
Eotitanopinae	■													
Lambdotheriinae	■													

[a] Wind River B=Huerfano A.
[b] Bridger A=Huerfano B.
[c] Bridger C and D=Washakie A.
[d] Washakie A=Bridger C and D.
[e] Uinta B=Washakie B.
[f] Diplacodon, Eotitanotherium, Protitanotherium.

ZONE 16: THEORETIC UINTA C 2

Titanotheres have thus far been determined from only the lower 100 feet of Uinta C. They are at present only partly known. When fully known we shall probably find close generic if not specific correlation between the upper fauna (now unknown) of Uinta C and the fauna of the lower levels (Chadron A) of the White River group. The passage from Eocene to Oligocene time probably occurs within the period of Uinta C (true Uinta) deposition. Scott is disposed to put all of Uinta C in the Oligocene.

COMPOSITE EOCENE AND LOWER OLIGOCENE SECTION AT BEAVER DIVIDE, WIND RIVER BASIN, WYO.

Most of the Oligocene sediments in the Rocky Mountain basin region have been eroded away. The only locality where fossil-bearing lower Oligocene sediments still overlie those of the upper Eocene is on the southern border of the Wind River Basin, Wyo., where the true *Titanotherium* zone overlies sediments containing a fauna similar to that of the *Diplacodon* zone (Uinta C). The geologic section observed at this point by the American Museum expedition of 1909 under Granger and N. H. Brown, who discovered this fauna in 1908, is as follows:

	Feet
Summit of lower Oligocene, *Oreodon* zone=Brule formation	540
Base of lower Oligocene, *Titanotherium* zone=Chadron formation	
Upper Eocene, *Diplacodon* zone=Uinta(?) formation	90
Middle Eocene (?), unfossiliferous=Bridger (?) formation	185
Lower Eocene, *Lambdotherium* zone=upper part of Wind River formation	265

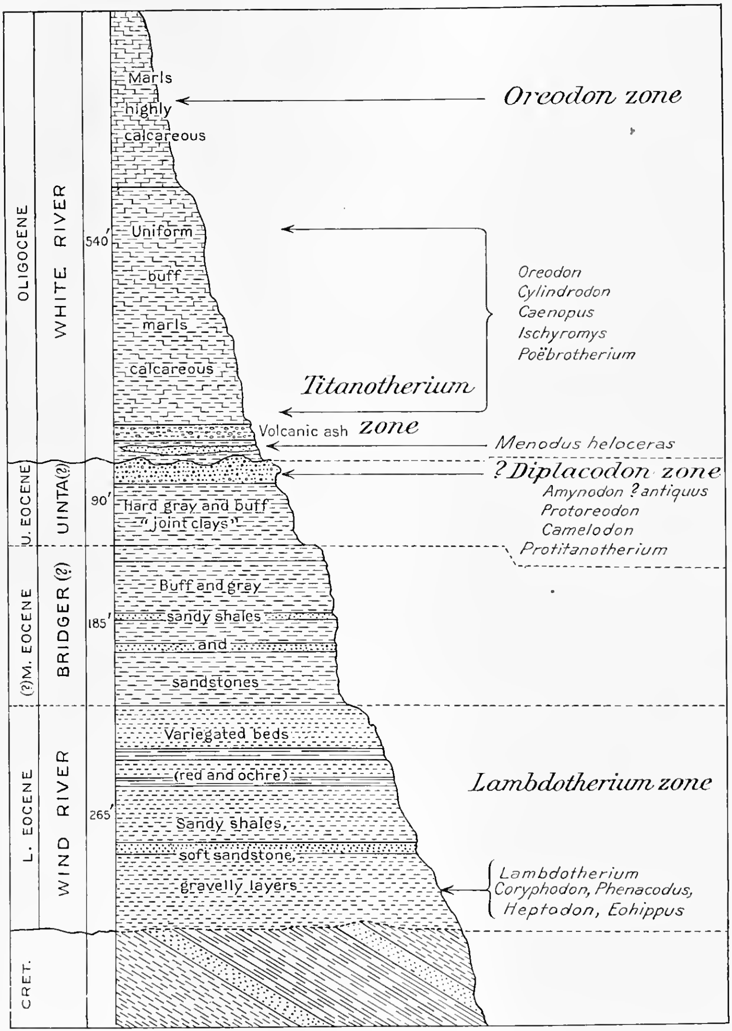


FIGURE 67.—Diagrammatic section of deposits at Green Cove, Beaver Divide, Wyo. (No. 6, fig. 35), from the *Lambdotherium* zone (Wind River) to the *Oreodon* zone (White River) at the summit

Chiefly after Granger (1910.1).

A single tooth of either *Diplacodon* or *Protitanotherium* has been found at Beaver Divide, Wyo. The correlation with Uinta C rests upon *Camelodon arapahovius* Granger, a species somewhat more progressive than *Protylopus* of Uinta C and somewhat more simple than *Leptotragulus*, characteristics that combine to place it among ancestral camels, in the Camelidae. In certain characters it agrees with *Leptotragulus profectus* of the *Titanotherium* zone of Pipestone Springs, Mont. The *Amynodon* found here agrees with the species *A. antiquus*, originally determined in Washakie B (=Uinta B). Two specimens of *Protoreodon* are referable to *P. parvus*, from the base of Uinta C or the summit of Uinta B.

Above this *Diplacodon*(?) level is a very marked erosional unconformity between the upper Eocene and the lower Oligocene; broad, shallow valleys (Sinclair and Granger, 1911.1, p. 99), indicating fairly mature topography, were excavated in the sediments of the *Diplacodon*(?) zone. After these valleys were cut the first deposits laid down were fine-grained buff-colored tuffaceous shales. In this tuff the American Museum exploring party of 1909 found a skull of *Menodus heloceras*, which belongs to the lower level of the *Titanotherium* zone, corresponding with Chadron A.

The volcanic ash comprising the sediments of the Oreodon titanothere zone, a few feet thick, is covered with a mud flow of volcanic material 46 feet thick, above which lies 540 feet of fine, wind-blown buff ash and dust. No clays have been found at this middle Oligocene horizon, which corresponds in age with the Brule formation of the White River group—only wind-laid ash and coarse gravel, perhaps deposited by torrents during occasional heavy rains. None of these sediments appear to have been much disturbed by water, and Sinclair and Granger (1911.1, p. 114) are inclined to believe that they accumulated under a drier climate than that which prevailed in Eocene time. These upper sediments contain a true *Oreodon* zone fauna.

FOURTH FAUNAL PHASE (LOWER OLIGOCENE)

LOWER OLIGOCENE MAMMALS

CORRELATION OF EUROPEAN AND AMERICAN FORMS

The lower Oligocene mammals represented by the fossils thus far discovered are listed below.

Peculiar to Europe:
- Paleotheres.
- Anoplotheres.
- Cenotheres.
- Gelocids.
- Amphicyonids.
- Viverrids.
- Cricetines (hamsters).
- Theridomyids.
- Sirenians (Halitherium).
- (Horses not recorded.)

Common to Europe and North America:
- Titanotheres (central Europe).
- Chalicotheres.
- Rhinoceroses (aceratheres and diceratheres).
- Amynodonts.
- Anthracotheres.
- Suillines.
- Entelodonts.
- Opossums.
- Hyaenodonts.
- Canids (dogs).
- Mustelids (martens).
- Machaerodonts (saber-tooth cats).

Peculiar to North America:
- Horses.
- Hyracodonts (rhinoceroses).
- Oreodonts.
- Camelids.
- Hypertragulids.
- Leptictids.
- Chrysochlorids? (insectivores).
- Ischyromyids (rodents).
- Leporids (hares).

ZONE 17: TITANOTHERIUM-MESOHIPPUS ZONE

[Chadron A, B, and C; Sannoisian of Europe]

The forms that constituted this rich world of lower Oligocene mammalian life were distributed through the Rocky Mountain basin region, but the sediments that contained the fossils have been eroded away except in a few isolated areas, such as those along Pipestone Creek, Mont.; at Beaver Divide, Wyo., south of the Wind River Basin; and at Bates Hole, Wyo. The areas in which these sediments were deposited lie east of the Rocky Mountains, in Saskatchewan, North Dakota, South Dakota, and Colorado. The chief fossil-bearing sediments exposed are in the localities shown below.

Recorded thickness of the Titanotherium zone in thirteen exposures of lower Oligocene deposits

	Feet
1. Cypress Hills, Saskatchewan (Lambe, 1908)	50–500
2. Pipestone Creek, Jefferson County, Mont. (Douglass, 1903)	300+
3. White Butte, N. Dak. (Douglass, 1903)	120
4. Big Badlands, S. Dak. (Hatcher, Darton) (typical area of *Titanotherium* zone)	180
5. Goshen Hole (Scotts Bluff), southeastern Wyoming (Darton), maximum thickness	200
6. Hat Creek, South Fork, Cheyenne River, Dawes County, Nebr.	100±

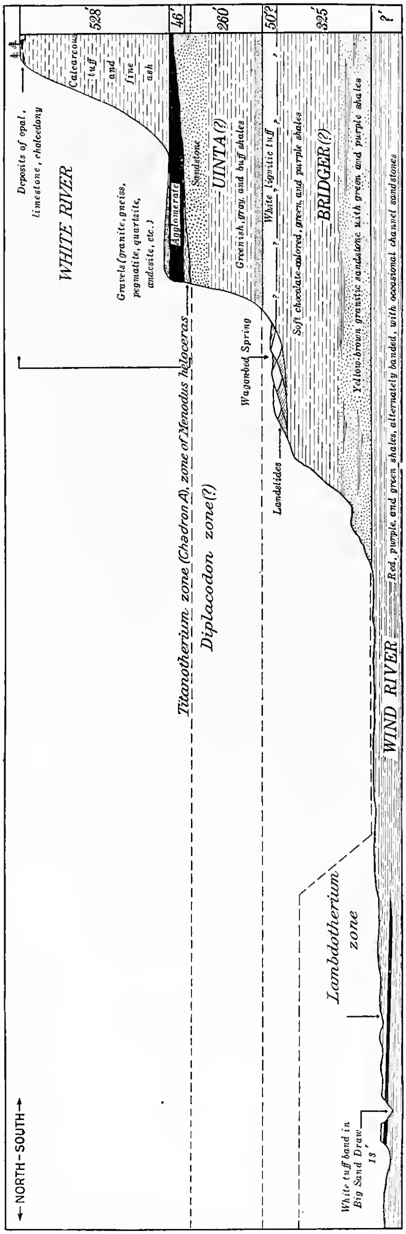


FIGURE 68.—Diagrammatic section across the Wind River Basin, Wyo., from Hudson to the top of Beaver Divide (No. 6, fig. 35) at Wagonbed Spring

Section from top of Wind River formation to top of lignitic tuff measured half a mile north of Wagonbed Spring; section from top of tuff to top of White River measured half a mile south of spring. Chiefly after Sinclair and Granger (1911.) Horizontally not drawn to scale.

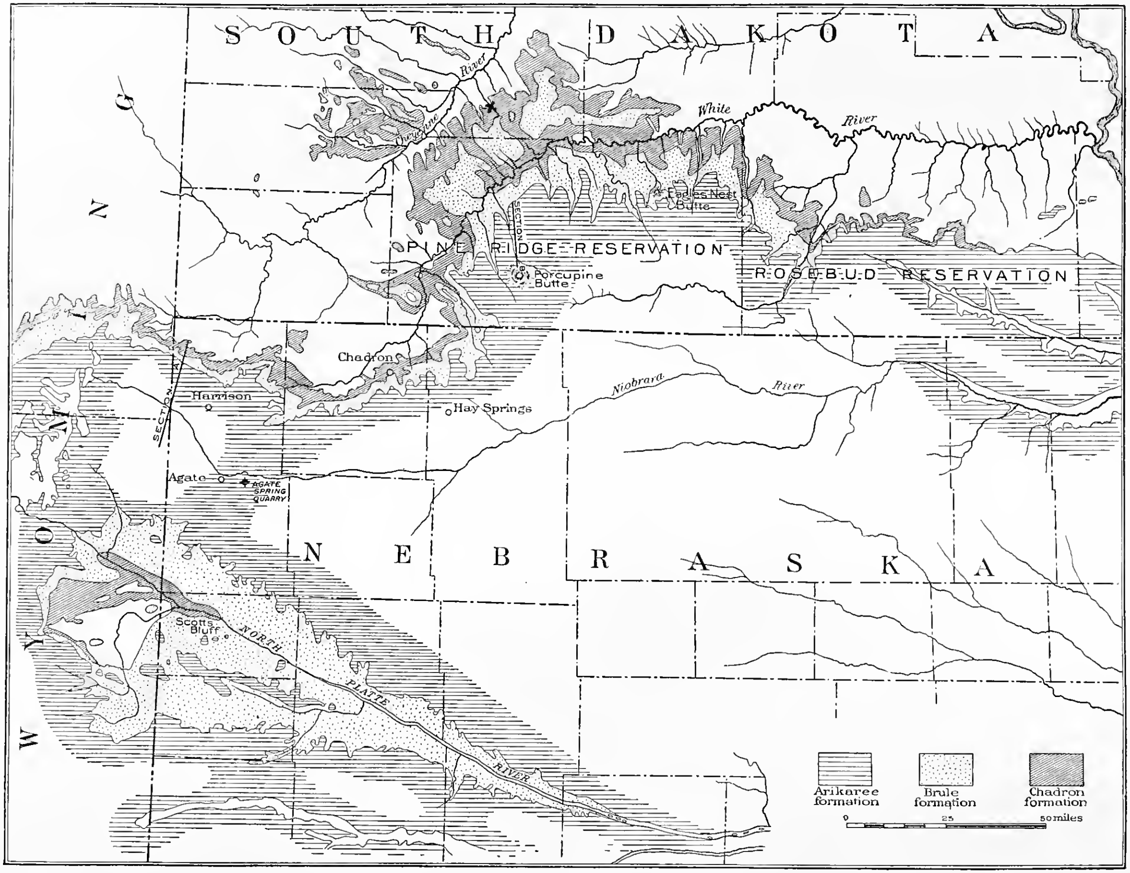


FIGURE 69.—Map showing exposures originally described as the "White River group" by Meek and Hayden (1862.1), as surveyed from Hayden's camp (×) on Bear Creek, Cheyenne River, S. Dak.

After Darton's survey of 1905, supplemented by observations of Matthew and Thomson (1906–1907). Modified from United States Geological Survey Bulletin 361, 1909, Pl. II. (Osborn and Matthew, 1909.321.) Areas greatly extended by subsequent exploration are divided into the Chadron and Brule formations of the Oligocene and the Arikaree formation of the lower Miocene. Later usage has restricted the term White River group to the beds of Oligocene age (Chadron and Brule formations).

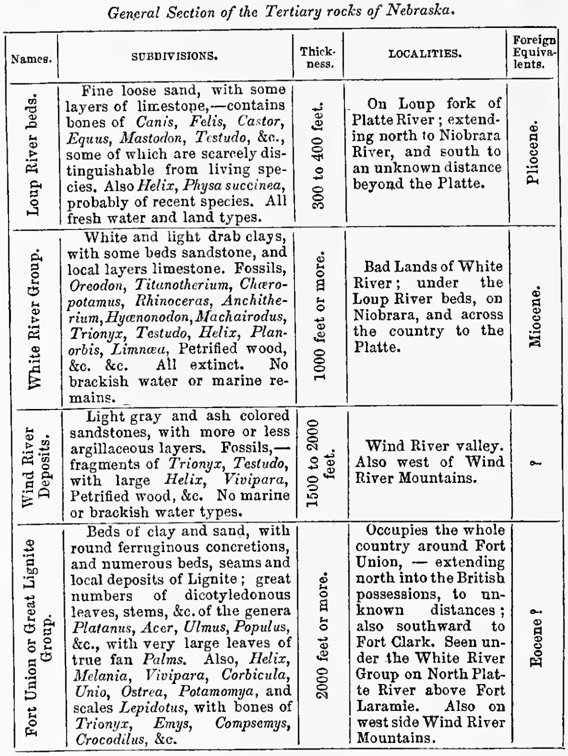
	Feet
7. Near Dickinson, S. Dak. (Douglass)	40–50
8. Pine Ridge, S. Dak. (Darton)	30–60
9. Beaver Divide, Wyo. (Granger)	46
10. Bates Hole, Natrona County, Wyo	(?)
11. Adelia, Sioux County, Nebr. (Darton), about	80
12. Between Platte River and Arkansas River drainage (Darton). ("Monument Creek group" of Hayden; Castle Rock conglomerate of Richardson, 1912.1)	300
13. Horsetail Creek, northeastern Colorado (Matthew, 1901.1), not over	100

The deposits at these localities, some of them indicated on the accompanying map, represent only the exposed parts of the lower Oligocene deposits of the great flood-plain system now known as the Chadron and correlated formations, the larger part of which is covered by the Brule and Arikaree formations. This flood plain extends 325 miles north and south and 300 miles east and west. We do not know whether it was wholly continuous. Such an area would embrace 97,500 square miles, which would not exceed the present Andean flood plains.

At the base of these sediments in South Dakota and northern Colorado there are abundant remains of titanotheres, certain of which are in stages of evolution no more advanced than those found at the base of Uinta C, *Diplacodon* zone. Consequently the faunistic relation between the titanotheres living in the mountain basins and those living on the Plains remains to be solved by future discovery. This relation may be revealed in the "missing" faunal zone. At present we may divide the life zones, in descending order, as follows:

17. *Titanotherium* zone:
    - Chadron C, levels 3, 2, 1:
        - Brontops robustus.
        - Menodus giganteus.
        - Brontotherium platyceras.
    - Chadron B:
        - Brontops dispar.
        - Menodus trigonoceras.
        - Brontotherium hatcheri.
    - Chadron A, levels 1, 2, 3:
        - Brontops brachycephalus.
        - Menodus heloceras.
        - Brontotherium leidyi.
16. Theoretic zone of Uinta C (upper levels, or Uinta C 2): Unknown or "missing."
15. *Diplacodon* zone of Uinta C (lower levels, or Uinta C 1):
    - Protitanotherium emarginatum.
    - P. superbum.
    - Diplacodon elatus.

It is very important to recall the fact that titanotheres have thus far been determined from only the lower 100 feet of Uinta C, that they are only partly known, and that when fully known we shall probably find a close generic if not specific correlation between the upper fauna (now unknown) of Uinta C and the fauna of the lower levels (Chadron A) of the White River group. The passage from Eocene to Oligocene time probably occurs within the period of deposition of Uinta C. Scott is disposed to put all of Uinta C in the Oligocene.



General Section of the Tertiary rocks of Nebraska.

Names.	SUBDIVISIONS.	Thickness.	LOCALITIES.	Foreign Equivalents.
Loup River beds.	Fine loose sand, with some layers of limestone,—contains bones of *Canis*, *Felis*, *Castor*, *Equus*, *Mastodon*, *Testudo*, &c., some of which are scarcely distinguishable from living species. Also *Helix*, *Physa succinea*, probably of recent species. All fresh water and land types.	300 to 400 feet.	On Loup fork of Platte River; extending north to Niobrara River, and south to an unknown distance beyond the Platte.	Pliocene.
White River Group.	White and light drab clays, with some beds sandstone, and local layers limestone. Fossils, *Oreodon*, *Titanotherium*, *Chœropotamus*, *Rhinoceras*, *Anchitherium*, *Hyænonodon*, *Machairodus*, *Trionyx*, *Testudo*, *Helix*, *Planorbis*, *Limnæa*, Petrified wood, &c. &c. All extinct. No brackish water or marine remains.	1000 feet or more.	Bad Lands of White River; under the Loup River beds, on Niobrara, and across the country to the Platte.	Miocene.
Wind River Deposits.	Light gray and ash colored sandstones, with more or less argillaceous layers. Fossils,—fragments of *Trionyx*, *Testudo*, with large *Helix*, *Vivipara*, Petrified wood, &c. No marine or brackish water types.	1500 to 2000 feet.	Wind River valley. Also west of Wind River Mountains.	?
Fort Union or Great Lignite Group.	Beds of clay and sand, with round ferruginous concretions, and numerous beds, seams and local deposits of Lignite; great numbers of dicotyledonous leaves, stems, &c. of the genera *Platanus*, *Acer*, *Ulmus*, *Populus*, &c., with very large leaves of true fan *Palms*. Also, *Helix*, *Melania*, *Vivipara*, *Corbicula*, *Unio*, *Ostrea*, *Potamomya*, and scales *Lepidotus*, with bones of *Trionyx*, *Emys*, *Compsemys*, *Crocodilus*, &c.	2000 feet or more.	Occupies the whole country around Fort Union, — extending north into the British possessions, to unknown distances; also southward to Fort Clark. Seen under the White River Group on North Platte River above Fort Laramie. Also on west side Wind River Mountains.	Eocene?

FIGURE 70.—Facsimile of the Meek and Hayden Tertiary section of 1862, showing original definitions of White River group and Wind River formation

The deposits are now known to include the following:

"Loup River beds" (lower Pleistocene fauna listed). The area includes deposits of the Pliocene and Miocene (Ogalalla formation of Darton).

"White River group," including lower Miocene (Arikaree formation of Darton) and Oligocene (Brule and Chadron formations of Darton). The "*Choeropotamus*" is *Ancodus americanus*, the ancodont of the Chadron formation (*Titanotherium* zone).

"Wind River deposits" (summit of the lower Eocene).

"Fort Union or Great Lignite group" (basal Eocene).

OLIGOCENE FLOOD-PLAIN SEDIMENTATION IN THE WESTERN GREAT PLAINS REGION

CONDITIONS OF DEPOSITION

A very long period of extremely slow sedimentation, east of the Rocky Mountains of Wyoming and Colorado, began in lower Oligocene time and extended without interruption to lower Miocene time, laying down the great deposits originally described as the White River group by Meek and Hayden (1862.1, p. 433) in the following language:

White River group * * * White and light drab clays, with some beds sandstone, and local layers limestone. Fossils: *Oreodon, Titanotherium, Chocropotamus, Rhinoceros, Anchitherium, Hyaenodon, Machairodus, Trionyx, Testudo, Helix, Planorbis, Limnaea,* petrified wood, &c., &c. All extinct. No brackish-water or marine remains * * * 1,000 feet or more * * * Badlands of White River; under the Loup River beds, on Niobrara, and across the country to the Platte. * * * Miocene.

This original definition appears to include all that has been determined subsequently and mapped by the United States Geological Survey (Darton, 1905) under three formations, namely, Chadron, Brule, and Arikaree, as shown in the accompanying illustration (fig. 69). Meek and Hayden did not, however, specifically define the upper limit of their White River group, and all the fossils listed by them as characteristic of the White River group apparently came from beds now classified as Oligocene. The name White River group has therefore for years been restricted to the beds of Oligocene age (Brule and Chadron formations).

This great flood-plain deposition was preceded by a long period of erosion in Eocene time. No sediments of Wasatch, Bridger, or Uinta age have been found on the Plains east of the Front Range of the Rocky Mountains, except in a small area of Huerfano sediment which lies within a mountain basin farther east. This fact is significant. It would appear, as stated at the beginning of this chapter, that sedimentation in this region was suspended after Denver, Lance, and Fort Union time. The Eocene gradients were so high that there were long periods of erosion, during which large areas of Upper Cretaceous beds were laid bare in the region that now includes North and South Dakota, western Nebraska, and Colorado, so that the lowest Oligocene sediments of the White River group, composing the *Titanotherium* zone (Chadron A), lie in gentle valleys of ancient formation that range in age from the Algonkian to the Denver formation and Dawson arkose. In Hayden's typical locality of the White River group—the Mauvaises Terres of early explorers—the Big Badlands between the Cheyenne and the White River of South Dakota—the underlying beds are composed entirely of the Pierre (Upper Cretaceous). At some places (Loomis, 1904.1, p. 432) the rivers depositing the *Titanotherium*-bearing beds washed out along their banks masses of the Pierre shale that contained characteristic Pierre fossils—*Baculites* and the bones of Cretaceous reptiles—and redeposited them in Oligocene sediments. On this level, the gently undulating surface of the Pierre, east of the Rocky Mountains and the Black Hills, meandered broad, sluggish streams, whose chan-

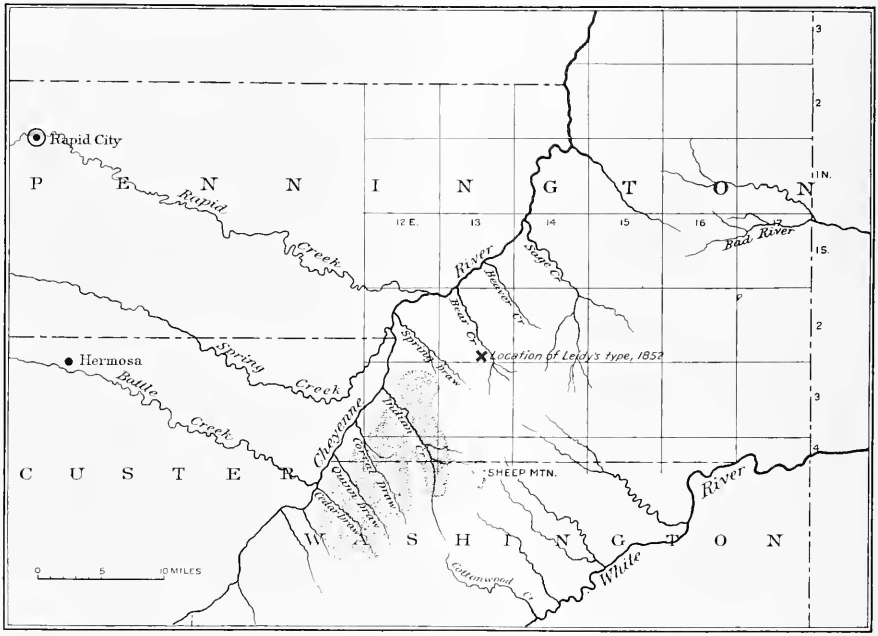


FIGURE 71.—Map showing tributaries of Cheyenne River, S. Dak., from the southeast and the type locality (X) of the "*Titanotherium* beds" of Hayden (Chadron formation), on Bear Creek; also principal collecting ground of Hatcher (dotted area), the chief fossiliferous area in the Big Badlands

nels ranged in width from a few hundred feet to half a mile. Beside these stream channels there were lagoons and areas of back water, some of them spreading into shallow lakes but none into vast sheets of fresh water. Savannas were interspersed with grass-covered pampas traversed by wide, meandering rivers that frequently changed their course. In these channels were deposited conglomerates and river sandstones, marked by cross-bedding, as well as calcareous grits In the shallow lagoons and back waters were deposited the fine clays and layers of fuller's earth. The deposits of gypsum represent periods of evaporation. In the lower part of the *Titanotherium* zone the deposits consist chiefly of fine flood-plain or overflow sediments interspersed with river sandstones and conglomerates, perhaps locally lacustrine, and occasional layers of volcanic ash.

This theory that the deposits of the western Great Plains region are of flood-plain and fluviatile origin has gradually replaced the older lacustrine theory that they were laid down in great fresh-water lakes. The lacustrine theory originated with Hayden, who, in his geologic introduction to Leidy's memoir of 1869 (1869.1, p. 18), observes: "One of the most interesting features in regard to this great fresh-water lake is the evidence of its growth from a germ, as it were, until it spread over the great area on which it has left its traces by the deposition of its peculiar sediments. * * * The basin-like character of this formation is most admirably shown." In the same memoir, Leidy (1869.1, p. 25) expressed some doubt as to the lacustrine theory, observing: "It is a remarkable circumstance that among the large quantity of fossil bones brought from the Mauvaises Terres and submitted to the examination of the author, certainly amounting to several tons in weight, there was detected no trace of remains of birds or fishes; and the same may be said of reptiles, except one species of turtle."

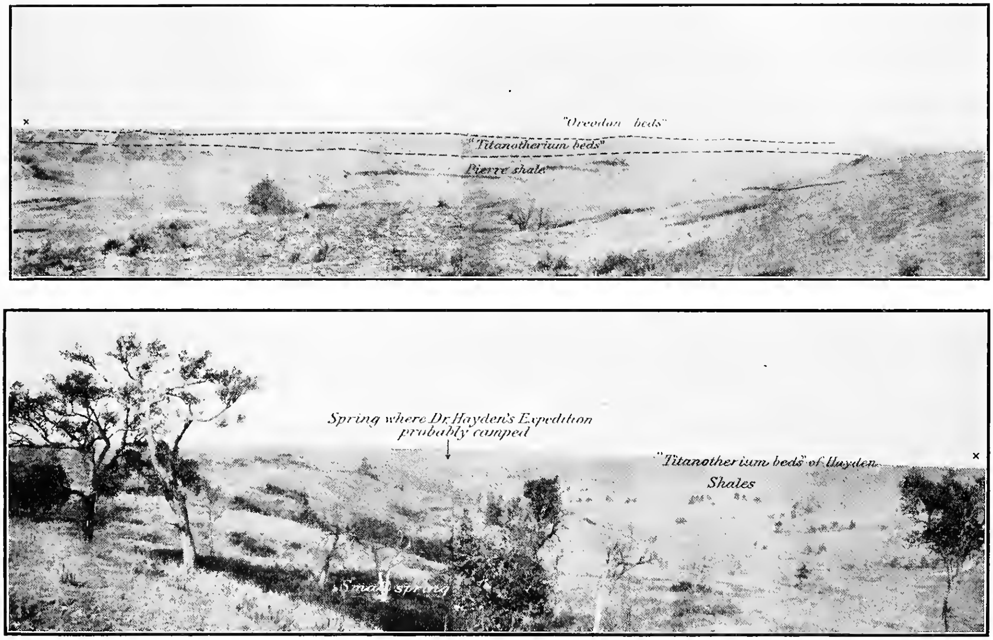


FIGURE 72.—Type locality of the "*Titanotherium* beds" of Hayden, on Bear Creek, S. Dak.

Panoramic view, connecting at X. Upper section, looking southeastward, up Bear Creek; lower section, looking northwestward, down Bear Creek. Am. Mus. negatives 104722–104726.

The lake-basin theory was generally adopted by geologists and paleontologists, reaching its apex in King's development of the lake theory both for the Plains and the mountain region. Johnson (1901.1), Gilbert (1896.1), Haworth (1897.1), and especially Davis (1900.1) reviewed the whole subject broadly in a critical way, developing the theory of fluviatile and flood-plain origin. Fraas (1901.1), Hatcher (1902.3), and more recently Darton (1905.2) set forth strong evidence for the theory of deposition in river channels, flood plains, back waters, lagoons, and shallow lakes. Among paleontologists Matthew (1899.2; 1901.1) was the first to attack the lacustrine theory of the origin of the Brule clay of the White River group and to advance reasons for believing that the sandstones were formed by river and flood-plain sedimentation and the clays in part by back water and lagoon and chiefly by eolian sedimentation. His paleontologic analysis showed that the fine Brule clays contain chiefly terrestrial and plains animals, whereas the river-channel sandstones that traverse these clays, although contemporaneous, contain chiefly forest and fluviatile animals.

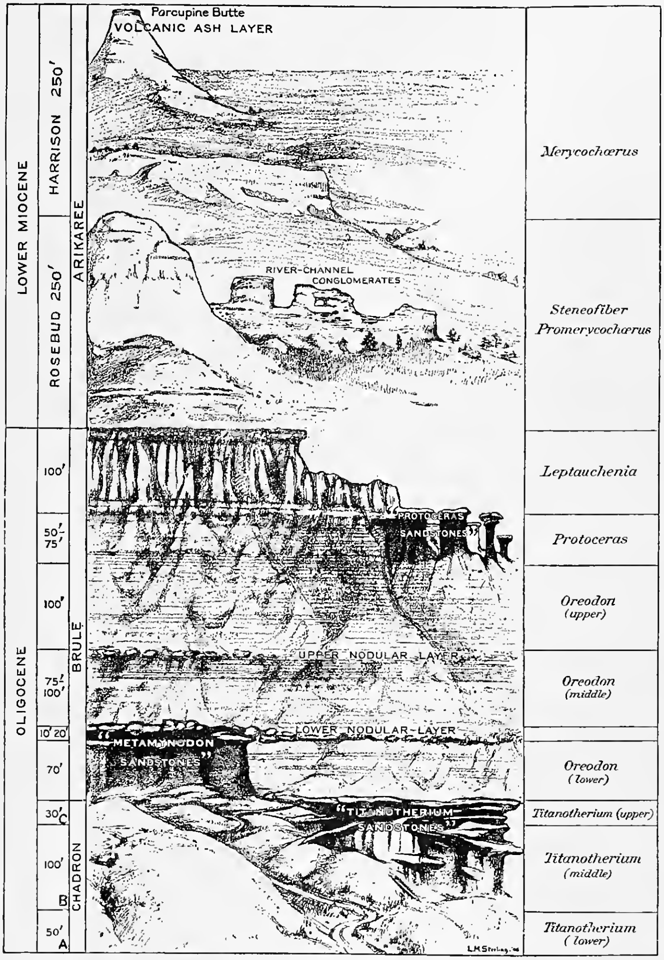


FIGURE 73.—Panoramic section of the Big Badlands of South Dakota

Modified from United States Geological Survey Bulletin 361, Pl. III. (Osborn and Matthew, 1909.321.) View southeastward from Cheyenne River, along line indicated on Figure 69, toward Porcupine Butte, across the Chadron, Brule, and Arikaree formations. This section illustrates the intrusion of river-channel deposits (the "*Titanotherium* sandstones," "*Metamynodon* sandstones," and "*Protoceras* sandstones") and river-channel conglomerates in "clays" of the *Titanotherium* and *Oreodon* zones. It shows also the characteristic erosion forms of these different layers. (See map forming fig. 69, vicinity of section B.)

The Testudinata as analyzed by Hay (1908.1) furnish evidence that during lower Oligocene time the Great Plains region was prevailingly dry land. In the sediments of the White River group there occur eight species of the Testudinidae, including one of the land tortoises, *Stylemys*, and one species of *Testudo*. *Testudo brontops* Marsh occurs in the *Titanotherium* zone (Chadron formation) and is generally found in the White River deposits of Colorado. Of water-living forms the White River group of South Dakota has furnished one species of small turtles related to the Chelydridae and now confined to Central America. In 1904 Loomis (1904.1) advocated the flood-plain origin of the "*Titanotherium* beds" and described two new river-living reptiles—*Chrysemys*, similar to the *Emys lativertebralis* Cope of the Wasatch; and *Alligator prenasalis* (Loomis), recently found by Loomis in the beds of Indian Draw, the first appearance of this genus in the Tertiary.

The nature of the sandstone or the clay in which their remains are found makes it impossible to separate the mammals of the Chadron formation (*Titanotherium* zone) into plains-dwelling and river-dwelling forms, because during floods both were swept into the streams, the skeletons being dissociated and the skulls and jaws separated. Doubtless also the remains of decaying carcasses were pulled apart by crocodiles and garpikes. Only three complete skeletons with skulls have been found intact, namely, the famous *Brontops robustus* of the Yale Museum, the *Brontops robustus* of the American Museum, and the *Menodus trigonoceras* of the Munich Museum. "For every even approximately complete skeleton," observes Hatcher (1902.3, p. 124), "there are scores of isolated skulls and other bones. Taking *Titanotherium* as an example, I have myself collected nearly 200 skulls of this animal, while the number of fairly complete skeletons at present known may be counted on the fingers of one hand."

SOUTH DAKOTA IN TITANOTHERIUM TIME

The best description of the conditions in the South Dakota region while it was inhabited by titanotheres is that given by Hatcher (1902.3, pp. 125–127), based on his own keen observations, which extended over many years of arduous exploration for remains of titanotheres:

The distribution, state of preservation, nature, and character of the animal and plant remains found in the clays and sandstones, as well as the distribution of the latter, absolutely preclude the possibility of their having been deposited in a vast lake and favor the presence of streams meandering through low, broad, level, open or wooded valleys subjected in part at least to frequent inundations, conditions very similar to those at present prevailing in the interior of South America, about the headwaters of the Orinoco, the Amazon, and the Paraguay and Parana Rivers.

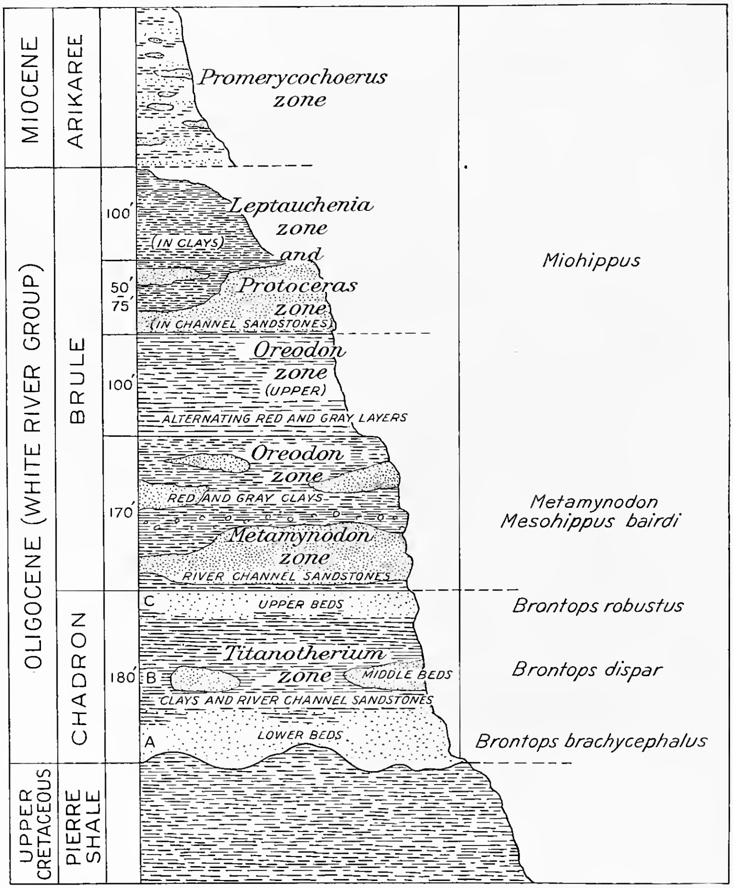


FIGURE 74.—Section of the Big Badlands of South Dakota showing the chief faunal zones of the Oligocene (White River group, No. 11, fig. 35) and the Miocene

The Chadron formation (*Titanotherium* zone) is shown as determined by the surveys of Hatcher; the divisions of the Brule formation (*Oreodon* and *Leptauchenia* zones) were first established by Wortman's observations; above is the Arikaree formation of Darton (*Promerycochoerus* zone).

Now it is evident that if such conditions prevailed in this region during the deposition of the White River beds there should remain certain evidences concerning it, such as filled-in river channels and small lagoons with their characteristic deposits and remains of the animal and vegetable life peculiar to each. Moreover, some indication at least of the forests should remain and be found somewhere in this vast region. With these and many other points constantly in mind the writer passed a considerable portion of the seasons of 1900 and 1901 in exploring these deposits. Particular attention was given to ascertaining whether or not they contained an aquatic fauna and flora. The sandstone lenses were especially examined with reference to this, for whether the deposits as a whole were of lacustrine origin or not, there could be little doubt as to the aqueous origin of the sandstones. Though for the most part remarkably barren of aquatic life, remains of *Trionyx*, fishes, and crocodiles were found, and in one locality the casts of unios were observed in great numbers. A search in the clays of the *Titanotherium* and overlying *Oreodon* beds was rewarded with greater success, for numerous thin layers of limestone, varying in thickness from a fraction of an inch to a foot or more and always of limited areal extent, were discovered at many horizons rich in the remains of fresh-water plants and Mollusca, such characteristically shallow-water forms as *Chara*, *Limnaea*, *Physa*, and *Planorbis* occurring in the greatest abundance. I have submitted these Mollusca to Drs. Dall, Pilsbry, and Stanton, and all have assured me that they belong to species inhabiting swamps and small ponds and could not have lived in the midst of a great lake; while Dr. Knowlton, who has examined the plants, finds in great abundance the stems and seeds of *Chara*, which, as all know, is distinctly an inhabitant of small springs, shallow ponds, and brooks. The presence of these thin limestone layers with such characteristically swamp plants and Mollusca as are *Chara* and *Physa* at various horizons throughout the White River series, and in the very midst of the region which was supposed to have been occupied by a great lake, and intercalated with the clays which advocates of the the lake theory maintain were deposited in the deep and quiet waters, would appear to preclude the possibility of the existence of such a lake in White River times. Moreover, remains of forests were found at several places and at different horizons throughout these beds. At various localities in the Hat Creek basin in Sioux County, Nebr., I discovered remains of the silicified trunks of trees and seeds belonging especially to *Hicoria* and *Celtis*. These were found at various horizons from the middle *Titanotherium* beds to the very top of the Loup Fork. And in South Dakota, some 12 miles north of White River, opposite the mouth of Corn Creek, I discovered the remains of a not inconsiderable forest. Here in the upper *Titanotherium* beds and lower *Oreodon* beds there occur, actu-

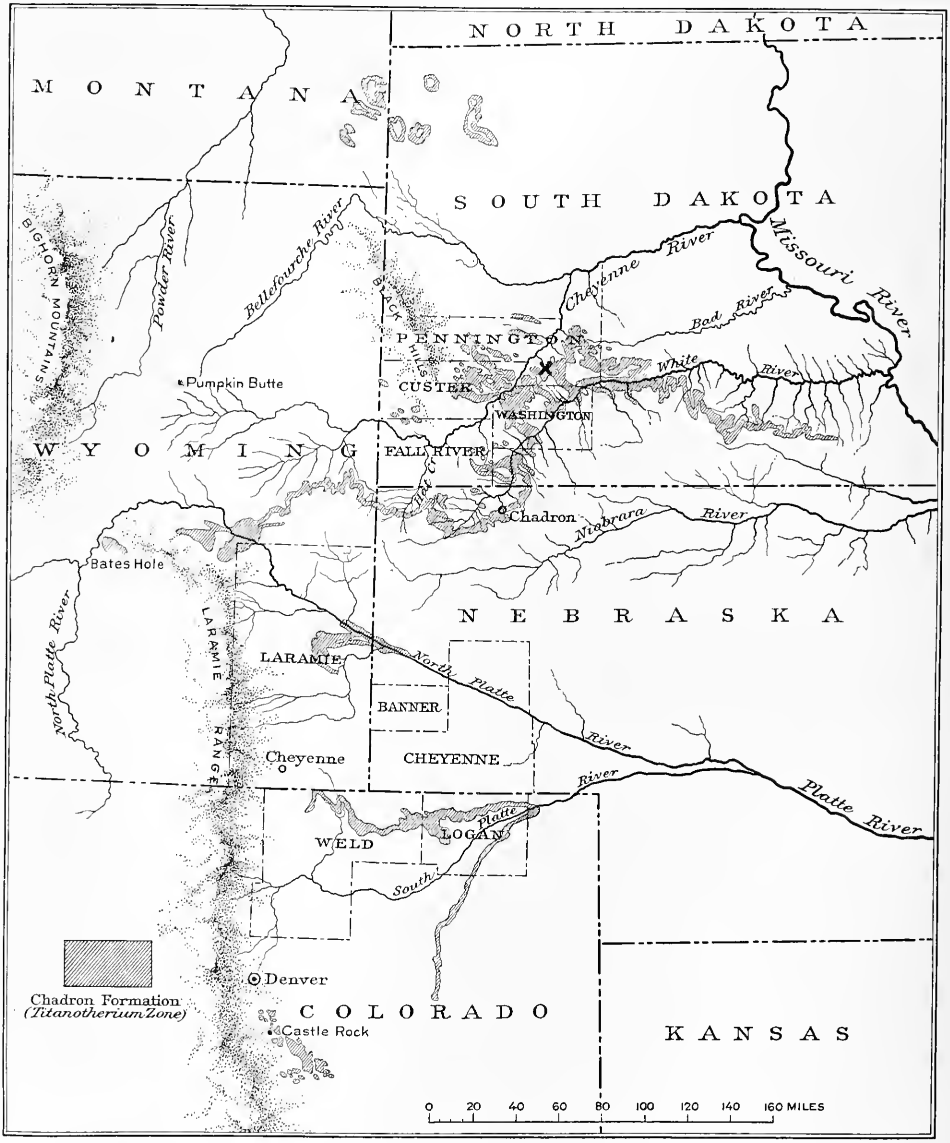


FIGURE 75.—Map showing principal exposures of the Chadron formation (*Titanotherium* zone) of Montana, South Dakota, Wyoming, Nebraska, and Colorado

Chiefly after Darton, 1905, United States Geological Survey. Includes the exposures at Castle Rock (Castle Rock conglomerate), south of Denver, in Weld and Logan Counties, Colo., where the early collections of Marsh and Cope were made; in the outlying localities of Bates Hole and Hat Creek, Wyo., from which the Reed and Hatcher collections were made; and in the Big Badlands of Pennington, Custer, and Washington Counties, S. Dak. The *Titanotherium* zone was first observed by Hayden at point X on map and was first subdivided faunistically by Hatcher.

> ally by hundreds, the silicified stumps and partially decayed trunks of trees, weathering out of the fine clays of these deposits. It was noticeable that only the knots and lower stumps had been preserved. Nothing like complete trunks were to be observed, and the entire aspect was that of the remains of a dead and decayed forest on the margin of some streams, where only the less destructible knots and stumps would endure sufficiently long to be finally covered up and preserved. In this same region there were discernible certain strata which seemed to indicate that during the deposition of these beds there has been at several horizons an accumulation of vegetable mold or humus, and on Dry Creek, some 5 miles northeast of Chadron, in Dawes County, Nebr., I observed near the base of the *Oreodon* beds a stratum of some 2 feet of dark-colored humus, clearly indicating that this region had not been occupied by a great lake while this stratum was being deposited.

Hatcher concludes that the sandstone, the conglomerate, and a part of the clay were deposited in river channels and that the lenses of limestone, which are rich in remains of aquatic plants and mollusks, were formed in shallow ponds and lakes that were scattered over the higher tablelands and the broad flood plains, where most of the finer clays were deposited by occasional inundations in the rivers and by wind. These conditions are similar to those now prevailing about the sources of Parana and Paraguay Rivers in central South America. There the rainy season extends from October to April, and the heaviest rains fall near its end, when the small rivers from the highlands are flooded and pour their waters over the flood-plain. The water, however, takes a long time to spread over the plain, and it is there highest in July and August and lowest in February. The flood plain of the Paraguay is 150 miles wide and broadens upstream. The flood plains of the upper Paraguay, the Amazon, and the Orinoco are confluent. Here we have a group of regions that are together probably larger than that occupied by the great White River group during Oligocene time—namely, 97,500 square miles.

RAPID FLUVIATILE SEDIMENTATION IN THE CYPRESS HILLS, SASKATCHEWAN

While the conditions thus described existed in the Big Badlands of South Dakota, the streams were much more active at places in areas to the south and north. "That the Cypress Hills Oligocene deposits were the result of rapidly flowing water from the west is evident," observes Lambe (1908.1, p. 7). He continues:

> The thick basal beds of rounded pebbles represent the work of a strong transporting force, such as would be supplied by a turbulent stream of considerable size carrying eastward material from the Rocky Mountains. The sands show false bedding as a result of varying currents. With the accumulation of material eastward, and consequent reduction of the transporting force, beds of finer material were deposited at a higher level and probably on extensive areas of overflow.

The beds that yield the most fossils are composed of a fine conglomerate, which on disintegration has freed the fossils. Associated beds of a rich brown coarse sand have also yielded some interesting remains. The vertebrate fauna of this region in Saskatchewan includes about 37 genera and 58 species, comprising among the fishes *Amia*, *Lepidosteus*, and catfishes; among the reptiles land tortoises, chelydrids, leather-backs (*Trionyx*), anguid lizards, palaeophid snakes, and true crocodiles; among the mammals opossums, anthracotheres, elotheres, agriochoerids, camels, tragulids (*Leptomeryx*), horses (*Mesohippus*), hyracodonts, true rhinoceroses (aceratheres), titanotheres (several lower Oligocene types), sciurid and ischyromyid rodents, beavers, hares, hyaenodonts, dogs (*Cynodictis*, *Daphaenus*), and cursorial saber-tooths (*Dinictis*).

These Saskatchewan beds are not only more than twice as thick as those in South Dakota but they have afforded a truer picture of the highly diversified reptilian and mammalian life during the time represented by the *Titanotherium* zone. The species of titanotheres that they contain belong chiefly to the lower (Chadron A) and middle (Chadron B) levels of the *Titanotherium* zone of South Dakota.

SLOW SEDIMENTATION IN SOUTH DAKOTA

As compared with the 500 feet of fluviatile deposits of the *Titanotherium* zone in Saskatchewan the bare 180 feet of sediments that represent the *Titanotherium* zone in South Dakota are very misleading as to the length of geologic time they represent. Deposition in South Dakota must have been extremely slow. The finer materials that border the river channels and compose the clays must have accumulated very gradually. That a very long period of geologic time elapsed while these sediments were being laid down is evident also from the great span of evolutionary change indicated by members of each phylum of the titanotheres found in this region. On the lowest levels are found primitive small-horned titanotheres, inferior in size to the smaller existing rhinoceroses; on the highest levels are found gigantic animals, of almost elephantine proportions, armed with great, powerful horns. As a basis for estimating the time required for the deposition of the South Dakota sediments, comparison may be made with existing conditions along the River Nile, which between Aswan and Cairo is building up its bed at the slow average rate of 10 centimeters, or 0.32 foot, per century. (Lyons, 1906.1, p. 334.) At this rate the deposition of the 180 feet of "*Titanotherium* beds," if composed entirely of fine clays, would have required some 55,000 years. On the other hand, if we apply Humphreys and Abbot's estimates for the Mississippi River system, namely 0.5 foot in 100 years, about 36,000 years would have been necessary for the deposition of the fine clay materials of the *Titanotherium* zone. The present author inclines to the opinion that the lower Oligocene evolution of the titanotheres demands a period of not less than 55,000 years, which would correspond with the present rate of sedimentation in the flood plain of the Nile.

GEOGRAPHIC DISTRIBUTION OF THE CHADRON FORMATION

The following list of localities at which remains of titanotheres have been collected includes some isolated spots where the Chadron formation is recognized by a few bones or a single skull, as well as points in the classic areas of the Great Plains where the history of the titanotheres is chiefly recorded.

Localities at which the principal types and collections of Oligocene titanotheres have been obtained

South Dakota

Region	Explorations	Locality	Type
"Mauvaises Terres of Nebraska," Big Badlands of Cheyenne and White Rivers of South Dakota. This region, the one most extensively explored, commonly known as the Big Badlands, lies between White and Cheyenne Rivers, southwestern South Dakota, extending over the border into Nebraska and Wyoming, including the basin of Hat Creek. The lower Oligocene has been well differentiated in this region, and the records are generally definite.	Successively explored by members of the American Fur Co. (1845), John Evans (1853), Meek and Hayden (1853), and by more recent explorers: Hatcher (for the U. S. Geological Survey, U. S. National Museum, and Yale University collections, 1886, 1887, 1888, 1902), Garman (for the Museum of Comparative Zoology, 1885), Wortman (for the American Museum of Natural History, 1892, 1894), Gidley and Thomson (for the American Museum of Natural History, 1902), Thomson (for the American Museum of Natural History, 1904), Darton (for the U. S. Geological Survey, 1905).	Bear Creek	Menodus (Titanotherium) proutii (Owen, Norwood, and Evans), Diploclonus (Megacerops) tyleri (Lull), Brontotherium (Titanops elatus) gigas Marsh, Menodus (Menops) varians (Marsh) Brontotherium tichoceras (Scott and Osborn), B. dolichoceras (Scott and Osborn), B. platyceras, B. leidyi Osborn, Brontops validus Marsh, Allops crassicornis Marsh, A. serotinus Marsh.
		Indian Draw	Brontotherium medium Osborn, B. hatcheri Osborn, Megacerops (Symborodon) copei Osborn, Allops (Megacerops) marshi Osborn.
		Quinn Draw	Diploclonus bicornutus (Osborn), Brontops brachycephalus Osborn, Brontotherium (Titanotherium) ramosum Osborn.
		Corral Draw	Allops walcotti Osborn.

Nebraska

Region	Explorations	Locality	Type
White River, northern Nebraska	Marsh and Clifford (for Yale University, 1874).	Dry Creek	Brontops robustus Marsh.
Hat Creek, Sioux County, Nebr. Hat Creek, a branch of the South Fork of Cheyenne River, rises in the canyon in the north front of Pine Ridge, Sioux County, and receives numerous branches, also heading in this front.	Hatcher (for the U. S. Geological Survey, 1886; for the Carnegie Museum, 1900), Peterson (for the Carnegie Museum, 1901, 1902).	Hat Creek	Brontops dispar Marsh.
Big Cottonwood Creek, Sioux County, Nebr. The exposures of the Titanotherium zone at the head of Big Cottonwood Creek are coextensive with those of the Hat Creek basin, which lies north of this locality. Much of Hatcher's collecting was done in exposures on the low divide connecting Big Cottonwood Creek with the exposures in the Hat Creek basin. Adelia is a station on the Chicago, Burlington & Quincy R. R., on the outskirts of this particular region.	Hatcher (for the U. S. Geological Survey, 1886; for the Carnegie Museum, 1900).		

Localities at which the principal types and collections of Oligocene titanotheres have been obtained—Continued

Colorado

Region	Explorations	Locality	Type
Northeastern Colorado, Logan and Weld Counties, exposures south of the Pawnee Buttes escarpment and some distance north of the South Platte River. The lower Oligocene was differentiated and explored by Cope in 1873, but it has hardly been touched by any subsequent work (Horsetail Creek beds of Matthew).	Marsh (for the Yale Museum, 1870), also field collectors.	Probably in Weld County, Colo.; near Gerry's ranch, Colo.; also 4 miles south of Pond Springs, Colo. Collector, Devendorf.	Brontotherium gigas Marsh, Menodus (Brontotherium) ingens Marsh, Brontotherium (Titanops) curtum Marsh.
Lower Oligocene has been recognized at other points in Colorado, as in the vicinity of Akron, but no adequate collections have been made for the identification of species.	Cope 1873, Matthew, Brown, Martin (for the American Museum of Natural History, 1898), Matthew, Brown (for the American Museum of Natural History, 1901).	Horsetail Creek, Colo.	Megacerops (Symborodon) acer Cope, M. (S.) altirostris Cope, M. (S.) bucco Cope, M. (S.) torvus Cope, Menodus (Symborodon) trigonoceras Cope, M. (S.) heloceras Cope, M. (S.) hypoceras Cope, Megacerops riggsi Osborn.
Castle Rock conglomerate (upper part of "Monument Creek beds"), Colorado.	Darton (for the U. S. Geological Survey, 1905, 1906). Richardson (for the U. S. Geological Survey, 1912).		

Wyoming

Region	Explorations	Locality	Type
Beaver Divide, Fremont County, Wyo.	Granger (for the American Museum of Natural History, 1910).		
Bates Hole, Natrona County, Wyo. Exposures lying between Bates Hole, at the north end of the Laramie Plains, and Beaver Divide, at some distance to the west, have been casually examined by W. H. Reed and W. D. Matthew, who have recognized a lower Oligocene fauna, but no systematic exploration has been made. A number of well preserved specimens of titanotheres (Univ. Wyoming Mus.) were found in this area.	Reed (for the University of Wyoming, 1907, 1908).		

Montana

Region	Explorations	Locality	Type
Pipestone Creek and Thompson Creek, Jefferson County, Mont. In southwestern Montana, at Pipestone Springs, McCarty Mountain, north of Dillon, and elsewhere, small scattered exposures. A considerable fauna, of small species, has been described from these beds.	Douglass (for the Carnegie Museum, 1899, 1901, 1903), Matthew (for the American Museum of Natural History, 1902).		

Saskatchewan

Region	Explorations	Locality	Type
Swift Current Creek, Cypress Hills, Saskatchewan.	McConnell and Weston (1883), Weston (1888, 1889), Lambe (1904).		Menodus angustigenis, M. selwynianus, Megacerops syceras, M. assiniboiensis, M. primitivus.

The Chadron formation was especially explored by Darton, under whose direction a map showing its general distribution (see fig. 8) was prepared. His description of this map may be paraphrased as follows:

> The most extensive outcrops are in the southwestern portion of South Dakota, in a district known as the Big Badlands. These extend along the valley of White River and in the adjacent divide between White River and Cheyenne River West of the latter the formation caps many of the divides extending to and up the eastern slopes of the Black Hills. The formation extends eastward to the vicinity of longitude 100°, and it extends westward along the foot of Pine Ridge through Dawes and Sioux Counties in Nebraska and Converse County, Wyo., to the north end of the Laramie Range. The formation probably underlies a large portion of western Nebraska, but it only reaches the surface at the foot of Pine Ridge and along the north Platte Valley west of Scotts Bluff. Isolated outcrops are also reported at Valentine and Lone Pine. The formation appears extensively in northeastern Colorado, on both sides of the valley of South Platte River. There are prominent exposures west of Akron, south of which the formation extends across the greater part of Washington County. South of Denver an extensive area caps the divide between the South Platte and the Arkansas Rivers, at the foot of the Rocky Mountains. The deposits in this area have been designated the Monument Creek formation. This consists of two members of which the upper [now called Castle Rock conglomerate; (Richardson, 1912.1)] has recently yielded *Titanotherium* remains. Other outlying areas of the formation occur in Bates Hole west of the Laramie Range [Wyoming], in Butte County, S. Dak., and in the southeastern corner of Montana.

An important additional exposure of the *Titanotherium* zone discovered by the American Museum expedition of 1909 is at Beaver Divide (Wagonbed Spring), in the southern rim of the Wind River Basin, near Hailey, Wyo. Here a deposit containing a skull of a primitive Oligocene titanothere was found overlying a deposit of upper Eocene age containing *Amynodon.*

The thickness of the Chadron formation varies, but in some places it reaches 180 feet. It consists of

> clays, sands, gravels, and sandstones, clay predominating greatly over the other materials. * * * This clay is of pale-greenish color, weathering in typical badland form and often having the peculiar character of fuller's earth. At the base of the formation there is usually a bed of gravel and sand merging upward into sands and sandy clays, which in the Big Badlands and western Nebraska are often of a reddish color. At various horizons through the formation there are beds of sandstone from a few inches to 4 feet in thickness and of local extent. Ordinarily these coarse materials exhibit current bedding and from their character and relations are clearly the products of running water. Beds of volcanic ash occur extensively in the Chadron formation in the Big Badlands and at intervals along the northern front of Pine Ridge (South Dakota).

Hatcher observes (1893.1, pp. 206–207):

> The clays greatly predominate, consist of very fine particles, and are quite compact. In places they are composed almost entirely of pure kaolin, but they often contain a considerable portion of sand. Near the bottom of the beds the color is often red or variegated, due to the presence in them of small quantities of red oxide of iron; but the prevailing color is a very characteristic and delicate greenish white. * * * Owing to the extreme minuteness of the particles forming the clays and the absence of sufficient cementing material in them, in most places they readily yield to the action of water and are quite rapidly eroded. The clays of the *Titanotherium* beds were probably derived from two sources, viz, from the Cretaceous clays and shales and from the kaolinization of granite feldspars.
>
> The sandstones are never entirely continuous and never more than a few feet thick. They present every degree of compactness, from loose beds of sand to the most solid sandstones. They are composed of quartz, feldspar, and mica and are evidently of granite origin. When solidified the cementing substance is carbonate of lime.
>
> The conglomerates, like the sandstones, are not constant, are of very limited extent, never more than a few feet thick. They are usually quite hard, being firmly held together by carbonate of lime. A section of the beds taken at any point and showing the relative position and thickness of the sandstones, clays, and conglomerates is of little [stratigraphic] value, since these vary much at different and quite adjacent localities.

These descriptions by Darton and Hatcher reveal a wide contrast between the composition of the *Titanotherium*-bearing beds and that of the upper Eocene deposits of the mountain-basin region.

COMPARISONS OF BASINS IN WESTERN UNITED STATES WITH THE FLOOD PLAIN OF THE NILE

The flood-plain deposition of the Nile, which has been very carefully studied, also throws light on the mode of formation of parts of the Chadron formation. The following passages are taken from "The physiography of the River Nile and its basin," by Capt. H. G. Lyons (1906.1, pp. 241, 311, 334):

> When rivers already loaded with sediment emerge from their mountain valleys of high slope on to a level plain under arid climatic conditions where the water table is at some distance from the surface their water sinks in almost at once instead of flowing on the surface and therefore deposits its load of sediment as an alluvial fan. This fan is built up most rapidly at its head, and as the floods of successive years come down new temporary channels are formed which divide and reunite, forming a network of channels, each by deposit building up banks for itself, which are probably cut through in the next season of the summer rainfall.
>
> While it is the finer silt which is deposited in the irrigation basins, on the shelving banks of the river, and on such parts of the flood plain as are annually flooded, it is the bottom load which is deposited in the bed of the river itself, and this consists of the coarser sand which the current can not carry so readily as the finer material. If the Nile mud is treated by levigation so as to remove the finest particles of clay and sand the residue is a fine whitish-gray sand, such as is seen forming sand banks in the Nile wherever the conformation of the river is such that the velocity of the flood current is reduced at that point.
>
> In this Aswan-Cairo reach of the Nile, then, we have to do with a river which is flowing with a low slope through an alluvial plain which it has formed and which, if uncontrolled, it annually floods, depositing on the flood plains part of its load of silt as the velocity of flood water is diminished.
>
> The Nile between Aswan and Cairo follows a depression in which it has gradually deposited a considerable thickness of alluvial mud, and now it meanders on the flood plain which it has formed. In earlier times side channels followed the lower margins of the valleys, and lagoons and swamps existed in the same part of the valley.

FAUNAL DIVISIONS IN THE CHADRON FORMATION

THREE FAUNISTIC LEVELS DETERMINED

In the series of sediments that were deposited on the uneven surfaces of the Pierre shale and that consist of fine clays, which were traversed and at many places secondarily eroded by river channels and which were very gradually accumulated during an extremely long period, we should not expect to find anything resembling clearly defined stratification or horizontal and vertical succession of species and genera. Nevertheless, we owe to the genius and the untiring exploration of Hatcher a division of the Chadron formation into lower, middle, and upper levels, which we shall designate Chadron A, Chadron B, and Chadron C, and which correspond to similar divisions of the deposits of the Rocky Mountain basins.

In his paper of 1893 (1893.1), "The *Titanotherium* beds," Hatcher remarked that these beds were so named by Meek and Hayden in 1857 from the genus *Titanotherium*, established by Leidy in 1852. Although we are obliged to replace the generic name *Titanotherium* by *Menodus* it seems best to retain *Titanotherium* as the historic zonal name for these significant beds.

The thickness of the "*Titanotherium* beds" at different localities in Wyoming, Colorado, the Dakotas, and Saskatchewan, as recorded above, varies, having a maximum of 500 feet and a minimum of 30 feet.

Hatcher, accepting a total of 180 feet as the maximum thickness of these beds in the Big Badlands of South Dakota, assigned 50 feet to the lower level, 100 feet to the middle, and 30 feet to the upper (1893.1, p. 210). During the field seasons of 1886, 1887, and 1888 Hatcher collected for the present monograph material including 105 nearly complete *Titanotherium* (*Menodus*) skulls and parts of numerous skeletons, as well as disarticulated bones, besides remains of many other associated animals. Early in the season of 1886 it became apparent that certain forms of skulls were characteristic of certain horizons in the "*Titanotherium* beds." This fact indicated the desirability of keeping, so far as possible, an exact record of the horizon from which each skull or skeleton was taken. From actual measurement the vertical range of the titanotheres in the Big Badlands was found to be about 180 feet. For convenience in keeping a record of horizons the beds were divided into three divisions of 60 feet each, and each of these three divisions was subdivided into three divisions of 20 feet each. As each skull or skeleton was dug out a separate letter or number was given to it and it was assigned to that subdivision of the beds from which it was taken.

STRATIGRAPHIC DISTRIBUTION OF SPECIES OF OLIGOCENE TITANOTHERES

In 1888 Hatcher drew up a manuscript table for Professor Marsh in which the lower, middle, and upper divisions of the "*Titanotherium* beds" were each subdivided into three levels, and in which he placed the letters assigned to many of the skulls found by him. In 1901 Hatcher revised this table for Osborn for use in the present monograph. In the summer of 1902 the United States Geological Survey sent Messrs. N. H. Darton and J. B. Hatcher to the Big Badlands of South Dakota for a resurvey of the localities where some of the skulls were found by Hatcher in order to determine precisely the elevation of these localities above the Pierre shale, at the base of the beds. Prof. Eberhard Fraas, of Stuttgart, accompanied the party and made some interesting observations on the mode of deposition of these beds. (Fraas, 1901.1.) This experienced geologist concluded that the "*Titanotherium* beds" consisted of river and flood-plain deposits whose surfaces were exposed during the dry seasons of the year; that parts of the overlying Brule clay—the beds in the middle *Oreodon* zone—were deposited in shallow lakes, the dissolved materials, of varying concentration, giving rise to the banded layers; and that the reddish strata of the *Oreodon* zone (Brule) were formed of eolian loess.

In the following table the results of records and observations made by Hatcher, indicated by the abbreviation J. B. H., are supplemented by the results of a few observations made by N. H. Darton of the United States Geological Survey, E. S. Riggs of the Field Museum, W. H. Reed of the University of Wyoming, and Walter Granger of the American Museum. The species are arranged in the five generic phyla determined by Osborn, namely, *Brontops*, *Allops*, *Menodus* (= *Titanotherium*), *Megacerops* (= *Symborodon*), *Brontotherium*.

Geologic succession of Oligocene titanotheres in the Chadron formation

[Levels (above Pierre shale except as otherwise indicated) mostly taken from J. B. Hatcher's field records of 1886, 1887, 1888. Genera and species of fossils determined by H. F. Osborn and W. K. Gregory]

	Level	Brontops	Allops	Menodus	Megacerops	Brontotherium	Classification uncertain
C. Upper Titanotherium zone	3	Brontops dispar?. Skull G, Nat. Mus. 4248. Record and level uncertain (J. B. H.).	Allops serotinus. Skull I, Nat. Mus. 2151. +80 feet. Same locality as H. Allops serotinus. Skull H, Nat. Mus. 4251. +77 feet; 34 feet below top.	Menodus giganteus. Field Mus. skull P5927. Near top of upper Titanotherium beds (E. S. Riggs). Menodus giganteus. Univ. Wyoming skull 3. Upper beds (W.H.Reed). Bates Hole, Wyo. Menodus giganteus. Skull r, Nat. Mus. 1212.	Megacerops copei. Skull V′, Nat. Mus. 4711. +65.4 feet, possibly in C2 (J. B. H.). ?Skull L′, Nat. Mus. 4700.	Brontotherium platyceras. Skull 12161, Field Mus. Upper levels (E. S. Riggs). Brontotherium medium. Skull w, Nat. Mus. 4256 (type); "from the extreme top of the Brontotherium beds. Oreodon teeth were found in digging it up" (J. B. H.). +81 feet, "well up in red clays" (J. B. H.). Brontotherium curtum. Skull Y′, Nat. Mus. 1211. +93.3 feet. Skull q, Nat. Mus. 4946. +89 feet. Skull g, Nat. Mus. 4244.	Skulls.
	2	Brontops dispar. Skull p, Nat. Mus. 1217. Brontops dispar?. Skull d, Nat. Mus. 4696. Brontops sp. Mounted skeleton, Am. Mus. 518. "Very high, 8–10 feet from top." (J. B. H.) "32 feet below the 3-foot siliceous limestone layer at top of Titanotherium series." (N. H. Darton, 1901.)	Allops serotinus Skull j, Nat. Mus. 4938.	?Menodus giganteus. Skull G′, Nat. Mus. 4291. "From middle beds or toward the top" (J. B. H.).		?Brontotherium hatcheri?. Univ. Wyoming skull 1. "Upper beds." Bates Hole, Wyo.	Skulls R′, W′.
	1	?Brontops dispar. Skull h, Nat. Mus. 4944.	Allops crassicornis. Skull Z′, Nat. Mus. 4289. "J. B. H. inclined to place this skull higher up."	Menodus proutii. Skull e, Nat. Mus. 4701. Level doubtful (J. B. H.).	Megacerops acer. Univ. Wyoming skull 2. "Upper beds about two-thirds up from base" (W. H. Reed). Bates Hole, Wyo.	Brontotherium medium?. Skull N′, Nat. Mus. 4699. Level? Brontotherium gigas. Skull H′, Nat. Mus. 4262.	Skulls M′, U′.
B. Middle Titanotherium zone	3	Brontops dispar. Skull D′, Nat. Mus. 4706. Level essentially correct (J. B. H.). Brontops robustus. Type skeleton, Yale Mus. 12048. 60 feet below summit (J. B. H.).		Menodus giganteus. Skull I′, Nat. Mus. 1220 (very large). Menodus trigonoceras. Skull O, Nat. Mus. 4257.	Megacerops bucco. Skull O′, Nat. Mus. 4705. Level rather doubtful (J. B. H.). +46.7 feet.	Brontotherium medium?. Skull u, Nat. Mus. 4716. Level? Brontotherium hatcheri. Type skull a, Nat. Mus. 1216.	Skulls S′, C′, F′, E′.
	2	Brontops dispar. Skull f, Nat. Mus. 4703. Level certainly B2 (J. B. H.). Skull D (type), Nat. Mus. 4941. Hat Creek. Level correct (J. B. H.). Skull K, Nat. Mus. 4290 (type of B. validus).	Allops marshi?. Skull t, Nat. Mus. 4942. Allops marshi?. Skull A′, Nat. Mus. 1215.		Megacerops sp. (or Brontotherium hatcheri). Skull Q′, Nat. Mus. 4255. "Certainly in middle beds, perhaps in middle level" (J. B. H.).	Brontotherium hypoceras. Skull l, Nat. Mus. 4273(?). Level probably correct (J. B. H.).	Skulls T′, P′, C B′.
	1	Brontops dispar. Skull (erroneously lettered P). Nat. Mus. 4245. Skull J, Nat: Mus. 4738. Hat Creek, Lower B, probably correct (J. B. H.). Brontops brachycephalus?. Skull M, Nat. Mus. 4259. +55.6 feet (J. B. H.). Level B, probably correct (J. B. H.). Brontops brachycephalus. Skull F, Nat. Mus. 4258. +71.4 feet (J. B. H.); +48.5 feet (N. H. Darton).		Menodus trigonoceras. Skull G′, Nat. Mus. 4291.			Skulls N, A, B No.? (a large skull).

Geologic succession of Oligocene titanotheres in the Chadron formation—Continued

	Level	Brontops	Allops	Menodus	Megacerops	Brontotherium	Classification uncertain
A. Lower Titanotherium zone	3	Brontops brachycephalus. Skull X′, Nat. Mus. 1214. Level probably correct (J. B. H.). Brontops brachycephalus?. Skull m, Nat. Mus. 4940. Level probably correct (J. B. H.).				Brontotherium ?hypoceras. Skull K′, Nat. Mus. 4702. Level very doubtful (J. B. H.).	Skulls v, I′.
	2	Diploclonus tyleri. Type skull. 35 feet above Pierre shale and 165 feet below top of formation (R. S. Lull).	Allops marshi?. Skull E, Nat. Mus. 1213. Level probably correct (J.B.H.).			Brontotherium leidyi (type). Skull R, Nat. Mus. 4249. Level correct (J. B. H.).	
	1	Brontops dispar??. Skull P, Nat. Mus.? (not 4245). "This skull in pieces found July 4, 1887, right at base of beds" (J. B. H.). Brontops brachycephalus. Skull c, Nat. Mus. 4261 (type). Lower levels (J. B. H.). Skull b, Nat. Mus. 4947 (marked 1991). +14.4 feet; 130.6 feet below top (J. B. H.). Very young skull (new born?), Univ. Wyoming. "From extremely low level" (W. H. Reed). Bates Hole, Wyo.	Allops walcotti (type). Skull Q, Nat. Mus. 4260. "Probably lower beds, level A, fine-grained sandstones" (J. B. H.).	Menodus heloceras. Skull, Am. Mus. 14576. At base of beds near Hailey, Wyo. (W. Granger).		Brontotherium leidyi. Skull, Carnegie Mus. 93. Hat Creek, Nebr., 15 or 20 feet from bottom of lower beds (J. B. H.).	

HATCHER'S COLLECTIONS, 1886-1888

According to a report delivered orally by Hatcher to the author in 1901, the collections made by him in 1886 included 24 skulls, some from Hat Creek, Nebr., and some from the Big Badlands of South Dakota, which were designated in his records and field notebooks by the letters A, B, C, etc., but which now bear United States National Museum numbers. In 1887 Hatcher collected from Sioux County, Nebr., mostly from Big Cottonwood Creek (adjoining Hat Creek), a second series of skulls, which he similarly designated by the letters A to K. Later in the same season he moved camp to the South Dakota Badlands and collected the skulls L to Z and a to w. Thus during the season of 1887 he collected 45 skulls. During the season of 1888 he collected another series of 24 skulls in the South Dakota Badlands, which he designated by the letters a′, b′, c′, to z′ but which Professor Marsh later relettered A′ to Z′. Subsequently the cataloguers of the United States National Museum assigned numbers to all these skulls. These revisions of the records have caused confusion, so that it is now doubtful whether certain skulls that bear capital letters and United States National Museum numbers belong to the series of 1886 from Hat Creek, Nebr., or to the series of 1887 from Big Cottonwood Creek and the South Dakota Badlands. Such uncertainty, of course, involves equal uncertainty as to the localities and geologic levels at which the specimens were obtained, but nearly all uncertainties have been settled by Dr. W. K. Gregory through careful examination of all the available evidence, with the assistance of Mr. J. W. Gidley, of the United States National Museum. The above table is based on these original and revised records.

This remarkable collection, now preserved in the United States National Museum, constitutes the reference standard as specifically determined by the author with the assistance of Messrs. Gidley and Gilmore and includes the skulls and jaws indicated below, which are enumerated in detail under the respective genera in Chapter VI:

Allops phylum: 24 skulls and lower jaws in four specific stages.
Diploclonus phylum: 1 skull in one specific stage.
Brontops phylum: 58 skulls and jaws in three specific stages.
Brontotherium phylum: 42 skulls and jaws in nine specific stages.
Megacerops phylum: 7 skulls and jaws in three specific stages.
Menodus phylum: 26 skulls and jaws in four specific stages.

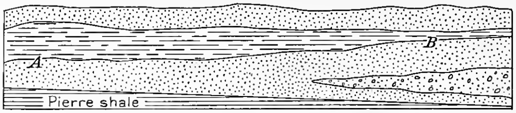


FIGURE 76.—Section showing the results of stratigraphic leveling in the Chadron formation (*Titanotherium* zone) in the badlands of White River, S. Dak., in June, 1901, by N. H. Darton

The results are affected by dip, by unconformity, and by variation in the thickness of the beds. In determining the dip the beds showing the nearest reliable contacts of the Chadron with the Pierre formation were selected for all the levelings, and as most of the distances determined were short and were measured along the strike of the low-dipping beds the angle of the dip is unimportant. The Chadron formation lies on a smooth plane of unconformity, and its basal member is generally continuous but was doubtless laid down against a sloping shore, and the layers are not synchronous throughout its extent. Nearly all the bones listed in the text, however, were found in an area so small that this unconformity is unimportant. The variation in the thickness of beds is the most important factor affecting the determination of the stratigraphic levels and one that could not be accurately determined, for the beds present so much variation in character that they can not be followed for a distance long enough to afford a basis for stratigraphic subdivision of the formation. A horizon 30 feet above the base of the formation at one point may represent a horizon 45 feet above it at another point; thus a bone found at *A* may have been deposited at the same time as a bone found at *B*.

SOURCES OF ERROR IN DETERMINING STRATIGRAPHIC LEVELS

It should be borne in mind that owing to the great difference in the thickness of the "*Titanotherium* beds" in different localities and to the irregular topography of the Pierre shale upon which the beds rest it often happens that the base of these beds at one point may correspond to the middle *Titanotherium* zone at others, so that an exact stratigraphic subdivision of the Chadron formation over wide areas is not at all possible. In spite of such opportunity for error only a few well-authenticated records (such as that of the type of *Brontops dispar*) appear to contradict Hatcher's statement that the titanotheres of advanced structural development are confined to the upper levels of the beds. One such striking exception is recorded by Prof. R. S. Lull (1905.1), who states that he found the type of *Diploclonus tyleri* at a point only 35 feet above the Pierre shale, at the base of the *Titanotherium* beds, which was there some 165 feet below their summit. Hence this skull is assigned to Hatcher's level A 3, although its large size and progressive structure would lead one to infer that it came from the upper *Titanotherium* zone (Chadron C).

Notwithstanding these discrepancies we are able to follow the evolution of five separate phyla of titanotheres, from the small animals of the lower *Titanotherium* zone (Chadron A), which have small horns, through intermediate types to the latest forms, which have highly specialized skulls, from the top of the "*Titanotherium* beds." This evolution was rather even and regular in the phyla *Brontotherium* and *Menodus* (= *Titanotherium*), but in the *Brontops* phylum it appears that some of the primitive types of the lower zone survived with little change into the middle zone (Chadron B), and that other primitive types evolved gradually into the more specialized species of the middle and upper zones.

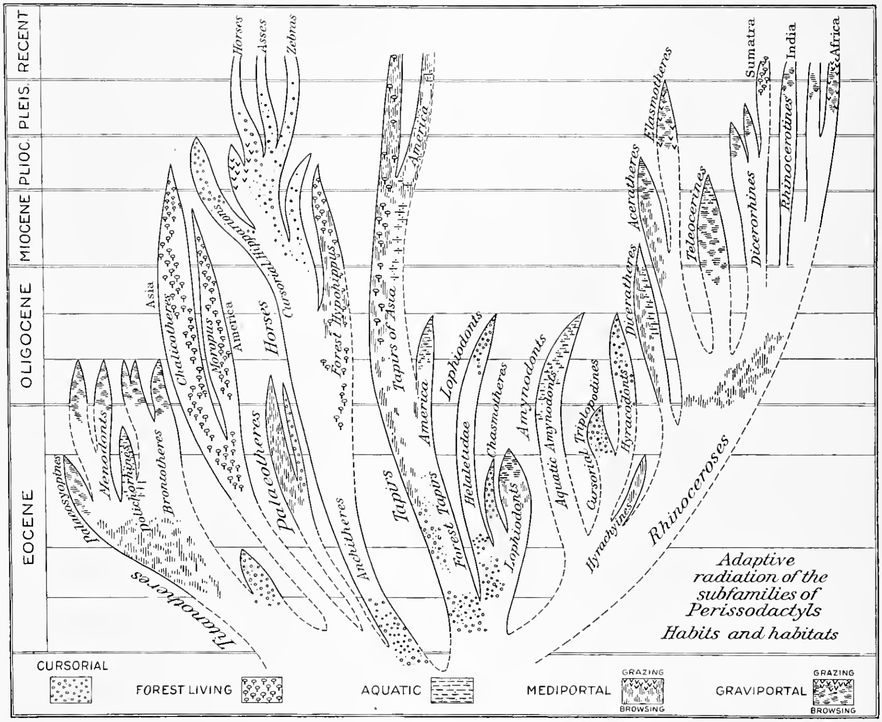


FIGURE 77.—The family tree of the Perissodactyla

Adaptive radiation of the 9 families and 35 subfamilies. Their divergence in limb and foot structure into cursorial, forest-living, mediportal, and graviportal types, and in tooth structure into browsing and grazing types, is indicated by respective symbols.

Height in feet above Pierre shale at which remains of titanotheres were found as determined in 1901 by J. B. Hatcher and N. H. Darton [a]

Specimen	Hatcher	Darton
Skull Y′ (?). "Big flat-horned skull in National Museum"; Nat. Mus. 1211 (?)		[b] 93. 3
Skull Q. Indian Draw. Probably skull "small q" was meant (Nat. Mus. 4946, Brontotherium curtum), "wrongly lettered Q"	[c] 89	88. 9
Large-horned red skull. Nat. Mus. 4256, Brontotherium medium (type)	81	81. 1
Skeleton. Am. Mus. 518, Brontops robustus?	(d)	(e)
Skull V′. Indian Draw. Nat. Mus. 4711, Megacerops copei (type)	65. 4	65. 3
Long-horned skull. West branch of Indian Draw. Brontotherium ramosum		62. 3
Skull M. Near Middle Corral Draw. Nat. Mus. 4259, Brontops brachycephalus	55. 6	55. 6
Skull "F." Quinn Draw, South Dakota. ?Nat. Mus. 4258, Brontops brachycephalus	71. 4	48. 5
Skull O′. South side of west fork of Corral Draw. Nat. Mus. 4705, Megacerops "bucco," female	46. 7	46. 7
Skull "I." Quinn Draw, South Dakota. Nat. Mus. 2151, "Allops serotinus," female	80	43. 5
Skull "H." Quinn Draw, South Dakota. Nat. Mus. 4251, Allops serotinus (type)	77–34	40. 7
Skull "little F." Quinn Draw, South Dakota. Nat. Mus. 4703, Brontops dispar	62	39. 0
Little skull "B." On fork of west fork of Corral (?Quinn, J. B. H.) Draw. Probably skull b, Nat. Mus. 4947, Brontops brachycephalus, female, aged	14. 4	14. 4

[a] In a letter to the author, dated July 31, 1901, Hatcher expressed grave doubts as to the accuracy of these levels on account of practical difficulties encountered in the field.

[b] From horizon of skull O′, Nat. Mus. 4705, to horizon of this skull there is a vertical upgrade of 46.6 feet.

[c] 27 feet above skull V′.

[d] Very high, 8 to 10 feet from top of titanothere zone (Hatcher).

[e] 32 feet below the 3-foot siliceous limestone layer at top of *Titanotherium* zone. The Pierre shale contact was far away, and although it was on a line of levels the dip in interval could not be ascertained precisely (Darton).

MAMMALIAN LIFE OF THE LOWER OLIGOCENE TITANOTHERIUM ZONE

The most highly characteristic feature of the Oligocene mammals as a whole, compared with the Eocene mammals, is their decided modernization, which is shown in the following table giving the percentages of the modern and the archaic families of the Oligocene Plains fauna as compared with those of the Eocene mountain-basin fauna.

Percentages of modern and archaic families in Eocene, Oligocene, and Miocene time

	Modern families or those closely related or ancestral to modern families	Archaic families supposed to be wholly extinct and not closely related to modern types
Basal Eocene	13	87
Lower and middle Eocene	32	68
Upper Eocene	42	58
Lower Oligocene	65	35
Miocene	86	14

This modernization of mammalian life is in part real and in part apparent, because the Plains fauna presents for the first time the full aspect of the upland, plains, and meadow life, especially the smaller and larger herbivorous ungulates. This life is, however, only partly revealed in the *Titanotherium* zone, in which conditions for the fossilization and preservation of the land fauna were less favorable than in the overlying *Oreodon* zone (Brule clay). In fact, remains of the small ungulates, such as the horses of the period (*Mesohippus*), are very rarely preserved in either the coarser or the finer sediments of the Chadron of South Dakota but are found more abundantly in the sediments of Pipestone Creek, Thompson Creek, and other areas in Montana and in the Swift Current Creek area of Saskatchewan. The entire *Titanotherium* zone fauna as listed by Osborn and Matthew (1909.321, pp. 103, 104) contains representatives of 6 orders and 24 families of mammals, which are of interest and value as showing the principal types of mammals that were in competition with the titanotheres in the struggle for existence.

Fish, reptile, and mammal fauna contemporary with the titanotheres

Common name or comparable form, babits or habitat, nature of deposits, etc.	Classific name	Region inhabited
	PISCES	
	Actinopterygii:	
Bowfins (Amia); rivers and streams	Amiidae—	
	Amia whiteavesiana Cope	Saskatchewan.
	Amia macrospondyla Cope	Do.
	Amia exilis Lambe	Do.
Gar pikes (Lepidosteus); rivers and streams	Lepidosteidae—	
	Lepidosteus longus Lambe	Do.
Catfishes (siluroids); rivers and streams	Siluridae—	
	Rhineastes rheas Cope	Do.
	Ameiurus cancellatus Cope	Do.
	Ameiurus maconnelli Cope	Do.
	REPTILIA	
Crocodiles and alligators; rivers and streams	Crocodilia:	
	Crocodilidae—	
	Crocodilus? sp. Lambe	Do.
	Alligator prenasalis (Loomis)	South Dakota.
	Squamata:	
	Anguidae—	
Compare Gila monster (Heloderma)	Peltosaurus granulosus Cope	Saskatchewan.
	Helodermoides tuberculatus Douglass	Montana.
	Glyptosaurus montanus Douglass	Do.
	Palaeophidae—	
Insufficiently known	Ogmophis compactus Lambe	Saskatchewan.
	Chelonia:	
Subterrestrial; wet and forested places	Dermatemydidae—	
	Xenochelys formosa Hay	South Dakota.
	"Anosteira ornata Leidy"	Saskatchewan.
Marsh turtles	Emydidae—	
	Graptemys inornata (Loomis)	South Dakota.
Land tortoises; characteristic of uplands, open country.	Testudinidae—	
	Testudo brontops Marsh	Do.
	Testudo exornata Lambe	Saskatchewan.
	"Stylemys nebrascensis Leidy"	Do.
Soft-shelled turtles; aquatic; remains found in fluviatile sandstones.	Trionychidae—	
	Platypeltis leucopotamica Cope	Saskatchewan, South Dakota.
	MAMMALIA	
	Marsupialia:	
	Didelphidae—	
Marsupials, opossum; small, forest-dwelling; arboreal.	Peratherium titanelix Matthew	Montana.
	?Peratherium valens (Lambe)	Saskatchewan.
	Ferae:	
	Hyaenodontidae—	
Cursorial, predacious, like the Thylacinus of Tasmania; resembling modern wolves in size.	"Pseudopterodon" minutus [a] (Douglass)	Montana.
	Hemipsalodon grandis Cope	Saskatchewan.
Comparable with hyena of Africa; powerful jaws.	Hyaenodon cf. H. cruentus Leidy	Saskatchewan, South Dakota.
	Hyaenodon cf. H. crucians Leidy	Do.
	Canidae—	
Analogous to the larger civets	Daphaenus dodgei Scott	South Dakota.
	Daphaenus cf. D. hartshornianus Cope	Saskatchewan.
	Daphaenus cf. D. felinus Scott [b]	Do.
	Daphaenus sp	South Dakota.
Analogous to the marten and mongoose	Nothocyon [c] paterculus (Matthew)	Montana.
	?Cynodon sp	South Dakota.
Mustelines	Mustelidae—	
Analogous to the marten and polecat	Bunaelurus infelix	Montana.

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[a] This is, in fact, an undescribed genus, more primitive than *Hyaenodon* and *Pterodon*, allied apparently to *Sinopa* and *Tritemnodon*.

[b] If Mr. Lambe's figure is correct this can hardly be *D. felinus;* it agrees much better with *D. dodgei* Scott.

[c] *Cynodictis* is not applicable to the American Oligocene species that have been called by that name. *Nothocyon* is next in priority among available names. The type, however (*N. geismarianus*), is a large and rather specialized species from the John Day formation. It may be necessary to separate the small species from the middle and lower Oligocene under the name *Pseudocynodictis* (Schlosser).

Fish, reptile, and mammal fauna contemporary with the titanotheres—Continued

Common name or comparable form, habits or habitat, nature of deposits, etc.	Classific name	Region inhabited
	MAMMALIA—continued	
	Ferae—Continued.	
	Felidae—	
Analogous to the leopard and cheetah	Dinictis fortis Adams	South Dakota.
	Dinictis fortis felina Leidy	Saskatchewan.
	Dinictis sp	South Dakota, Montana.
	Insectivora:	
	Leptictidae—	
Possibly like the modern Gymnura of the East Indies.	Ictops acutidens Douglass	Montana.
	Ictops thomsoni Matthew	Do.
	Ictops montanus Douglass	Do.
	Ictops intermedius Douglass	Do.
	Ictops tenuis Douglass	Do.
	Ictops major Douglass	Do.
	?Solenodontidae—	
Allied to the Solenodon of the West Indies(?)	Micropternodus borealis Matthew	Montana.
	?Chrysochloridae—	
Fossorial, like the Cape golden moles	Apternodus mediaevus Matthew	Montana, Wyoming.
	"Xenotherium"[d] unicum Douglass	Montana.
	Nothocyon "lippincottianus" (Cope)	Saskatchewan.
	Glires (Rodentia):	
	Ischyromyidae—	
Burrowing; analogous to marmots, prairie dogs, and the like.	Titanotheriomys veterior (Matthew)	Montana, Wyoming.
	Titanotheriomys "Ischyromys typus Leidy"	Assiniboia.
Squirrels and ground squirrels (spermophiles).	Prosciurus vetustus Matthew	Montana.
	Prosciurus jeffersoni Douglass	Do.
	Prosciurus ?saskatchewensis (Lambe)	Saskatchewan.
Like small heteromyids	Cylindrodon fontis Douglass	Montana, Wyoming, Saskatchewan.
	Castoridae—	
Possibly cursorial; foot slender	Eutypomys parvus Lambe	Do.
	Heteromyidae—	
Found in Chadron clays; like pocket mice; Perognathus.	Adjidaumo (Gymnoptychus) minor Douglass	Montana.
	Adjidaumo (Gymnoptychus) minimus Matthew.	Do.
	Leporidae—	
Rabbits; remains found in the Chadron clays	Palaeolagus temnodon Douglass	Do.
	Palaeolagus brachyodon Matthew	Do.
	Palaeolagus "turgidus Cope"	Saskatchewan.
	Perissodactyla:	
Grazing, upland rhinoceroses; cursorial; found in the Chadron clays.	Hyracodontidae—	
	Hyracodon priscidens Lambe	Assiniboia.
	Hyracodon sp	Montana, Wyoming, South Dakota.
Amphibious rhinoceroses; found in the channel sandstones.	Amynodontidae—	
	Metamynodon sp	Do.
	Rhinocerotidae—	
Small rhinoceroses of rather slender proportions, probably of browsing habit; remains found chiefly in clays.	Trigonias osborni Lucas	Do.
	Trigonias sp	Do.
	Leptaceratherium trigonodum Osborn	Do.
	Caenopus mitis Cope	Assiniboia, South Dakota.
	Caenopus "occidentalis Leidy"	Assiniboia.
	Caenopus exiguus Lambe	Do.
	Caenopus cf. C. platycephalus Osborn	South Dakota.
	Caenopus sp. div	Montana, Colorado, South Dakota.
	Lophiodontidae—	
	Colodon (= Mesotapirus) occidentalis Leidy	South Dakota.
	Equidae—	
Very small, slender-limbed horses, cursorial; grazers and browsers. Abundant in clays; rare in sandstones.	Mesohippus celer Marsh	Colorado, South Dakota.
	Mesohippus westoni Cope	Saskatchewan.
	Mesohippus latidens Douglass	Montana.
	Mesohippus montanensis Osborn	Do.
	Mesohippus proteulophus Osborn	South Dakota.
	Mesohippus hypostylus Osborn	Do.
	Mesohippus precocidens Lambe	Saskatchewan.

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[d] Name preoccupied by *Xenotherium* Ameghino, 1904, a genus of edentates.

Fish, reptile, and mammal fauna contemporary with the titanotheres—Continued

Common name or comparable form, habits or habitat, nature of deposits, etc.	Classific name	Region inhabited
	MAMMALIA—continued	
	Artiodactyla:	
Suillines abundant and characteristic. Difficult to place. Small, compact, didactyl feet and fairly long limbs, cursorial. Ribs and abdomen small. Common in clays and sandstones.	Entelodontidae—	
	Archaeotherium mortoni Leidy	South Dakota.
	Archaeotherium clavum Marsh	Do.
	Archaeotherium crassum Marsh	Colorado.
	Archaeotherium ingens Marsh	South Dakota.
	Archaeotherium coarctatum Cope	Saskatchewan.
	Dicotylidae (=Tagassuidae)—	
Like the peccaries, rare	Perchoerus sp	South Dakota.
	Leptochoeridae—	
Little known, rare	Stibarus montanus Matthew	Montana.
	Anthracotheriidae—	
Analogous to pigs. Occur chiefly in the clays	Ancodus americanus Leidy	South Dakota.
	?Anthracotherium sp	Do.
	Oreodontidae (=Agriochoeridae)—	
Peccary-like, but of grazing habits. Rather scarce, not abundant as in later life zones. Browsing. Agriochoerus partly arboreal proportions like the larger cats.	Bathygenys alpha Douglass	Montana.
	Limnenetes platyceps Douglass	Do.
	Limnenetes anceps Douglass	Do.
	Oreodon (=Merycoidodon) hybridus Leidy	South Dakota.
	Oreodon (=Merycoidodon) bullatus Leidy	Do.
	Oreodon (=Merycoidodon) affinis Leidy	Do.
	Oreodon (=Merycoidodon) "culbertsonii Leidy."	Saskatchewan.
	Agriochoerus maximus Douglass	Montana.
	Agriochoerus minimus Douglass	Do.
	Agriochoerus sp	South Dakota.
	Agriochoerus "antiquus Leidy"	Saskatchewan.
	Hypertragulidae—	
Analogous to existing chevrotains of Africa	Trigenicus socialis Douglass	Montana.
	?Trigenicus mammifer Cope	Saskatchewan.
	?Trigenicus speciosus Lambe	Do.
	?Leptomeryx esulcatus Cope	Do.
	Leptomeryx sp. div	South Dakota.
Analogous to Hyaemoschus	Heteromeryx dispar Matthew	Do.
	?Heteromeryx transversus Cope	Saskatchewan.
	"Anthracotherium pygmaeum" Lambe [e]	Do.
Grazing, upland, cursorial, like the smaller antelopes of Africa and the guanacos of South America.	Camelidae—	
	Eotylopus primaevus Matthew	Wyoming.
	?Leptotragulus profectus Matthew	Montana.
	"Poëbrotherium wilsoni Leidy"	Saskatchewan.

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[e] Based upon a part of a "right upper molar," which from Mr. Lambe's figure appears to be a left lower molar, probably of a hypertragulid comparable to *Heteromeryx*.

NOTES ON THE HABITAT OF THE FAUNA OF THE CLAY AND SANDSTONE AS A WHOLE

Matthew was the first to distinguish between the upland forms, found chiefly in the clays (flooded plains), and the lowland and aquatic forms, found in the sandstones (river channels). The following discriminations have been made:

1. *Typical grazing group of open plains.—Hyracodon, Oreodon, Mesohippus, Eotylopus, Poebrotherium.* Note the cropping front teeth, associated with delicately cut and progressively long-crowned grinders, small, compact feet, and, except in *Oreodon*, long, slender limbs. *Colodon* may belong here.

2. *Browsing group of bush country and forest.*—Titanotheres, *Metamynodon, Caenopus, ?Entelodon, ?Anthracotherium, ?Ancodon, ?Agriochoerus.* All large-sized fighting beasts, with coarse, heavy enamel on cheek teeth; front teeth adapted to lip browsing. *Metamynodon* may very likely have been amphibious; the others probably were not. *Entelodon* is somewhat of an enigma; *Sus* is the nearest analogue but not a close one.

3. *Small bush or forest-dwelling browsers.—Heteromeryx, Leptomeryx, Trigenicus.* Analogous to the modern tragulines and probably of similar habits.

4. *Carnivora.*—The hyaenodonts are analogues of the wolves. The ancestral canids are analogues of the mustelines and viverrines. True mustelines are scarce. *Dinictis* is the only cat.

5. *Rodentia.*—Rabbits much like modern "cottontails" of the Great Plains. Heteromyids have appeared, but no true mice (Muridae) until the middle

Oligocene. Ischyromyids are abundant and include terrestrial (?) and arboreal (?) forms; whether fossorial forms existed or not is not proved. *Eutypomys*, though referred to the Castoridae, is not at all analogous to the modern beaver but rather to a large squirrel or spermophile.

6. *Insectivora.*—The leptictids have rather sharp-cusped teeth and are intermediate in type between opossums and tree-living erinaceids. The moderate wear of the teeth is evidence against the theory that their food was worms or other terrigenous forms. There are no obvious arboreal adaptations in the limbs and feet; perhaps they may have been semi-arboreal. Their survival, unaltered as to cheek teeth, from the basal Eocene is suggestive of some special protection, such as spines. As for the zalambdodonts, they may have been fossorial, *Xenotherium* being molelike, but the evidence is insufficient.

7. *Marsupialia.*—Rare. Precisely like small opossums in the structure of the teeth.

8. *Aves.*—No birds have been recorded in this fauna, although they probably existed and may have been even numerous and varied.

9. *Reptilia.*—Crocodiles and trionychids occur in the sandstone lenses; probably they were aquatic forms analogous to modern crocodiles and soft-shell turtles. In the clays *Testudo* occurs; also *Xenochelys*, probably similar in habits to modern land tortoises and marsh turtles. The lizards are apparently analogous to the Gila monster and to some of the swift-footed anguid lizards. Burrowing amphisbaenids occur in the *Oreodon* zone but have not yet been discovered in the lower Oligocene; no doubt they formed part of the fauna; also other lizards and many snakes.

10. *Batrachia.*—No batrachians have been recorded, but there is no reason to suppose that they were absent or rare.

11. *Pisces.*—A few fragments of fresh-water fishes, similar to those characteristic of muddy rivers of to-day, are recorded from the Swift Current beds in Canada. They will doubtless be found in the sandstones and other stream deposits of the *Titanotherium*-bearing beds of the United States.

SECTION 3. ADAPTIVE RADIATION, PRIMARY AND SECONDARY, THROUGH CHANGE OF ENVIRONMENT A CAUSE OF THE DIVERSIFICATION OF THE TITANOTHERES

HABITAT OF THE UNGULATES

The present geographic features of modern equatorial Africa, consisting of a high central plateau, river borders, savannas, and forests, exhibit a close parallel to what we believe were those of the known titanothere region of North America in Eocene and lower Oligocene time. These conditions may also be compared with those found in the existing flood plains at the headwaters of the great rivers of South America east of the Andes in the warm temperate and subtropical but not in the tropical belt.

Adaptive radiation: Favorite habitats of existing perissodactyls and elephants

[See fig. 78]

RHINOCEROSES

Rhinoceros sondaicus. Java. Typically a forest dweller, occasionally found in alluvial swamps. A browser.

Rhinoceros (Dicerorhinus) sumatrensis. Hilly forest districts of Sumatra. A browser.

Rhinoceros (Opsiceros) bicornis. Bush-covered country and open plains; forested foothills in the dry season. Fairly abundant on the top of the Aberdare, British East Africa (elevation 9,000 feet). A browser, feeding on shrubs, roots, leaves, etc.

Rhinoceros unicornis. Grassy jungles of India. A grazer.

Rhinoceros (Ceratotherium) simus. Savannas and grassy plains, with swamps or water holes for wallowing. A grazer.

TAPIRS AND ELEPHANTS

Tapirus roulini. Pinchaque tapir of the high region of the Andes and Cordilleras. A browser.

Elasmognathus bairdi. A hill dweller, seeking lowlands during rainy seasons. A browser.

Tapirus terrestris. A forest dweller. Lowlands of Brazil and Paraguay. A browser, feeding on palm leaves, fruits, water plants.

Tapirus indicus. Lowlands and forests of India. A browser.

Elephas (Loxodonta) africanus. Less typically a forest animal than *E. indicus.* Savannas, dry country, and forests. Ranges from the seacoast to points beyond the alpine heath zone of Mount Kenia and the bamboo belt of other African mountains. Ascends and descends steep places with wonderful facility. A browser and grazer.

HORSES AND ZEBRAS

Equus burchelli. Essentially a plains dweller; often found in sparse savannas.

E. grevyi. Grevy's zebra. Low plateaus, thorn bush and feather grass country that has gravelly soil. Essentially a dweller in open plains and savannas.

E. quagga (extinct). The quagga. A karoo dweller. Frequents open, arid plains.

E. zebra. Mountain zebra. Hilly and mountainous country.

E. przewalskii. Przewalski horse. Gobi Desert. A steppe dweller.

ASSES

Equus asinus. Abyssinian ass. Wiry hedge and upland country.

E. hemionus kiang. The kiang. Desolate plains in the vicinity of lakes and rivers. High table-lands of Tibet (15,000 feet). Coarse wiry pasture and rough hard yellow grass.

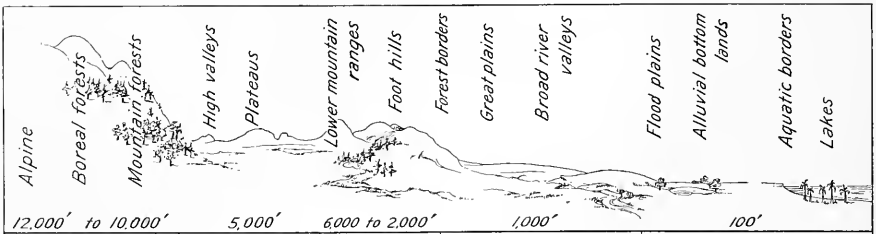
E. asinus somalicus. Striped African ass. Borders of the Nubian Desert.

E. hemionus onager. Persian wild ass. Migrates from the plains to the hills in summer. The onager of Persia.

POLYPHYLY AMONG HOOFED MAMMALS

THE TITANOTHERES AND OTHER EXTINCT FORMS

It is astonishing to find within relatively small geographic areas both Eocene and Oligocene remains of many kinds of titanotheres, which lived close together under very similar climatic conditions, the more so because the known geographic distribution of the titanotheres in Eocene time is confined to the central Rocky Mountain region and extends only from the Wind River Basin of Wyoming on the north to the White River Basin of Utah on the south, a distance of



HABITAT	BROWSERS Conifers Hard woods	GRAZERS Hard siliceous grasses	BROWSERS Shrubs Lesser forests	GRAZERS Grass jungles Grassy meadows Bush country	BROWSERS Savannahs Reeds and swamps Jungles Lake-border reeds Swamps
Rhinoceroses		C. simum (Africa) Hyracodonts (North America)	D. sumatrensis (Sumatra)	R. unicornis (India) O. bicornis (Africa) Aceratheres (Europe, Asia, N. America)	R. sondaicus (Java) Amynodonts (Wyoming) Metamynodonts (South Dakota)
Elephants Mastodons		E. africanus — — (Savannahs of Africa)	— — — — — — — — Elephas indicus (Forests of India)	E. africanus Palaeomastodonts Mastodonts	Hippopotami Manatee Dugong
Horses Asses Zebras		E asinus (Africa) E. przewalski (Asia steppes) E. zebra — — — — (Africa plateaus)	Hypohippids — E. zebra	— — — — — — — — — Hypohippids E. burchelli E. grevyi E. quagga	
Tapirs	Tapirus roulini (High Andes) (South America)		Tapirus bairdi (South America)		Tapirus indicus T. americanus (Lowlands S. America)
Titanotheres		Telmatheres (High plains) Menodonts — —	Symborodonts (Hilly regions) — — — — — — —	Manteoceratines Brontotheres (Flood plains) — Menodonts Brontopines	Dolichorhines Metarhines Palaeosyopines

FIGURE 78.—Geographic cross section showing the nature of the habitats of the larger existing ungulates and of the titanotheres as illustrating adaptive radiation

The upper row shows the present geographic distribution of the ungulates in continental Africa and the theoretic geographic features of the Rocky Mountain region in Eocene and Oligocene time—namely, high valleys, plateaus, foothills, plains, river valleys, flood plains, bottom lands, and river and lake borders. The second row shows the corresponding present distribution of the plant foods of different types of browsing and grazing, cursorial, graviportal, and semiaquatic quadrupeds. The four next lower rows show, in descending order, the corresponding adaptive radiation of the rhinoceroses, extinct and living; of the elephants and mastodons and the typical aquatic hippopotami and sirenians; of the plateau, plains, and forest types of horses; of the mountain, foothill, and lowland types of tapirs. The bottom row shows the theoretic adaptive radiation of the principal types of titanotheres—telmatheres and menodonts of the higher levels; symborodonts in the foothills; manteoceratines, brontotheres, brontopines, and menodonts on the flood plains; dolichorhines, metarhines, and palaeosyopines on the lowlands and river borders.

480 kilometers (298 miles). The continental extent of the distribution of the titanotheres, which is still unknown, was undoubtedly far greater, including, perhaps, the larger part of the North American continent and certainly extending into Asia. In Oligocene time the known geographic distribution was somewhat larger, including an area extending from Colorado to southern Alberta and measuring from north to south about 1,200 kilometers (746 miles). Titanotheres lived also in eastern Europe, both in Transylvania and Rumelia, also in Mongolia.

Our present knowledge of the geologic horizons of the titanotheres is still extremely meager regarding certain strata. The extent of our knowledge is summarized below.

Geologic horizons of the known genera and subgenera of the titanotheres

Lower Oligocene; upper, middle, and lower levels: *Brontops, Diploclonus, Allops, Menodus, Brontotherium, Megacerops.*

Upper Eocene; Uinta C (true Uinta): *Telmatherium, Manteoceras, Diplacodon, Protitanotherium, Eotitanotherium.*

Upper Eocene; Washakie B and Uinta B: *Metarhinus, Rhadinorhinus, Mesatirhinus, Dolichorhinus, Manteoceras, Telmatherium, Diploceras.*

Middle Eocene; upper part of Bridger formation: *Mesatirhinus, Manteoceras, Palaeosyops, Telmatherium.*

Middle Eocene; lower part of Bridger formation: *Limnohyops, Palaeosyops, Eometarhinus.*

Lower Eocene; Wind River formation: *Lambdotherium, Eotitanops.*

As compared with what we observe among the hoofed animals living to-day these titanotheres certainly dwelt near one another under very similar conditions of climate but in different feeding ranges and local habitats; they sought the same watercourses, and their remains were entombed in similar deposits. As the whole tendency of discovery up to the present time has been to multiply the phyla, to separate and diversify the titanotheres, the probability is that many other kinds of titanotheres lived in other parts of North America and Asia.

The evolutionary principle underlying these diversities Osborn (1902. 214, p. 353) has called adaptive radiation, which is the application to paleontology of the idea of divergence as conceived and developed successively by the studies of Lamarck, Darwin, Huxley, and Cope.[11] Radiation is a broader principle than divergence, because it implies evolution in every direction possible to the organism. The idea of radiating branches from central forms assists the imagination, because the known radiations of extinct animals must be supplemented by the unknown radiations, and it is most remarkable how these missing radii have been discovered in group after group of animals. Such adaptive "radiation" is either "continental"—that is, it occurs where diversities in food, soil, or climate prevail over large areas—or "local"—that is, it occurs where marked diversities prevail in relatively small areas. The radiation among the titanotheres in southern Wyoming and northern Utah seems to have been largely "local," indicating that the physiography of the mountain basin was highly diversified.

One of the results of adaptive radiation is polyphyletic evolution, the existence within families of a large number of independent minor branches that may pursue more or less divergent evolution in local or continental regions but that may come together in river and flood-plain basins, so that their fossil remains are found in the same localities and deposits. Polyphyletic evolution has been discovered so frequently, among both the mammals and the lower forms of life, that it may be considered the rule and monophyletic evolution along single lines the exception. Some of the examples of polyphyletic evolution among extinct mammals that have been determined in comparatively recent years are the following:

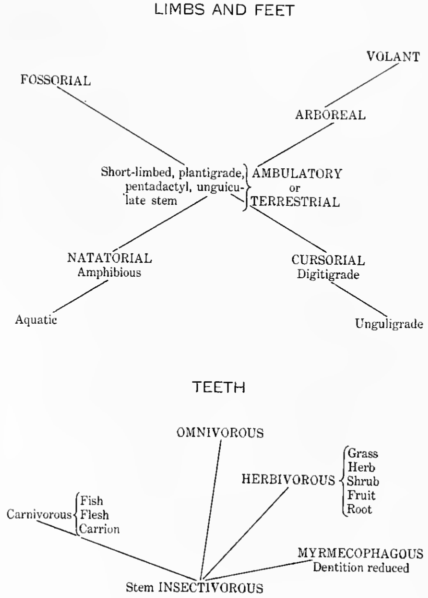


FIGURE 79.—Original radiation of the unguligrade Herbivora, Carnivora, and Insectivora, showing the adaptations of teeth, limbs, and feet to various habits and environments

	Contemporaneous branches, or phyla
Oreodonts (Cope, Wortman, Peterson, Matthew, Douglass)	7–9
Lophiodonts (Osborn, Depéret)	5–7
Anthracotheres (Stehlin, Depéret, Andrews)	6–8
Rhinoceroses (Osborn)	8–9
Horses (Osborn, Gidley, Matthew)	8–9
Titanotheres (Osborn)	10–12
Elephants and mastodons (Osborn)	7–10

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[11] See also Osborn, H. F., 1902.214; 1905.267; 1910.345; 1910.346; Stevenson-Hamilton, J., 1912.1; Sclater, P. L., 1894.1; Lydekker, R., 1893.1; Gregory, J. W., 1896.1; Blanford, W. T., 1888.1; Kobelt, W., 1902.1; Schimper, A. F. W., 1903.1; Lönnberg, E., 1912.1; Roosevelt and Heller, 1914.1.

THE EXISTING AFRICAN ANTELOPES

The polyphyly among the titanotheres and other extinct Perissodactyla presents a marked contrast to the impoverished conditions among the existing members of the same order when we consider that in all parts of Asia and Africa only five kinds of existing rhinoceroses can be distinguished by the characters of the skeleton and teeth alone, that only six or eight kinds of horses, asses, and zebras in the same great region can be distinguished by their hard parts, and that, similarly, among the tapirs of Asia and South America only three kinds can be distinguished. This contrast between present monophyly and former polyphyly is due to the fact that the order Perissodactyla, though formerly a dominant group, is now a declining group.

In the existing Bovidae, especially those in the great continent of Africa, we have a parallel to the ancient polyphyly of the titanotheres and other Perissodactyla. The Bovidae is a family that includes the cattle and antelopes and that is now in the highest stage of radiation and adapted to a great variety of physiographic and biotic conditions, as shown in the primary and secondary adaptations in the seven subfamilies of the African antelopes.

The African antelopes: Subfamilies, habits, and environment

Subfamilies and habits	Environment
Antilopinae (browsers and grazers):	
Gazelles	Plains and deserts.
Pallahs (impalas)	Thorny bush and glades.
Springbucks	High veldts.
Gerenuks	Deserts and bush.
Saigas	Steppes.
Bubalidinae (mostly grazers):	
Gnus	Open plains.
Hartebeests	Open forests or plains.
Blesboks	
Sassabies	Open rolling country.
Tragelaphinae (browsers and grazers):	
Elands	Open forests and flats.
Koodoos	Stony hills.
Bush bucks	Forests.
Bongos	Dense forests.
Situtungas	Swamps and lagoons.
Hippotraginae (grazers):	
Roan antelopes	Thin forests.
Sable antelopes	Rolling uplands.
Gemsboks	Open deserts.
Addaxes	Waterless deserts.
Neotraginae (browsers and grazers):	
Klipspringers	Hills, mountains.
Oribis	Thin forests.
Dik-diks	
Cephalophinae (mostly browsers):	
Duikers	Dense forests and bush.
Cervicaprinae (grazers on succulent plants near water):	
Water bucks	Open forests and stony hills.
Lechwes	Reed swamps, river borders.
Kobs	Open swampy plains.
Reedbucks	Slopes of hills.
Rhebucks	Flat table mountains.

An incipient or attempted adaptation to a grazing life is seen in the teeth of certain titanotheres. Most titanotheres are browsers. Broadly speaking, herbivorous animals that live on open plains are grass eaters and tend to become gregarious in habit and cursorial in locomotion, whereas those that prefer the shady depths of the forests are browsers, are of solitary habit, and are mediportal in locomotion. There are exceptions, such as the black rhinoceros (*Rhinoceros* (*Opsiceros*) *bicornis*), which now frequents the treeless plains of East Africa but which is habitually a browser, although it is at times a grazer. The long-necked giraffes are fond of rather dry and fairly open country and are not found in strictly forested regions, yet they are wholly browsers, being especially fond of the leaves of certain thorny acacias, notably *Acacia giraffa*, and the related short-necked okapi, which is found only in the dense forests of the Congo, is a browser.

The principles of adaptation shown in the skull and teeth of Perissodactyla to browsing and grazing habits are described in Chapters V and VI of this monograph. The adaptation of the limbs of the Perissodactyla to speed and weight are described in Chapter VII.

In general, the competition and range for food among hoofed animals is accompanied by lengthening of the limbs from medium-paced (mediportal) types to either swift-moving (cursorial) types or heavy-bodied (graviportal) types. Similarly, adaptation of the grinding teeth to browsing habits is seen in the short-crowned (brachyodont) types, and transition to the grazing habit is accompanied by lengthening (hypsodontism) of the crowns of the grinding teeth. Such changes are accompanied by changes in the proportions of the head to adapt the action of the teeth to browsing or to grazing. We observe a passage from short-headed (brachycephalic) to long-headed (dolichocephalic) forms of skull. In adaptive radiation every possible combination of lengthening and of shortening of skull, tooth, limb, and foot may arise, as well as notable coincidences of structure in different forms, for similar kinds of food may be found and similar feeding habits may be acquired in widely separated habitats or greatly different environments. Contrasts in structure, such as those shown below, are equally notable.

Contrast in structure between browsing and grazing types

Browsing types (brachyodont)	Grazing types (hypsodont)
Short-headed (brachycephalic)	Long-headed (dolichocephalic).
Straight-headed (orthocephalic)	Bent-headed (cyptocephalic).
Short-limbed (brachymelic, brachypodal).	Long-limbed (dolichomelic, dolichopodal).

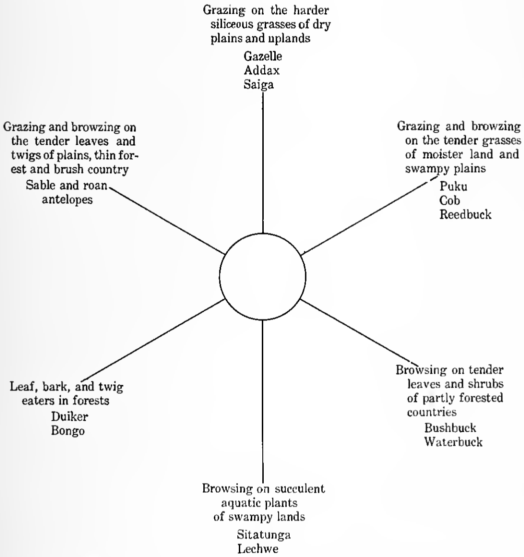

FIGURE 80.—Adaptions in the structure of the skull and teeth of Herbivora to diverse habits of feeding

Double or even multiple adaptive radiation is continually in operation, first, in the structure of skull and tooth, which is dependent on the nature of the food, and, second, in the structure of foot and body, which is dependent on the nature of the soil. Thus may arise cursorial (long-limbed) grazers (long-toothed), graviportal (heavy-limbed) grazers (long-toothed), or cursorial (long-limbed) browsers. There is no fixed law of correlation of structure of skull and tooth such as was supposed by Cuvier. The law of correlation as restated by Osborn (1902.214) is as follows:

Structure of feet (correlated chiefly with structure of limb and body) and structure of teeth (correlated chiefly with structure of skull and neck) diverge independently in adaptation respectively to obtaining food (by feet) and eating food (by teeth) in different environments. Each structural feature is evolved directly to perform its own mechanical functions or purposes, yet in such a manner that each is consonant with the other.

CONTINENTAL ADAPTIVE RADIATION OF THE AFRICAN ANTELOPES

The African antelopes are divided into seven subfamilies, all mediportal to cursorial in limb structure but widely different in tooth and skull structure, as shown in the table on page 124.

The 133 or more species (Sclater, 1894.1) embraced in these seven subfamilies seek food and protection from enemies on the varied surface of the African continent in habitats including no less than 17 different kinds of country.

Each type of habitat has food peculiarly favorable to certain feeding habits to which the structure of the teeth and skull is specifically adapted. Each type of habitat demands modifications of limb, foot, and hoof structure for movement in the search for food and escape from enemies.

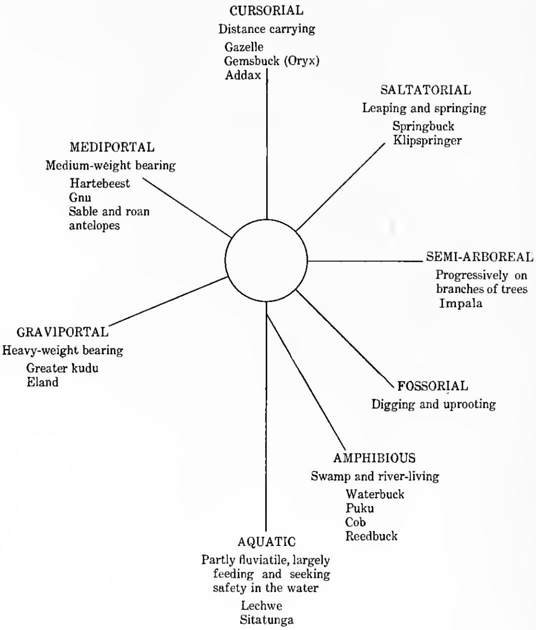

FIGURE 81.—Convergent adaptations in the structure of the limbs and feet of ungulates

Certain gazelles are independent of watercourses. The adaptive radiations indicated above occur independently within different subfamilies.

The theory of the evolution of the antelope is that in mid-Tertiary time a divergent primary radiation divided them into seven subfamilies, each with its distinctive mode of life. During a long period of geologic time the Bovidae have undergone secondary radiations (A–Q, fig. 82), by which certain branches of these subfamilies have become adaptively convergent toward certain branches of other subfamilies through the adoption of similar habits and habitats. Thus analogous genera and species arise independently in each subfamily. For example, waterless deserts were sought both by the addax, among the Hippotraginae, and by the gazelle, among the Antilopinae; reeds, river borders, and lagoons were sought both by certain Cervicaprinae, such as the lechwes and kobs, and by certain of the Tragelaphinae, such as the situtungas.

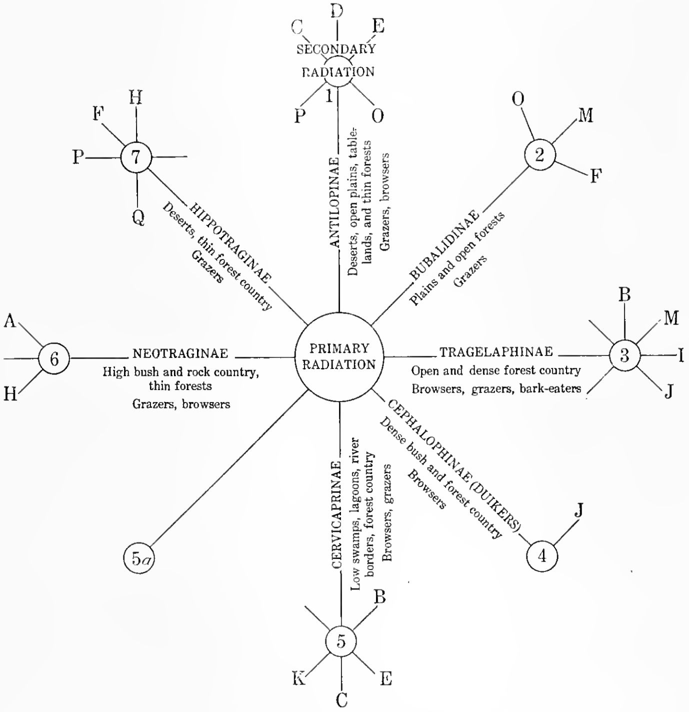

FIGURE 82.—Adaptive radiation in the feeding habits of antelopes, as observed by Stevenson-Hamilton in 1912

1–7, Primary radiations; A–Q, secondary radiations

ADAPTIVE RADIATION IN THE FEEDING HABITS OF ANTELOPES

The habits and habitats of the antelopes, as noted by Stevenson-Hamilton (1912), are as follows:

1. *Antilopinae*.—The impalas (*Apyceros melampus*) cling to neighborhoods of dense thorny bush, to which they fly for refuge. More partial to browsing than to grazing. Food consists largely of leaves and shoots, but they eat young and tender grass freely after early rains. Staple diet leaves and fruit of certain acacias, also twisted bean pods of the same. In March fruit of marula is eaten. Toward the end of the dry season they completely strip the bush of everything edible up to the extreme height which they are able to reach. * * * The springbucks (*Antidorcas euchore*) are typical of the high veldt fauna of South Africa. The only member of the gazelle group in this region. Love high, open tablelands. * * * The typical African races of gazelles include 14 species, Grant's, Thomson's, Speke's, etc. Inhabitants of wide, open plains or sandy deserts. Largely independent of water.

2. *Bubalidinae*.—Antelopes of large size, large, moist rhinarium; including *Bubalis* (= hartebeest), *Damaliscus* (= bastard hartebeest), *Connochaetes* (= gnu, or wildebeest). *Bubalis* (= hartebeest), eight species, with everywhere same characteristics; frequent open or forest country or treeless plains; essentially grass eaters; like to drink regularly. Young carried about eight months. * * * *Damaliscus*, bontebuck (*D. pycargus*), blesbuck, tsessebe (sassaby) (both *D. albifrons*), grass-eating antelopes, favoring rather open and fairly flat country, never hills or thick jungle, partiality for shady patches of bush or forest for shelter during the hot hours. * * * *Connochaetes* (gnu, or wildebeest), white-tailed or black (*C. gnu*) and brindle or blue (*C. tautrinus*). Prefer open, rolling country interspersed with thick thorn or other bush. Sometimes remain in the open, bare spaces or plains where they can see for long distances. Essentially grass-eating animals. Pasture cropped closely. Sociable, gregarious.

3. *Tragelaphinae*.—Elands and bushbucks, inyalas, kudus, situtungas. Elands (*Taurotragus oryx*), plains type, graze with horses, donkeys, and cattle but browse by preference, favoring the grass only when fresh and green, sometimes cropping the tops of young river reeds. Gestation period eight and a half months. * * * Bongo (*Boocercus euryceros*), fond of the most dense forest, leaves and twigs of a certain kind of undergrowth, which grows from 6 to 8 feet in height. Young shoots all nipped off if bongo have been feeding. Also (?) bark eaters. * * * Bushbucks (*Tragelaphus scriptus*), forest dwellers, solitary, nocturnal, prefer densely wooded gullies, or kloofs, of South Africa. Browsers on the leaves of various small shrubs and trees; eat grass sparingly when the latter is fresh and green; roots and tubers form further articles of diet. * * * Inyalas (*Tragelaphus angasi*), very local and rare. Exhibit intense localization, probably due to the presence of some peculiar foodstuff, limited in quantity but necessary to the health of the individual animal. Probably browse on various leaves, shrubs, and fruits, bean pods and acacias, fruit of the marula; grass eaten when it is young and of good quality. * * * Situtungas (*Tragelaphus spekei*), semiaquatic animals, almost amphibious by nature. Great elongation of hoofs. Strong swimmers. Rapid locomotion upon dry land very difficult. Frequent extensive reed and papyrus swamps bordering lakes and large rivers. * * * Kudus (*Strepsiceros strepsiceros*), love stony or rather broken ground, covered with thorn scrub. Gregarious, more than most antelopes, a browser, subsisting chiefly on the leaves of thorn acacias and bush shrubs, together with the fruits of the marula and other trees.

4. *Hippotraginae.*—Sable and roan antelopes *Hippotragus*, oryx and addax, distinguished by the presence of horns in both sexes and small rhinarium or bare space on the muzzle. Sable (*H. niger*) to a great extent, though not entirely, a grass eater. Prefers thin forest country, interspersed with alternate thickets for shade, and open vleis for grazing. Regular drinker, seldom found more than a few hours from water. Gestation period about 270 days. * * * Roan antelope (*H. equinus*) favors rather upland, rolling country, not too thickly wooded, such as the middle veldt, but when persecuted takes readily to forest or the same environment as the sable antelope. A grass eater, and drinks regularly * * * [Genus *Oryx*.] The gemsbuck (*O. gazella*) of South Africa separated from its nearest generic relative (*O. beisa*) of German East Africa by an interval of 1,500 miles. Fairly numerous in Kalahari Desert, maintaining its security owing to its independence of water, able to quench thirst from moist tubers and roots. Generally found in small troops. The beisa (*O. beisa*) inhabits the Kilimanjaro district, British East Africa, Somaliland and the Sudan, east of the Nile. Sometimes found in herds of 50. Period of gestation eight and a half to ten months. White oryx (*O. leucoryx*) is found west of the Nile. Essentially a desert animal and like the gemsbuck apparently associates in small parties. [Genus *Addax*.] The addax [*A. nasomaculatus*] distantly related to both oryxes and roan and sable antelopes, pale sandy color. An inhabitant of waterless sandy deserts of northern Africa.

5. *Neotraginae.*—Klipspringers (*Oreotragus oreotragus*), like the chamois, prefer small shrubs and grasses growing among the stones. Live on natural moisture of the grass and nightly dews. * * * Oribi (*Ourebia*) frequents open grass country or plains not too thickly forested. Grass feeders, seldom found any distance from water. Eight species.

6. *Cephalophinae.*—Lovers of dense bush and forest of central and southern Africa. Thirty-eight species. Duiker (*Cephalophus grimmi*), solitary animal, fond of bush country. Never far from covert. Mainly browsers. Nibbles leaves and young shoots of various acacias, small shrubs. Grass consumed when young and fresh. Red duiker (*C. natalensis*), dense forests and bush. Blue duiker (*C. monticola*), essentially a browser, favors shelter or dense covert.

7. *Cervicaprinae.*—Animals of large or medium size. Water buck (*Cobus ellipsiprymnus*), open forest country, eastern Africa, favor banks of large rivers, prefer succulent herbage, but are partial to rough and broken country, stony hillsides, and vicinity of fairly thick bush; grass feeders. During dry season frequent banks of streams for succulent herbage. * * * Sing-sing water buck (*Cobus defassa*), habits similar to above. * * * The lechwe (*C. lechwe*) is smaller than the water buck. Hoofs elongated and pointed. Frequent great reed swamps and river borders, northern Rhodesia. Next to the situtunga, the most aquatic of all antelopes, standing knee or even belly deep in large shallow lagoons. Come ashore to graze, food consisting of grass and young reeds. * * * Gray's water buck (*C. maria*), frequent river bottoms and reedy grass. Stand in shallow water. * * * Puku (*C. vardoni*), less aquatic than the lechwe, approaching in this respect the water buck—that is, found close to but not in the water. Frequent swampy plains. * * * Uganda cob (*C. thomasi*), fond of open, rather swampy plains, near rivers or permanent water. Grazes on young shoots of grass. * * * Common reedbuck (*Cervicapra arundinum*), lowlands of Natal and Zululand, Transvaal bush country, etc. Favors grassy or reedy valleys near streams or permanent water of some kind. Occasionally met with in thin bush. Food consists entirely of grass. Do not take to water when alarmed. * * * Mountain reedbuck (*Cervicapra fulvorufula*), lower slopes of hills covered with rocks and loose stones, mingled with scattered bush and long grass. Grass eaters, at night descending from hills to nearest water. Affecting sides rather than tops of hills. * * * Bohor reedbuck (*Cervicapra redunca*), favoring open vleis and bush or swamp land. Like the neighborhood of water. * * * Gray rhebuck (*Pelea capreolus*), unlike mountain reedbuck, frequent flat tops of the table mountains; common in South Africa as well as higher levels of the ranges. Grass feeders, and descending at night to drink after the manner of the mountain reedbuck.

[Note vertical physiographic distribution of the genus *Cervicapra*.]

CAUSES OF VARIATION AND POLYPHYLY AMONG QUADRUPEDS

Change of physical environment.—A series of meteoric and biotic changes—that is, changes of season, of climate, or of rainfall, the appearance of new enemies, the introduction of new plants or the crowding out of old ones—will cause a change of food supply, which will cause a change of habitat, which in turn will cause a change of browsing or grazing habits that will affect locomotion—the use of the limbs in the search for food—and modify the form of the hoofs, because of the change of soil. The browsing mountain moose (*Alces*) of eastern Idaho, for example, has a hoof of very different form from that of the water-living forest moose of Maine. Among the new enemies that may appear are certain insect pests, such as flies or ticks, which may drive quadrupeds away from feeding ranges that are otherwise favorable into regions, perhaps not far distant, where food is scarcer and the general conditions are more adverse, and where, perhaps, the young are exposed to new dangers.

Such changes may bring about (1) a change of habit or (2) a change in habitat or environment, either of which, as a general law, culminates in (3) change of function, followed by (4) change of structure. (5) A change of function or habit certainly brings about a new "incidence" of selection or new set of causes tending to survival or extinction.

Change of appetite.—Variations in appetite are undoubtedly among the chief causes of local divergence. Stevenson-Hamilton (1912.1, pp. 97–158) noted the fastidious choice of food by each of the principal species of African antelopes, and other wild animals are very fastidious and seek an astonishing variety of food in the course of a single season. The predilection for certain kinds of food is very strong, and departures from it lead to adaptive radiation. Similarly Sampson (1905.1) records that the white-tailed deer (*Odocoileus virginianus*) browse on many kinds of plants in the course of a year.

Local polyphyly through reunion of phyla.—Animals that have diverged through migration or through geographic segregation or separation may later be brought together in one region. For example, the mule deer (*Odocoileus hemionus*) and the white-tailed deer (*O. virginianus*), which have probably evolved in different regions of the United States, are now found together in the same region in the West. In Miocene time the American rhinoceroses were joined in the western plains by certain European rhinoceroses. Thus continental radiations from great countries like Africa, Asia, or America may pour some of their branches into a single small region, mingling many distinct phyla.

Hypsodont or grazing types may mingle with brachyodont or browsing types in the same locality through their choice of grasses or of shrubs as their principal article of diet. Independently in the same region in southern Wyoming two of the branches of the titanotheres (*Telmatherium* and *Dolichorhinus*) began to acquire long-crowned teeth, while two others (*Palaeosyops* and *Limnohyops*) retained persistently short-crowned teeth.

HABITS OF THE RHINOCEROSES PARALLEL TO THOSE OF THE OLIGOCENE TITANOTHERES

Mingling of browsing and grazing rhinoceroses in Africa.—In equatorial Africa the Nile is an insuperable barrier between two species of rhinoceros, the "white rhinoceros," which is confined to the west bank, and the "black rhinoceros," which ranges along the east bank; yet these two species were formerly found together in the same regions of South Africa. The large grazing "white rhinoceros," *R.* (*Ceratotherium*) *simus*, has hypsodont teeth and grazes in the open country, particularly in the wide, grassy valleys, though it was frequently met on the high veldt of Matabele and Mashonaland, feeding at night or in the cooler parts of the morning and evening. Its food consists entirely of grasses. Its sight is bad, but its scent and hearing are acute. On the other hand, the smaller browsing "black rhinoceros," *R.* (*Opsiceros*) *bicornis*, which has brachyodont teeth, was formerly common on the slopes of Table Mountain and on the Cape Flats and closely overlapped *R.* (*Ceratotherium*) *simus* in certain parts of its range; it frequented bush-covered country more than open grass lands and was often found in rocky, stony districts. It is partly nocturnal in its habits. Its food consists entirely of leaves, twigs, and sometimes of the roots of certain bushes and shrubs, but seldom of grass (Roosevelt and Heller, 1914.1). Its adaptations are essentially those of a browser, for it prefers the twigs and small roots of certain shrubs which it finds on the treeless plains of East Africa (Stevenson-Hamilton, 1912.1). It has a considerable vertical geographic range,[12] being found also on the high plateau near the glaciers of Mount Kenya. (J. W. Gregory, 1896.1, p. 267.)

Habits of Asiatic rhinoceroses.—The existing species of Asiatic rhinoceroses differ in habitat; they do not mingle. *Rhinoceros unicornis* or *indicus*, which has relatively hypsodont grinders, frequents the swampy, grassy jungles of the plains of India. The *R. sondaicus* of Burma and Java has shorter grinders. As observed by Blanford (Lydekker, 1893.1, vol. 2, sec. 4, p. 470), it "is more an inhabitant of the forest than of the grass, and although it is found in the alluvial swamps of the sudarbans, its usual habitat appears to be in hilly countries. It has been observed at considerable elevations both in Burma and Java." Indeed there is much evidence that it probably ascends occasionally to as much as 7,000 feet above sea level. Its food consists largely of twigs and smaller branches. The third species of Asiatic rhinoceros, the Sumatran rhinoceros (*R.* (*Dicerorhinus*) *sumatrensis*), which has relatively short-crowned teeth, inhabits hilly forest districts and has been observed in Tenasserim at an altitude of 4,000 feet above the sea. According to Lydekker, it is a good swimmer and is said to have been seen swimming in the sea in the Mergui Archipelago, possibly traveling in search of new feeding grounds or to avoid certain unfavorable conditions.

Thus we find among the rhinoceroses three lines of adaptation to habitat and to food radiation—first, both hypsodont (grass-loving) and brachyodont (browsing) forms; second, a considerable geographic vertical range both in *R.* (*Ceratotherium*) *simus* and *R. sondaicus;* third, the occasional assumption of semiaquatic habits.

All these conditions were partly paralleled among the Oligocene titanotheres, which, however, attained no extreme hypsodontism.

HABITS OF THE EXISTING TAPIRS PARALLEL TO THOSE OF THE EOCENE TITANOTHERES

The Eocene titanotheres, although inferior in the structure of their grinding teeth, were nearest in form and in body adaptations to the existing tapirs. In the Tapiridae we find these principles of adaptive radiation—great vertical geographic range, including choice between upland and lowland habitat, and assumption of more or less aquatic life. The teeth are short-crowned (brachyodont), are crested (lophodont), and are superior in mechanism to the cone and crescent (bunoselenodont) grinders of the titanotheres. These principles are observed as follows:

1. According to J. E. Gray (1872.1, p. 486) *Tapirus pinchaque* ascends to very great heights in the Andes. M. Goudot "obtained a young female tapir at an elevation of about 1,400 meters—nearly up to the snow level on the Peak of Tolima in New Granada—about 1843." According to Gray (1872.1, pp. 487, 488) Tschudi, in the "Fauna peruana" (p. 213), says, "This species of tapir [*T. roulini*] is found in Peru on the eastern slope of the Cordilleras at an elevation of 7,000 or 8,000 feet, which is above the snow line."

2. On the other hand, the tapirs (*T. bairdi*) from Mexico and the Isthmus of Panama, which have been referred to the genus *Elasmognathus* by Gill, are more generally confined to the lower hills or occupy an intermediate habitat. Captain Dow observes (1867.1, p. 214):

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[12] Gregory attributes this range to the white rhinoceros, but his observation actually refers to the black rhinoceros, as Heller has pointed out.

> Thus far all examples of *T. bairdi* [*Elasmognathus*] have been found exclusively on the Atlantic side of the Isthmus [of Panama], and north of the Chagres River. Their favorite haunts appear to be in the hills lying at the back of Sion Hill and the adjoining stations of the Panama Railway. It is only during the rainy season that they seem to seek the lowlands, for it is only in that season they are captured.

Similarly *Tapirus* (*Elasmognathus*) *dowi* was found in the highlands of Guatemala, Nicaragua, and Costa Rica.

3. The opposite extreme from mountain-living habits is furnished by the typical South American tapir (*T. terrestris*), which inhabits the forest districts of Brazil, Paraguay, and the northern part of Argentina. This species is fond of gamboling in the water and rolling in soft mud and swims and dives like a capybara; it is not improbable that it may also walk along the beds of shallow rivers and lakes, as was observed to be the habit of a specimen of the Malayan tapir (*Tapirus indicus*). In Brazil, in districts remote from cultivation, the food of the tapir is composed largely of palm leaves, but at certain seasons of the year these animals subsist almost exclusively on fallen fruits, and in some districts swampy grasses and water plants form their chief food.

VERTICAL GEOGRAPHIC RANGE OF QUADRUPEDS

The rhinoceroses as a group have a wide vertical geographic distribution, ranging from sea level to the snow belt. The black rhinoceros, although it prefers the lower grassy plains, is found also on the high plateaus near the glaciers of Mount Kenya. (Gregory, 1898, op. cit., p. 263.[13]) As above noted, the tapirs as a group range from sea level to the snow belt, 8,000 feet above sea level. Some species are exclusively low-level forms (*T. terrestris*); others range from sea level well up into the mountains (*T. bairdi*); still others inhabit the higher Andes (*T. pinchaque*). The elephants also enjoy a wide vertical range; *Elephas* (*Loxodonta*) *africanus* is said to ascend and descend steep places with wonderful facility, and footprints of the modern Asiatic elephants have been seen among the eternal snows of the highest mountains (Pohlig, 1891.1, p. 328).

VERTICAL GEOGRAPHIC RANGE OF THE TITANOTHERES

Thus, judging by analogy with the other Perissodactyla and from what we know to be true also of the horses, it is probable that the titanotheres enjoyed a considerable vertical geographic range in the Rocky Mountain region in Eocene time and that this may have entered into the causation of their local adaptive radiation.

TEN CHIEF HABITAT ZONES OF MAMMALS

Wide climatic and physiographic differences, if concentrated in a geographically restricted area, facilitate local adaptive radiation. For example, grassy meadows favorable to shrubs bring grazers and browsers together. That much more extreme contrasts are by no means unnatural is shown along the coasts of Mexico, where there is an abrupt transition from an extremely moist, warm lowland to a dry, cool upland. Similarly abrupt transitions are observed in parts of the Andes and the Himalayas.

It is consequently not difficult to account for the fact that seven or eight different phyla of titanotheres lived together in southern Wyoming and northern Utah in middle and upper Eocene time, for the entire region was varied and mountainous.

The life zones of mammals have been set forth admirably by Kobelt (1902.1) and should be studied in connection with the vegetation zones of Schimper (1903.1). Some mammals are strictly confined to their typical habitat zones—that is, they are intensely localized. Certain antelopes, such as *Tragelaphus angasi*, the inyala (Stevenson-Hamilton, 1912.1, p. 135), probably feed upon only a single plant and are limited in range to its distribution. Many Herbivora, such as elephants, rhinoceroses, and horses, are very plastic and have great diversity of habitat in the course of the change in seasons and under varying conditions of competition.

Life zones are defined by land and water, by moisture and aridity, by depression and elevation, by low and high temperature, by the distribution of insects, and especially by the presence of vegetation adapted to grazing or browsing. Life zones are therefore defined sharply in some places and feebly in others. The ten zones discriminated are described below.

1. *Mountain or alpine habitat.*—High mountains and mountain ranges with the snow and timber lines at altitudes of 6,000 to 12,000 feet or more. Thinly forested or tundra-like lands, adapted both to grazing and browsing ungulates having relatively short limbs and feet adapted to climbing. The Artiodactyla are represented by many forms, some of which range far above timber line, including goats (*Capra*), rupicaprines (*Rupicapra*, *Nemorhaedus*, *Oreamnos*), mountain sheep (*Ovis*), vicuñas (*Lama vicunna*) at certain seasons, Pudu deer (*Pudua*). The Perissodactyla that invade these high forest zones are only certain tapirs of the Andes (*Tapirus pinchaque* and *T. roulini*).

2. *Mountain forest habitat.*—Lower mountain ranges and foothills, dry or well watered, well wooded, with river valleys. This zone includes the dry tropical woodlands (such as those of India), which are favorable to the larger ungulates; also the tropical rain forests (Asia, Africa, North America), generally unfavorable to large ungulates. In Asia the especial habitat of many deer, bovines, antelope, browsing perissodactyls, such as *Rhinoceros sondaicus* of Java, typically a forest dweller, *R.* (*Dicerorhinus*) *sumatrensis* of Sumatra. In the northern latitudes of North America, the typical home of the deer (*Odocoileus*), moose (*Alces*), wapiti

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[13] Gregory inadvertently attributes this range to the white rhinoceros.

(*Cervus*), mountain caribou (*Rangifer*), at elevations of 2,000 to 8,000 feet. On these levels in South America are found among the Tapiridae *T.* (*Elasmognathus*) *bairdi*, a hill dweller seeking the lowlands during the rainy season; also *T.* (*Elasmognathus*) *dowi.* In the equatorial belt of Africa both the high forests and lower forested foothills favorable to the growth of shrubs and trees attract also the elephants.

Vertical distribution of life zones of ungulates

Family or phylum	Peaks and highest mountain ranges; 6,000 to 12,000 feet. Browsers	High desert and drier uplands and plains, table-lands, plateaus, mesas; 5,000 to 15,000 feet. Grazers	Lower mountain ranges, foothills, well wooded and watered; forest lands; tributary river valleys; 2,000 to 8,000 feet. Browsers	Great plains and larger river valleys, broad grassy meadows, rolling country; sea level to 6,000 feet. Grazers	Alluvial bottom lands, delta and flood-plain deposits, swamps and jungles, forests and partly forested lowlands; river or sea level. Browsers and grazers	Rivers and lakes, river or lake level. Browsers
Ruminants	Mountain sheep, goat, deer, and elk (summer).	Pronghorn antelope	Deer, moose, elk, caribou (winter).	Buffalo and wapiti, or elk.		
Rhinocerotidae (recent and extinct types).		Hyracodon nebrascensis. Three long toes. Rhinoceros (Ceratotherium) simus. Meadows and sparse forests.	Rhinoceros sondaicus. Java; typically a forest dweller. R. (Dicerorhinus) sumatrensis. Inhabitant of hilly forest districts. R. (Opsiceros) bicornis. Two-horned "black" rhinoceros of Africa. Often seen on slopes of table mountains; feeds on roots, leaves, etc.	Rhinoceros unicornis; inhabits grass jungles. R. (Ceratotherium) simus. Large two-horned rhinoceros of Africa; inhabitant of grassy valleys on high veldt. R. (Opsiceros) bicornis. Found on Cape flats, in bush-covered country. Coenopus and Diceratherium. Three-toed animals.	Rhinoceros sondaicus. Occasionally seen in alluvial swamps. Aceratherium. Four-toed rhinoceros.	Metamynodon Amphibious rhinoceros.
Equidae (horses, zebras, asses).		Equus hemionus, E. kiang. Kiang and dziggetai. Inhabit table-lands of Tibet, 15,000 feet high. Prefer desolate places near lakes and rivers, and coarse wiry pasture of rough, hard yellow grass. E. onager. The onager of Persia. E. hemippus. Syrian wild ass. E. asinus. Feeds on wiry desert grasses. E. zebra. Feeds on plains grasses. E. przewalskii. Inhabits northern deserts.	Equus zebra, mountain zebra.	Equus hemionus onager. Migrates to the hills in summer. E. asinus somalicus. Inhabits Nubian desert. E. quagga. The quagga of South Africa; extinct. A karroo dweller. E. burchelli. Burchell's zebra; found north of Orange River; often seen in sparse forests, but predominantly a plains dweller. E. grevyi. Low plateaus with gravelly soil. Seen in thick thorn bush and tall feathery grass. Essentially an inhabitant of the open plains.		
Tapiridae (tapirs)	Tapirus roulini T. pinchaque. Inhabits slopes of Cordilleras.	Tapirus roulini T. pinchaque. Tapir of the high regions of the Andes.	Tapirus bairdi. Hill dweller, seeking lowlands at rainy season. T. dowi.		Tapirus americanus. Common tapir of forests and lowlands of Brazil and Paraguay. A forest dweller, feeding on palm leaves, fruits, and water plants. T. indicus.	
Proboscidea (elephants).			Elephas africanus. Ascends and descends steep places with wonderful facility.	Elephas africanus. Less typically a forest animal than E. indicus; found in comparatively open country; also in forests. E. indicus. Typically a forest animal.		
Sirenians, chalicotheres, hippopotami.					Macrotherium. Moropus. Chalicotherium.	Manatee. Dugong. Hippopotamus.

3. *Boreal forest habitat.*—Characteristic of north temperate zones with cold winters. The "temperate rain forests" of Schimper, partly interspersed with meadowlands. This zone includes the whole of primitive northern Europe and North America south of the tundra zone. In Asia it includes the whole of Siberia, grading on the south into the high "steppe" and high "plateau" regions and on the north into the Arctic tundras or barren grounds. It is the great boreal zone of North America, favored both by woodlands and meadows and by sufficient rainfall. The ungulates are very numerous, especially genera of Bovidae, Cervidae, and Suidae.

4. *Tundras and barren ground habitat.*—In this low-lying, north circumpolar region trees are scarce or absent, except the willows and birches of the river bottoms, and the subsoil is frozen throughout the year. The ungulates are now represented only by the musk ox (*Ovibos moschatus*) and several species of reindeer (*Rangifer*); formerly by the mammoth and the horse in Alaska and Siberia during the period of greater forestation.

5. *Higher plains and plateaus.*—Mesas, table-lands (as in Tibet and the Himalayas), and the desert plateaus of the Rocky Mountains and Andes, altitude 3,000 to 6,000 feet or more; vegetation scattered, sparsely forested, both grasses and shrubs abundant; or rocky and open country with occasional forests. Climate generally severe in winter. This zone grades into the "high steppes" of Asia, the veldt of South Africa, the high plains of North America. It is mostly open country adapted to grazers with hypsodont teeth, long limbs, and slender feet, or to the cursorial and gregarious Herbivora.

6. *High steppe and desert habitat.*—Treeless and arid wastes, steppes, and deserts of central Asia (such as the Desert of Gobi) or of Persia and Asia Minor, reaching an altitude of 6,000 feet, usually not so rich in flora and fauna as the high plateau. Climate extremely severe in winter. Inhabited chiefly by grazers. In Asia, among the Equidae we find the kiang (*Equus kiang*) of Tibet, the dziggetai (*E. hemionus*) of Mongolia, the wild horse (*E. przewalskii*) of the Desert of Gobi or the Kobdo district of western Mongolia. The kiang of Tibet and Turkestan prefers desert places near lakes and rivers, seeking coarse, wiry pasture and rough, hard grasses. The dziggetai ranges from the lowland steppes of Turkestan to the high plateaus (1,680 meters) of the deserts of Mongolia. In this zone among the Artiodactyla we find the wild Bactrian camel (*Camelus bactrianus*), the saiga antelope (*Saiga tartarica*), and the Persian gazelle (*Gazella gutturosa*).

7. *Low desert habitats.*—Steppes and sandy deserts of northern Africa, Syria, Arabia, Mesopotamia, and the northern borders of the Arabian Sea; rocky countries covered with sparsely vegetated areas and thin forests, scattered shrubs, and thorny bushes. Except in temperature and altitude this zone is like that of the high steppes; its vegetation is sought mostly by cursorial browsers and grazers with coloration of the desert; in Africa *Gazella dorcas*, *Addax*, *Oryx leucoryx*, and among the Equidae the north African wild ass (*Equus asinus*), the Somaliland ass (*Equus somaliensis*), the Assyrian *E. hemippus*, and the onager (*E. onager*), which grazes in the low deserts of Kutch and Rajputana. Neither the rhinoceroses nor the tapirs have ever had representatives in these low-lying desert belts.

8. *Plains habitat.*—Great plains and larger river valleys; broad, grassy meadows bordering glades partly forested or not forested at all, extending from sea level to an altitude of 6,000 feet in northern latitudes. The tropical grasslands or savannas of Africa, the llanos of the Orinoco, the campos of Brazil, the semiarid karoos and veldts of South Africa are partly included in this zone, although they also approach the high steppe habitat. This zone is generally adapted to grazing, hypsodont types, mostly long-headed and cursorial. It is the natural habitat on the Great Plains of North America of the buffalo (*Bison bison*), of the pronghorn antelope (*Antilocapra americana*), and formerly of the wapiti (*Cervus canadensis*). Similarly on the plains of equatorial Africa are found numerous species of antelope (mostly grazers), oxen (grazers), giraffes (true browsers), the black rhinoceros, *R.* (*Opsiceros*) *bicornis* (browsers and grazers), and all species of zebra. The ungulates in this open country are either cursorial or graviportal and are well defended by horns. The Tapiridae have never been adapted to a country of this kind. The giraffes frequent the savanna and the thorn-forested country (xerophilous woodland of Schimper).

9. *Lower river valleys habitat.*—Alluvial bottom lands, delta and flood-plain deposits, swamps and jungles, forested or grassy lowlands near rivers or sea level, typically the home of browsers rather than grazers, with feet and limbs adapted to soft soil, limbs both of mediportal and graviportal type, with some cursorial types (such as situtungas) having spreading feet. The Artiodactyla include many bovines, some antelopes (such as situtungas), chevrotains, suillines, the Liberian hippopotamus (*Choeropsis liberiensis*), and the primitive traguline (*Dorcatherium*) of West Africa. Among the Asiatic rhinoceroses *R. sondaicus*, a browsing, brachyodont type,

is occasionally seen in these alluvial bottoms. Similarly, the Sumatran rhinoceros, *R.* (*Dicerorhinus*) *sumatrensis*, also brachyodont, occasionally frequents such a region. *Tapirus indicus* inhabits this low forest belt in India, and *T. terrestris* is the common tapir of the forests and lowlands of Brazil and Paraguay. Among extinct forms the chalicotheres (*Moropus*, etc.) are found here.

10. *Aquatic, river and lake border habitat.*—Rivers, bayous, and lakes, frequented especially by aquatic browsing types with limbs adapted to swimming or to aquatic life and the teeth adapted to the softer kinds of food. Here we find the ungulates represented by their partly degenerate and specialized offshoots the sirenians, the Artiodactyla by the common hippopotamus or the water buffalo of the Philippines. Either the lower river valleys or the rivers themselves were undoubtedly the habitat of the extinct rhinoceroses known as amynodonts; also, possibly, of the Miocene *Teleoceras*, a short-limbed river-frequenting animal. Among the titanotheres there are evidences of aquatic adaptation in species of the genus *Mesatirhinus*.

CONCLUSIONS AS TO HABITATS OF THE TITANOTHERES

We have no evidence that titanotheres formerly inhabited alpine, high steppe, or low desert regions. Neither the teeth nor the feet predispose us to speculate upon such a habitat, nor have we any geologic evidence of it. There remain to be considered the "mountain," the "forest," the "boreal," or north temperate, the "plains," the "river valleys," the "rivers and lagoons."

The earliest known types of titanotheres, which are subcursorial in limb structure, developed in a partly open and partly forested country, frequenting meadows, lower river valleys, and plains that were flooded during certain seasons of the year. There is reason to believe that one of their upper Eocene radiations (*Metarhinus*) became amphibious or even aquatic. Some authors (Riggs, 1912.1, p. 36) believe that *Dolichorhinus*, as well as the short-footed *Palaeosyops*, was semiaquatic. The habits of these animals are more fully considered in Chapter V.

In Oligocene time the titanotheres entered the savanna-like Great Plains region of western North America, which was in part open country, in part country traversed by undulating rivers and by river bottoms bordered with forests.

In dentition the titanotheres, both in Eocene and Oligocene phyla, are chiefly a browsing family, though they show incipient indications of adaptation to the grazing habit.

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FISHER, CASSIUS ASA.

1906.1. Geology and water resources of the Big Horn Basin, Wyo.: U. S. Geol. Survey Prof. Paper 53, 72 pp., 16 pls., 1906.

Discusses briefly the character, thickness, and distribution of the Wasatch formation (p. 33).

FRAAS, EBERHARD.

1901.1. On the aqueous *vs.* eolian deposition of the White River Oligocene of South Dakota (translation by H. F. Osborn): Science, new ser., vol. 14, No. 345, pp. 210–212, Aug. 9, 1901.

"*Titanotherium* beds" formed by river and flood-plain deposits exposed during dry season. Middle "*Oreodon* beds" deposited by a shallow lake with dissolved materials of varying concentration (cf. banded layers). Upper "*Oreodon* beds" formed by eolian loess.

GARDNER, JAMES HENRY.

1910.1. The Puerco and Torrejon formations of the Nacimiento group: Jour. Geology, vol. 18, pp. 702–741, 1 pl., 9 figs., 1910.

Gives historical review. Topography, structure, and physiographic record of the Puerco-Torrejon district described. Considers that an unconformity exists between the two formations, to which the group name Nacimiento is given.

GIDLEY, JAMES WILLIAMS.

1904.1. See Matthew, William Diller, 1904.1.

1917.1. [The 1910 collection near the Davis ranch, Powder River valley, Wyo.] In Wegemann, C. H., Wasatch fossils in so-called Fort Union beds of the Powder River basin, Wyo., and their bearing on the stratigraphy of the region: U. S. Geol. Survey Prof. Paper 108, p. 59, 1917.

GILBERT, GROVE KARL.

1896.1. The underground waters of the Arkansas Valley in eastern Colorado: U. S. Geol. Survey Seventeenth Ann. Rept., pt. 2, pp. 553–601, pls. 56–68, figs. 45–49, 1896.

Rocky Mountain deposits may be of fluviatile and not of lacustrine origin.

GRANGER, WALTER.

1909.1. Faunal horizons of the Washakie formation of southern Wyoming: Am. Mus. Nat. Hist. Bull., vol. 26, pp. 13–23, pls. 2–6, 1 map, Jan. 19, 1909.

Divides "Washakie beds" into two horizons, characterized by fauna and lithology. Lower horizon=upper Bridger; upper horizon=lower and middle "Uinta" (Uinta A and B).

1910.1. Tertiary faunal horizons in the Wind River Basin, Wyo., with descriptions of new Eocene mammals: Am. Mus. Nat. Hist. Bull., vol. 28, pp. 235–251, pls. 20–23, 6 figs., July 16, 1910.

Determines two distinct faunal horizons in Wind River beds—the *Lambdotherium* zone and an earlier horizon.

1911.1. See Sinclair, William John, 1911.1.

1912.1. See Sinclair, William John, 1912.1.

1914.1. On the names of lower Eocene faunal horizons of Wyoming and New Mexico: Am. Mus. Nat. Hist. Bull., vol. 33, pp. 201–207, Mar. 31, 1914.

Names "Clark Fork," "Sand Coulée," and "Gray Bull beds" of Big Horn, Wyo., and "Almagre" and "Largo beds" of New Mexico. Correlates the lower Eocene of New Mexico with that of the various Wyoming basins.

1914.2. See Sinclair, William John, 1914.1.

1917.2. Notes on Paleocene and lower Eocene mammal horizons of northern New Mexico and southern Colorado: Am. Mus. Nat. Hist. Bull., vol. 37, pp. 821–830, Dec. 5, 1917.

1918.1 (and Matthew, W. D.). A revision of the lower Eocene Wasatch and Wind River faunas: Am. Mus. Nat. Hist. Bull., vol. 38, pp. 565–657, 1918.

GRAY, DR. J. E.

1872.1. Notes on a new species of tapir (*Tapirus leucogenys*) from the snowy regions of the Cordilleras of Ecuador and on the young spotted tapirs of tropical America: Zool. Soc. London Proc., 1872, pp. 483–492, pls. 21–22.

GREGORY, JOHN WALTER.

1896.1. The Great Rift Valley, 422 pp., London, John Murray, 1896.

HARRIS, GILBERT DENNISON.

1892.2. See Dall, William Healey, 1892.2.

HATCHER, JOHN BELL.

1893.1. The *Titanotherium* beds: Am. Naturalist, vol. 27, pp. 204–221, 3 figs., Mar., 1893.

General description. Accepts lacustrine theory of deposition.

1894.1. Discovery of *Diceratherium*, the two-horned rhinoceros, in the White River beds of South Dakota: Am. Geologist, vol. 13, pp. 360–361, May, 1894.

Top of White River correlated with John Day formation.

1895.1. On a new species of *Diplacodon*, with a discussion of the relations of that genus to *Telmatherium:* Am. Naturalist, vol. 29, pp. 1084–1093, pls. 38–40, fig. 1, Dec., 1895.

1902.3. Origin of the Oligocene and Miocene deposits of the Great Plains: Am. Philos. Soc. Proc., vol. 41, pp. 113–131, 1902.

Summarizes facts and accepts theory of small lakes, flood plains, river channels, and pampas as prevailing conditions during Oligocene and Miocene time. Gering, Arikaree, Ogalalla, Monroe Creek, Harrison, and "Nebraska" of Scott. Classification of the Oligocene and Miocene. "Lake-bed" hypothesis of origin disproved in favor of fluviatile, flood-plain, and eolian hypothesis.

HAWORTH, ERASMUS.

1897.1. Physical properties of the Tertiary [of Kansas]: Kansas Univ. Geol. Survey, vol. 2, pp. 247–284, pls. 36–44, 1897.

Rejects "lake-basin" hypothesis in favor of hypothesis of fluviatile origin of Tertiary of Kansas.

HAY, OLIVER PERRY.

1905.1 The fossil turtles of the Bridger Basin: Am. Geologist, vol. 35, pp. 327–342, June, 1905.

Evidence for flood-plain rather than lacustrine origin of the Bridger. Discussion of life and climatic conditions.

1908.1 The fossil turtles of North America: Carnegie Inst. Wash. Pub. 75, 568 pp., 113 pls., 704 figs., 1908.

HAY, ROBERT.

1889.1. Northwest Kansas, its topography, geology, climate, and resources: Kansas State Board Agr. Sixth Bienn. Rept., pp. 92–116, 2 maps, 4 figs., 1889.

See especially discussion of the Tertiary geology of Kansas.

HAYDEN, FERDINAND VANDIVEER.

1858.1. Notes on the geology of the Mauvaises Terres of White River, Nebr.: Acad. Nat. Sci. Philadelphia Proc., vol. 9, pp. 151–165, 1858.

Refers to Bear Creek, Pennington County, S. Dak. Type locality of *Mesohippus boirdii*.

1862.1. See Meek, Fielding Bradford, 1862.1.

1869.1. Geological report of the exploration of the Yellowstone and Missouri Rivers, by F. V. Hayden, under the direction of William F. Raynolds, 174 pp., 1 map, Washington, 1869.

1871.2. Report of F. V. Hayden. In [Fourth Annual] Preliminary report of the United States geological survey of Wyoming and portions of contiguous territories, pp. 9–81, 1871.

A general account of the topography and geology (type description) of the Bridger Basin (pp. 54–58). Considers upper portion of Washakie Basin sediments, as either an extension eastward of the Bridger beds or as a separate deposit of the same age. Notes occurrence of vertebrate fossils.

1873.1. Preliminary field report of the United States geological survey of Colorado and New Mexico: U. S. Geol. Survey Terr. Third Ann. Rept., pp. 105–251, 1869, reprinted 1873. [Reprinted in 1873 in First, Second, and Third Annual Reports of the Geological Survey of the Territories. In the text of this monograph reference is made to the reprinted edition.]

Names and briefly describes "Green River shales," Bridger "group," Wasatch "group," and Bear River "group." Designates Tertiary deposits between Creston and Bitter Creek along Union Pacific Railroad as "Washakie group" (p. 190).

1881.1. Geological and geographical atlas of Colorado and portions of adjacent territory, U. S. Geol. and Geog. Survey Terr., 1877, corrected to 1881.

HELLER, EDMUND.

1914.1. See Roosevelt, Theodore, 1914.1.

HILLS, RICHARD CHARLES.

1888.1. The recently discovered Tertiary beds of the Huerfano River basin, Colo.: Colorado Sci. Soc. Proc., vol. 3, pp. 148–164, 1 map, 1888.

Beds first described. Upper half suspected to be of Wasatch age.

1889.2. Additional notes on the Huerfano beds: Colorado Sci. Soc. Proc., vol. 3, pp. 217–223, 1889.

Mammals reported from upper division. Bridger age indicated.

Hills, Richard Charles—Continued.

1891.1. Remarks on the classification of the Huerfano Eocene: Colorado Sci. Soc. Proc., vol. 4, pp. 7–9, 1891.

Series divided into Huerfano, Cuchara, and Poison Canyon beds. Huerfano=Bridger; other two=lower Eocene.

Hovey, Edmund Otis.

1908.1. See Willis, Bailey, 1908.1.

Irving, John Duer.

1896.1 The stratigraphical relations of the Browns Park beds of Utah: New York Acad. Sci. Trans., vol. 15, p. 252, pl. 18, Sept., 1896.

The beds in Browns Park valley assigned to the Pliocene.

Johannsen, Albert.

1914.1. Petrographic analysis of the Bridger, Washakie, and other Eocene formations of the Rocky Mountains: Am. Mus. Nat. Hist. Bull., vol. 33, pp. 209–222, 2 figs., Mar. 31, 1914.

Considers Bridger and "Washakie" rocks largely tuffs modified by slight transportation. The older Eocene rocks are considered more strictly sedimentary.

Johnson, Willard Drake.

1901.1. The High Plains and their utilization: U. S. Geol. Survey Twenty-first Ann. Rept., pt. 4, pp. 601–741, pls. 113–116, figs. 300–329, 1901; Twenty-second Ann. Rept., pt. 4, pp. 631–669, pls. 55–65, figs. 236–244, 1902.

Tertiary deposits of the Plains, of fluviatile and flood-plain origin.

King, Clarence.

1876.1. Geological and topographical atlas accompanying the report of the Geological Exploration of the 40th Parallel, 1876.

1878.1. Systematic geology: U. S. Geol. Expl. 40th Par. Rept., vol. 1, 803 pp., 21 pls., 12 maps, 1878.

Gives the name "Vermilion Creek" to the Wasatch beds of southern Wyoming; considers them as lowest Eocene and unconformable with the overlying Green River beds. The name "Uinta group" is given to the uppermost 400 feet of the sediments in the valley of White River; considered to lie unconformably on lower beds and to represent uppermost Eocene Mammals collected by Marsh are listed. Area is mapped, and relationships of Bridger with other Eocene deposits of the basin are set forth.

Knowlton, Frank Hall.

1902.1. Fossil flora of the John Day Basin, Oreg.: U. S. Geol. Survey Bull. 204, 153 pp., 17 pls., 1902.

Geology (pp. 14–20, 102–108). Mascall formation referred to upper Miocene.

1909.1. The stratigraphic relations and paleontology of the "Hell Creek beds," "*Ceratops* beds," and equivalents, and their reference to the Fort Union formation: Washington Acad. Sci. Proc., vol. 11, No. 3, pp. 179–238, Aug. 14, 1909.

Kobelt, W.

1902.1. Die Verbreitung der Tierwelt, 576 pp., Leipzig, 1902.

Lambe, Lawrence Morris.

1908.1. The Vertebrata of the Oligocene of the Cypress Hills, Saskatchewan: Canada Geol. Survey Contr. Canadian Paleontology, vol. 3, pt. 4, 65 pp., 8 pls., 1908.

Leidy, Joseph.

1869.1. The extinct mammalian fauna of Dakota and Nebraska, including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America: Acad. Nat. Sci. Philadelphia Jour., 2d ser., vol. 7, 472 pp., 30 pls., 1869.

Lindgren, Waldemar.

1915.1. The igneous geology of the Cordilleras and its problems. In Problems of American geology (Silliman Memorial Lectures, 1913), pp. 234–286, 1 map, Yale Univ. Press, 1915.

Lönnberg, Einar.

1912.1. Mammals collected by the Swedish zoological expedition to British East Africa, 1911: K. svenska Vet.-Akad. Handlingar, Bd. 48, No. 5, 1912.

Loomis, Frederic Brewster.

1904.1. Two new river reptiles from the titanothere beds: Am. Jour. Sci., 4th ser., vol. 18, pp. 427–432, 4 figs., Dec., 1904.

Flood-plain origin of the "*Titanotherium* beds."

1905.1. The Tertiary of Montana: Carnegie Mus. Mem., vol. 2, pp. 203–224, pl. 22, 1905.

Chiefly a description of *Ictops*, *Xenotherium*, and other lower White River mammals.

1907.1. Origin of the Wasatch deposits: Am. Jour. Sci., 4th ser., vol. 23, pp. 356–364, 3 figs., May, 1907.

Treats of the Big Horn Basin Wasatch; divides the beds into three faunal levels, lists fossils from each level, and gives sections. The Wasatch is considered a flood-plain deposit, the upper 1,000 feet of which appear to overlap in time the base of the Wind River.

Lull, Richard Swann.

1905.1 *Megacerops tyleri,* a new species of titanothere from the Bad Lands of South Dakota: Jour. Geology, vol. 13, No. 5, pp. 443–456, pls. 3–4, 1905.

Lydekker, Richard (editor).

?1893.1. The new natural history, vols. 1–4 (American reprint of "The Royal natural history," published 1893–1896).

Lyons, H. G.

1906.1 The physiography of the River Nile and its basin, 441 pp., 48 pls., 1 map, Egypt Survey Dept., 1906.

Rate of deposition (p. 334).

McMaster, John Bach.

1881.1. See Osborn, Henry Fairfield, 1881.8.

Marsh, Othniel Charles.

1871. 3. On the geology of the eastern Uintah Mountains: Am. Jour. Sci., 3d ser., vol. 1, pp. 191–198, 1871.

Short account of the expedition to Uinta Basin in 1870. Considers Uinta Basin deposits synchronous with those of Bridger Basin on paleontologic evidence. Considers the fossils as indicating much greater age than Miocene of eastern Rocky Mountain basins.

1875. 2. Ancient lake basins of the Rocky Mountain region: Am. Jour. Sci., 3d ser., vol. 9, pp. 49–52, January, 1875.

1877. 1. Introduction and succession of vertebrate life in America: Am. Jour. Sci., 3d ser., vol. 14, pp. 337–378, 1877.

Plate showing successive horizons named from characteristic genera. Names *Diplacodon* zone (p. 354).

1891. 2. Geologic horizons as determined by vertebrate fossils: Am. Jour. Sci., 3d ser., vol. 42, pp. 336–338, October, 1891.

1898. 1. The comparative value of different kinds of fossils in determining geological age: Am. Jour. Sci., 4th ser., vol. 6, pp. 483–486, December, 1898.

Value of a form depends upon its modifiability in accordance with changing conditions.

Matthew, William Diller.

1897. 2. A revision of the Puerco fauna: Am. Mus. Nat. Hist. Bull., vol. 9, pp. 259–323, Nov. 16, 1897.

Points out the distinct separation of species of upper and lower beds and adopts Wortman's proposed name, Torrejon for the upper beds.

1899. 1. A provisional classification of the fresh-water Tertiary of the West: Am. Mus. Nat. Hist. Bull., vol. 12, pp. 19–75, Mar. 31, 1899.

1899. 2. Is the White River Tertiary an eolian formation? Am. Naturalist, vol. 33, pp. 403–408, May, 1899.

Summary of the paleontologic evidence against the "lake-basin" hypothesis.

1901. 1. Fossil mammals of the Tertiary of northeastern Colorado: Am. Mus. Nat. Hist. Mem., vol. 1, pt. 7, pp. 353–447, 1901.

Stratigraphy of White River deposits ("Horsetail Creek," "Cedar Creek," and "Martin Canyon beds") and of "Loup Fork" formation ("Pawnee Creek beds"). Evidence as to mode of deposition (chiefly eolian); analysis of faunas; correlation of horizons; systematic descriptions.

1902. 1. List of the Pleistocene fauna from Hay Springs, Nebr.: Am. Mus. Nat. Hist. Bull., vol. 16, pp. 317–322, Sept. 25, 1902.

Lists for comparison the faunas of Hay Springs (Nebr.), Silver Lake (Oreg.), and Washtucna Lake (Wash.).

1903. 1. The fauna of the *Titanotherium* beds at Pipestone Springs, Mont.: Am. Mus. Nat. Hist. Bull., vol. 19, pp. 197–226, 19 figs., May 9, 1903.

1904. 1. (and Gidley, J. W.). New or little-known mammals from the Miocene of South Dakota: Am. Mus. Nat. Hist. Bull., vol. 20, pp. 241–268, 15 figs., July 20, 1904.

Upper Miocene "Loup Fork beds," geology and faunal list. Lower Miocene "Rosebud beds" (new name). New Carnivora and Rodentia.

1906. 1. Hypothetical outlines of the continents in Tertiary times: Am. Mus. Nat. Hist. Bull., vol. 22, pp. 353–384, 7 figs., Oct. 25, 1906.

1907. 1. A lower Miocene fauna from South Dakota: Am. Mus. Nat. Hist. Bull., vol. 23, pp. 169–219, 26 figs., 1907.

"Lower Rosebud" and "Upper Rosebud" deposits and faunas; comparison with American Oligocene and Miocene faunas. New Carnivora, Rodentia, Artiodactyla.

1908. 1. Mammalian migrations between Europe and North America: Am. Jour. Sci., 4th ser., vol. 25, pp. 68–70, January, 1908.

1909. 1. The Carnivora and Insectivora of the Bridger Basin, middle Eocene: Am. Mus. Nat. Hist. Mem., vol. 9, pt. 6, pp. 289–559, pls. 44–52, 118 figs., 1909.

History of exploration. Stratigraphy and faunal divisions. Condition of deposition.

1909. 2. See Osborn, Henry Fairfield, 1909. 321.

1914. 1. Evidence of the Paleocene vertebrate fauna on the Cretaceous - Tertiary problem: Geol. Soc. America Bull., vol. 25, pp. 381–402, Sept. 15, 1914.

1918. 1. See Granger, Walter, 1918. 1.

Meek, Fielding Bradford.

1862. 1 (and Hayden, F. V.). Descriptions of new Lower Silurian (Primordial), Jurassic, Cretaceous, and Tertiary fossils, collected in Nebraska by the exploring expedition under command of Wm. F. Raynolds, with some remarks on the rocks from which they were obtained: Acad. Nat. Sci. Philadelphia Proc., vol. 13, pp. 415–447, 1862.

Wind River deposits considered intermediate in age between Fort Union and White River.

Mercer, Henry Chapman.

1899. 1. The bone cave at Port Kennedy, Pa., and its partial excavation in 1894, 1895, 1896: Acad. Nat. Sci. Philadelphia Jour., 2d ser., vol. 11, pt. 2, pp. 269–286, Feb. 4, 1899.

Referred to the Pleistocene, but without comparison with other cave formations and faunas.

Merriam, John Campbell.

1901.1. A contribution to the geology of the John Day Basin [Oreg.]: California Univ. Dept. Geology Bull., vol. 2, pp. 269–314, pls. 6–8, fig. 1, 1901.

Geology, faunas, and floras of the Cretaceous (Chico and Knoxville), Eocene (Clarno), Oligocene (John Day), Columbia River lava, Miocene (Mascall), Pliocene (Rattlesnake), Quaternary (p. 269).

Nickles, John M.

1924.1. Geologic literature on North America, 1785–1918: U. S. Geol. Survey Bull. 746 (Bibliography), 1167 pp.; Bull. 747 (Index), 658 pp., 1924.

Osborn, Henry Fairfield.

1878.3 (and Scott, W. B.). Palaeontological report of the Princeton Scientific Expedition of 1877: Princeton Coll. E. M. Mus. Geol. Archaeol. Contr., No. 1, 107 pp., Sept. 1, 1878.

A general account of the Bridger badlands, with notes on analysis of the rocks.

1881.8 (and McMaster, J. B.). A memoir upon *Loxolophodon* and *Uintatherium*, two genera of the suborder Dinocerata, accompanied by a stratigraphical report of the Bridger beds in the Washakie Basin by J. B. McMaster: Princeton Coll. E. M. Mus. Geol. Archaeol. Contr., vol. 1, No. 1, pp. 5–54, 1881.

Topography and geology described. Section given and important fossil localities indicated. Osborn notes for first time difference in fauna between beds of the two basins and considers "Washakie" as somewhat later than Bridger. First stratigraphic section with geologic location of species. Error in stratigraphy.

1887.30. See Scott, William Berryman, 1887.1.

1887.37 (and Scott, W. B.). Preliminary report on the vertebrate fossils of the Uinta formation collected by the Princeton expedition of 1886: Am. Philos. Soc. Proc., vol. 24, No. 126, pp. 255–264, 1887.

1890.51. See Scott, William Berryman, 1890.1.

1892.67 (and Wortman, J. L.). Fossil mammals of the Wasatch and Wind River beds, collections of 1891: Am. Mus. Nat. Hist. Bull., vol. 4, pp. 81–147, Oct. 20, 1892.

Geology of the Big Horn Basin (Wortman), p. 135. Analysis and description of the fauna (Osborn). Considers Wind River beds distinct from and successive to the Wasatch of Big Horn Basin.

1893-82. Rise of the Mammalia [vice-presidential address before American Association for the Advancement of Science]: Am. Jour. Sci., 3d ser., vol. 46, pp. 379–392, 448–466, November, December, 1893; Am. Assoc. Adv. Sci. Proc., vol. 42, pp 189-227, 1894.

1894.89. A division of the eutherian mammals into the Mesoplacentalia and Cenoplacentalia [terms subsequently altered to Meseutheria and Ceneutheria]: New York Acad. Sci. Trans., vol. 13, pp. 234–237, June 4, 1894.

Osborn, Henry Fairfield—Continued.

1894.90 (and Wortman, J. L.). Fossil mammals of the lower Miocene White River beds, collection of 1892: Am. Mus. Nat. Hist. Bull., vol. 6, pp. 199–228, pls. 2–3, July 28, 1894.

Succession of species in the White River "Miocene" [Oligocene].

1895.95 (and Earle, Charles). Fossil mammals of the Puerco beds, collection of 1892: Am. Mus. Nat. Hist. Bull., vol. 7, pp. 1–70, Mar. 8, 1895.

Wortman (field notes, pp. 1, 2) divides the Puerco into upper and lower beds, with two thin yet distinct fossil-bearing strata in the lower bed and one (?) thicker stratum in the upper. Gives the localities of both levels and estimates the thickness of the combined beds (upper and lower) at 800 to 1,000 feet.

1895.98 (and Peterson, O. A.). Fossil mammals of the Uinta Basin, expedition of 1894 (geologic levels by O. A. Peterson): Am. Mus. Nat. Hist. Bull., vol. 7, pp. 71–105, 17 figs., May 18, 1895.

Divides Uinta Basin deposits into three horizons; the three faunal levels (horizons A, B, C), with faunal lists. New genera and species, especially of *Mesonyx*, *Telmatherium*, *Sphenocoelus*, and *Elotherium*.

1895.105 (and Wortman, J. L.). Perissodactyls of the lower Miocene White River beds: Am. Mus. Nat. Hist. Bull., vol. 7, pp. 343–375, pls. 8–11, Dec. 23, 1895.

Oligocene.

1897.126. The Huerfano lake basin, southern Colorado, and its Wind River and Bridger fauna: Am. Mus. Nat. Hist. Bull., vol. 9, pp. 247–258, Oct. 20, 1897.

1900.182. The geological and faunal relations of Europe and America during the Tertiary period and the theory of the successive invasions of an African fauna: Science, new ser., vol. 11, No. 276, pp. 561–574, Apr. 13, 1900.

1900.187. Correlation between Tertiary mammal horizons of Europe and America, an introduction to the more exact investigation of Tertiary zoogeography, preliminary study with third trial sheet: New York Acad. Sci. Annals, vol. 13, No. 1, pp. 1–72, July 21, 1900.

1901.200. Corrélation des horizons mammifères tertiaires en Europe et en Amérique: Cong. géol. internat., 8e sess., Compt. rend., pp. 357–363, 1901.

1901.201. See Fraas, Eberhard, 1901.1.

1902.214. The law of adaptive radiation: Am. Naturalist, vol. 36, pp. 353–363, May, 1902.

1905.267. Ten years progress in the mammalian palaeontology of North America: Cong. internat. zool., 6e sess. (Bern, 1904), Compt. rend., pp. 86–113m, pls. 1–15; Am. Geologist, vol. 36, pp. 199–229, October, 1905.

1907.294. Tertiary mammal horizons of North America: Am. Mus. Nat. Hist. Bull., vol. 23, pp. 237–253, 3 figs., Mar. 30, 1907.

1909.321 (and Matthew, W. D.). Cenozoic mammal horizons of western North America, with appendix, Faunal lists of the Tertiary Mammalia of the West, by William Diller Matthew: U. S. Geol. Survey Bull. 361, 138 pp., 2 pls., 14 figs., January, 1909.

1910.341. The paleontologic correlation through the Bache fund: Science, new ser., vol. 31, No. 794, pp. 407–408, Mar. 18, 1910.

Osborn, Henry Fairfield—Continued.

1910.342. Correlation of the Cenozoic through its mammalian life: Jour. Geology, vol. 18, No. 3, pp., 201–215, April–May, 1910; Outlines of geologic history, pp. 251–264, Chicago Univ. Press July, 1910.

1910.345. Paleontologic evidences of adaptive radiation: Pop. Sci. Monthly, vol. 77, pp. 77–81, July, 1910.

1910.346. The age of mammals in Europe, Asia, and North America, 635 pp., 220 figs., New York, Macmillan Co., 1910.

1912.376. Correlation and paleogeography: Geol. Soc. America Bull., vol. 23, pp. 232–256, 1912.

1919.494. New titanotheres of the Huerfano: Am. Mus. Nat. Hist. Bull., vol. 41, pp. 557–569, 7 figs., 1919.

Peale, Albert Charles.

1876.1. Report on stratigraphy—Cenozoic formations: U. S. Geol. and Geog. Survey Terr. Eighth Ann. Rept., pp. 75–180, 13 pls., 5 maps, 1876.

"Washakie" treated as distinct group. Contains table of localities, authorities, references, etc. (p. 146).

1879.1. Report on the geology of the Green River district: U. S. Geol. and Geog. Survey Terr. Eleventh Ann. Rept., pp. 511–542, pls. 47–54, 1879.

Peterson, Olof August.

1895.1. See Osborn, Henry Fairfield, 1895.98.

1914.1. A new titanothere from the Uinta Eocene: Carnegie Mus. Annals, vol. 9, pp. 29–52, pls. 6–10, figs. 1–14, 1914.

Diploceras osborni, from horizon B.

1914.2. A small titanothere from the lower Uinta beds: Carnegie Mus. Annals, vol. 9, pp. 53–57, pl. 11, figs. 1–2, 1914.

Heterotitanops parvus, from horizon A.

1914.3. Some undescribed remains of the Uinta titanothere *Dolichorhinus:* Carnegie Mus. Annals, vol. 9, pp. 129–138, figs. 1–7, 1914.

From Uinta A.

1914.4. A correction of generic name: Carnegie Mus. Annals, vol. 9, p. 220, 1914.

Pohlig, Hans.

1891.1. Dentition und Kraniologie des *Elephas antiquus* Falc. * * * Nachträge: K. Leop.-Carol. deutsche Akad. Naturforscher Nova Acta, Band 57, pp. 285–459, 1891.

Powell, John Wesley.

1876.1. (and White, C. A.). Invertebrate paleontology of the Plateau province. In Powell, J. W., Report on the geology of the eastern portion of the Uinta Mountains and a region of country adjacent thereto, pp. 74–135, U. S. Geol. and Geog. Survey Terr., 1876.

Ransome, Frederick Leslie.

1915.1. The Tertiary orogeny of the North American Cordillera and its problems. In Problems of American geology (Silliman Memorial Lectures, 1913), pp. 287–376, 1 map, Yale Univ. Press, 1915.

Richardson, George Burr.

1912.1. The Monument Creek group: Geol. Soc. America Bull., vol. 23, pp. 267–276, 1 fig., 1912.

Describes the Dawson arkose and Castle Rock conglomerate forming the "Monument Creek group" of Colorado and discusses their relation to the Denver and Arapahoe formations

Riggs, Elmer Samuel.

1912.1. New or little known titanotheres from the lower Uintah formations: Field Mus. Nat. Hist. Pub. 159 (Geol. ser., vol. 4, No. 2), pp. 17–41, pls. 4–12, figs. 1–2, June, 1912.

Discusses stratigraphy of lower part of lower horizon of Uinta Basin and gives general and detailed sections, with exact stratigraphic position of various species of titanotheres.

Roosevelt, Theodore.

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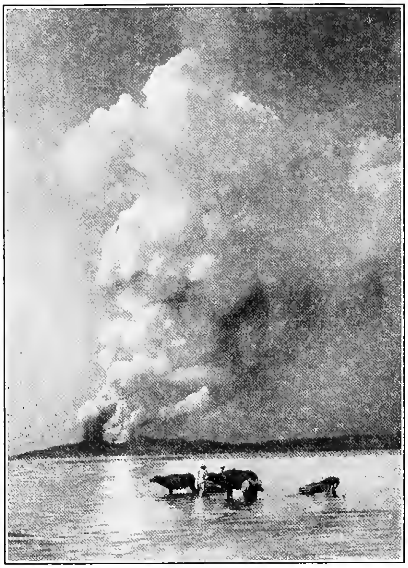
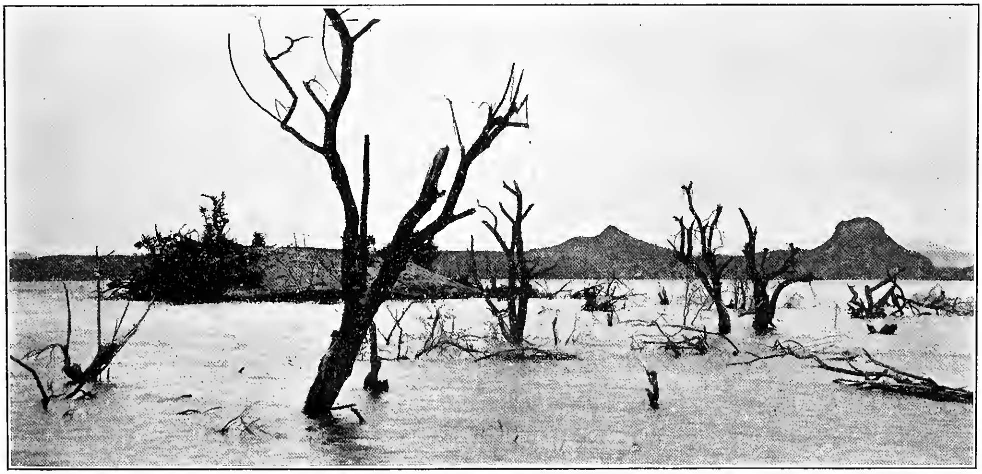
Origin of the primates (vol. 15, pp. 419–436).



A. ERUPTION OF THE CRATER OF TAAL, PHILIPPINE ISLANDS, JANUARY, 1911

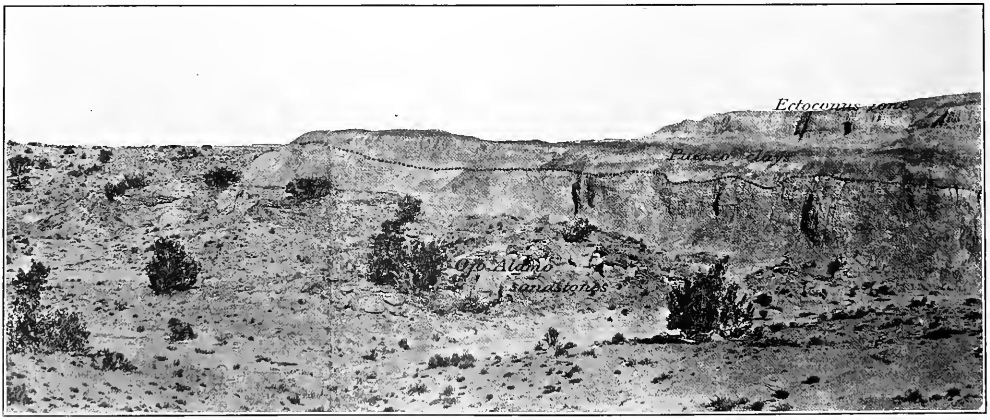


B. FLOODED AREA

Submerged layers of volcanic cinders, ashes, and mud, in which are entombed the bodies of men and the carcasses of animals. (After Dean C. Worcester.) Comparable to volcanic ash deposits of Bridger age in southern Wyoming

A. OJO ALAMO, SAN JUAN COUNTY, N. MEX., LOOKING NORTH

Contact (indicated by arrows) between Ojo Alamo sandstone and clay of Puerco formation is observed directly back of the trading store

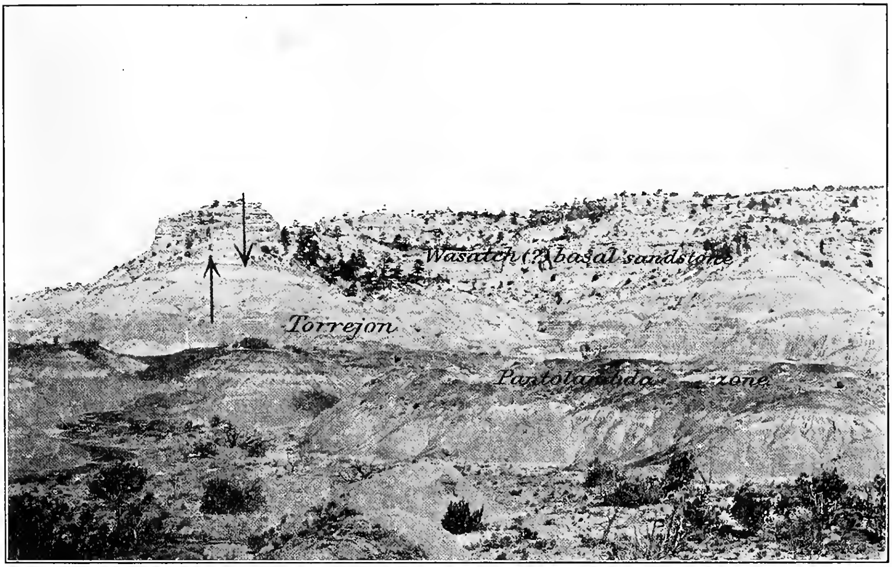


B. EXPOSURES OF PUERCO FORMATION EAST OF OJO ALAMO, N. MEX.

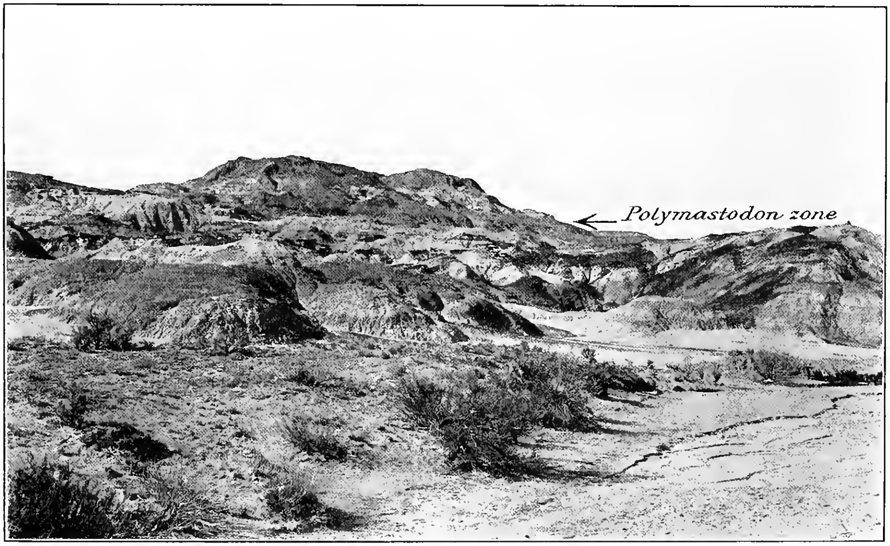
Puerco rests on eroded surface of Ojo Alamo sandstones; contact indicated by dotted line. The dark stratum at top to the right is the lower level (*Ectoconus* zone) of the Puerco formation

CRETACEOUS AND BASAL EOCENE CONTACTS IN NEW MEXICO

Photographs by W. J. Sinclair, 1913. (After Sinclair and Granger, 1914.1)



A. UPPER BEDS OF TORREJON FORMATION, WEST FORK OF TORREJON ARROYO, SANDOVAL COUNTY, N. MEX.
The Torrejon is overlain unconformably by the basal sandstones of the Wasatch(?) formation



B. EXPOSURES OF PUERCO FORMATION 3 MILES EAST OF OJO ALAMO, N. MEX.

BASAL EOCENE AND LOWER EOCENE CONTACTS IN NEW MEXICO
Photographs by W. J. Sinclair, 1913. (After Sinclair and Granger, 1914.1)

A. EOHIPPUS-CORYPHODON ZONE (LOWER PART OF WASATCH FORMATION, LEVEL BIG HORN B), LITTLE SAND COULEE

First appearance of *Eohippus*. Am. Mus. negative 18565

B. PHENACODUS-NOTHODECTES-CORYPHODON ZONE (BASAL PART OF WASATCH FORMATION, LEVEL BIG HORN A), ABOUT 4 MILES NORTH OF RALSTON

Am. Mus. negative 18563

LOWER WASATCH STRATA RESTING ON BASAL WASATCH STRATA, CLARK FORK BASIN, PARK COUNTY, WYO.

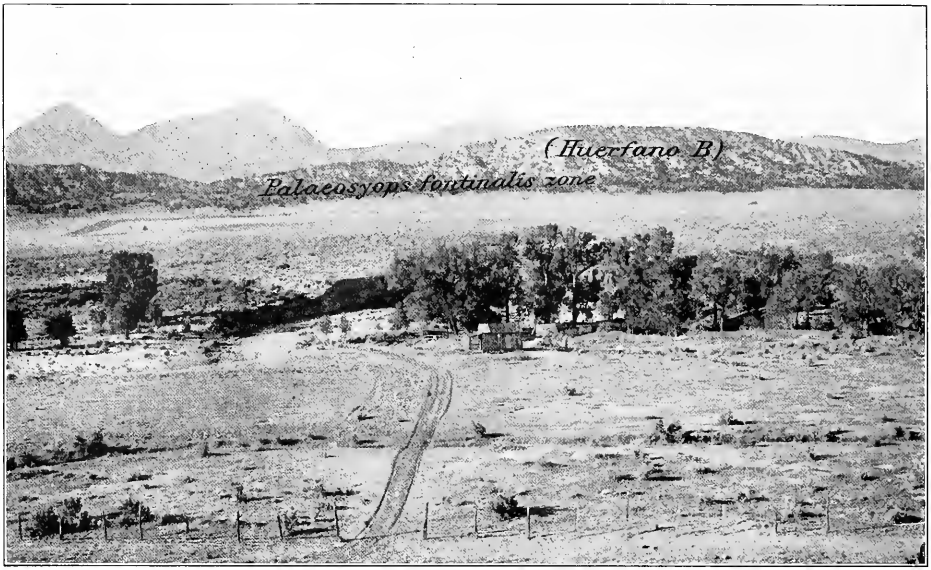
A. TYPICAL "LYSITE" LOCALITY, AT COTTONWOOD DRAW, NORTH OF LOST CABIN, WIND RIVER BASIN, WYO.

Shows the *Heptodon-Coryphodon-Eohippus* zone (level Wind River A), with Paleozoic hills in the background. (After Granger, 1910.1.) Am. Mus. negative 18393

B. TYPICAL "GRAY BULL" LOCALITY, 4 MILES SOUTH OF OTTO, BIG HORN BASIN, WYO.

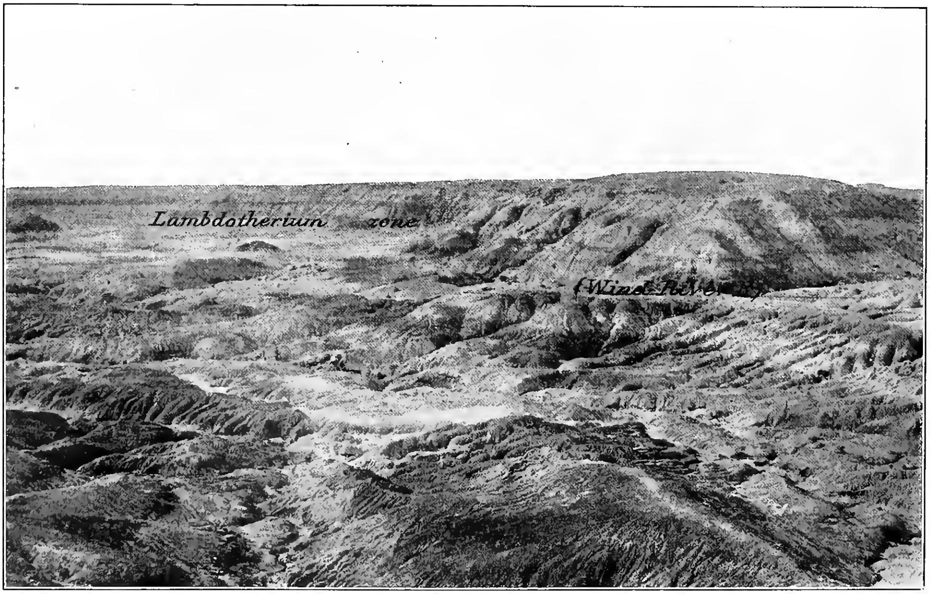
Shows the *Systemodon-Coryphodon-Eohippus* zone (level Big Horn C), with the excavation of the skeleton of *Eohippus osbornianus* in the foreground. Am. Mus. negative 18450

EXPOSURES OF WASATCH FORMATION AND TYPICAL WIND RIVER DEPOSITS IN WYOMING



A. A TYPICAL HUERFANO LOCALITY, 2 MILES WEST OF GARDNER, HUERFANO BASIN, COLO.

Palaeosyops fontinalis zone (level Huerfano B). A cedar-covered ridge in middle distance, and eruptive peaks in the background. The type of *Eometarhinus* and referred specimens of *Palaeosyops fontinalis* were found at this site. Am. Mus. negative 104715



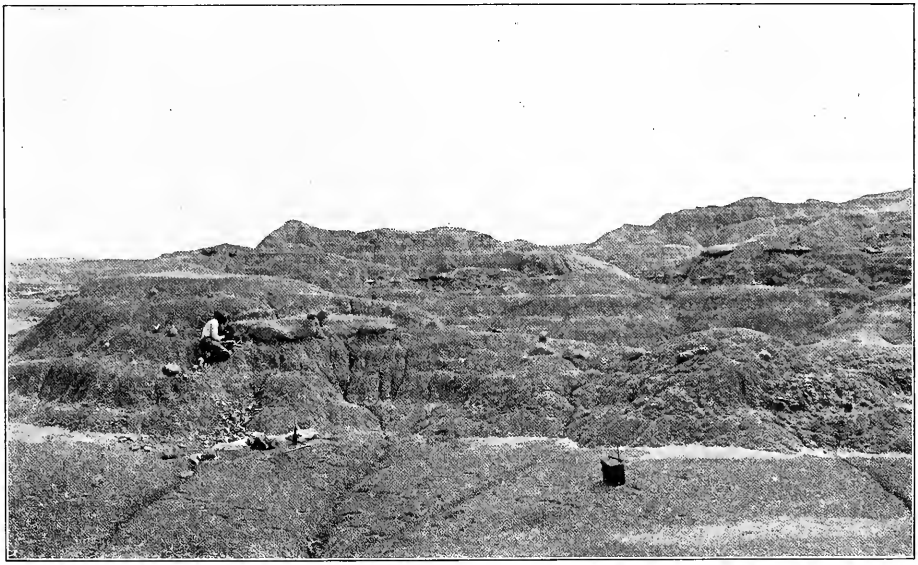
B. A TYPICAL "LOST CABIN" LOCALITY, ON ALKALI CREEK, EAST OF LOST CABIN, WIND RIVER BASIN, WYO.

Lambdotherium zone (level Wind River B). The types of *Lambdotherium popoagicum*, *Eotitanops borealis*, and *E. gregoryi* were found at this site. Am. Mus. negative 18392

TYPICAL HUERFANO FORMATION OF COLORADO AND WIND RIVER FORMATION OF WYOMING

A. HENRYS FORK TABLE, LOOKING NORTHWARD ACROSS HENRYS FORK, BRIDGER BASIN, WYO.

Uintatherium zone (levels Bridger C and D) and *Metarhinus* zone (level Bridger E) with Bishop ("Wyoming") conglomerate at the top. The Burnt Fork "white layer" (w and arrow) separates level Bridger C 2 from Bridger C 3. Am. Mus. negative 18152



B. GRIZZLY BUTTES, SOUTH OF MOUNTAIN VIEW, UINTA COUNTY, WYO.

Palaeosyops paludosus-Orohippus zone (level Bridger B). Excavation by Granger of the type skull of *Limnohyops priscus* (Am. Mus. 11687). Am. Mus. negative 18089

TYPICAL BRIDGER FORMATION (LEVELS UPPER C, D, E, AND LOWER B) OF WYOMING, MIDDLE AND UPPER (?) EOCENE

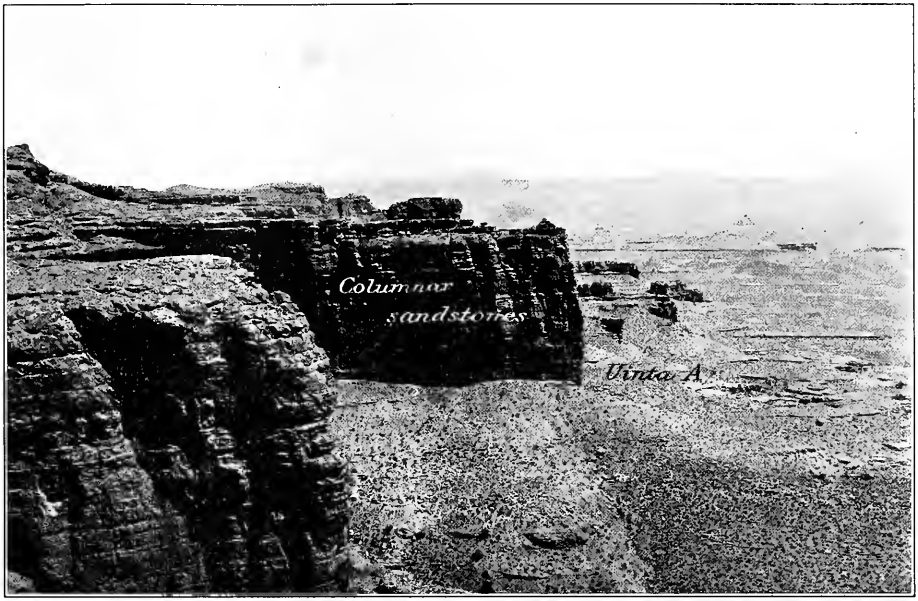
A. NORTHWEST POINT OF HAYSTACK MOUNTAIN, HEAD OF BITTER CREEK, SWEETWATER COUNTY, WYO.

Eobasileus-Dolichorhinus and *Metarhinus* zones (levels Washakie B 2 and B 1). (After Granger.) Am. Mus. negative 18213. (See figs. 60 and 61)

B. VIEW SOUTHEASTWARD FROM LACLEDE STATION ON OVERLAND STAGE TRAIL, SWEETWATER COUNTY, WYO.

Lower brown sandstones of *Uintatherium* zone (level Washakie A) in middle distance. Haystack Mountain and the *Eobasileus-Dolichorhinus* and *Metarhinus* zones in the background. (After Granger.) Am. Mus. negative 18223

TYPICAL "WASHAKIE" FORMATION (LEVELS B 2 AND B 1 OVERLYING LEVEL A 1), WYOMING; MIDDLE AND UPPER EOCENE



A. COLUMNAR SANDSTONES, TOP OF LEVEL UINTA A, WHITE RIVER CANYON, UINTA BASIN, UTAH

(After Riggs, 1912.1.) Field Mus. negative

B. PANORAMIC VIEW, WHITE RIVER CANYON, 4 MILES BELOW WAGONHOUND BEND, UINTA BASIN, UTAH

Bluffs on right bank of river belong to the unfossiliferous level Uinta A. Photograph by Riggs. Field Mus. negative

MIDDLE EOCENE OF NORTHERN UTAH (LEVEL UINTA A)

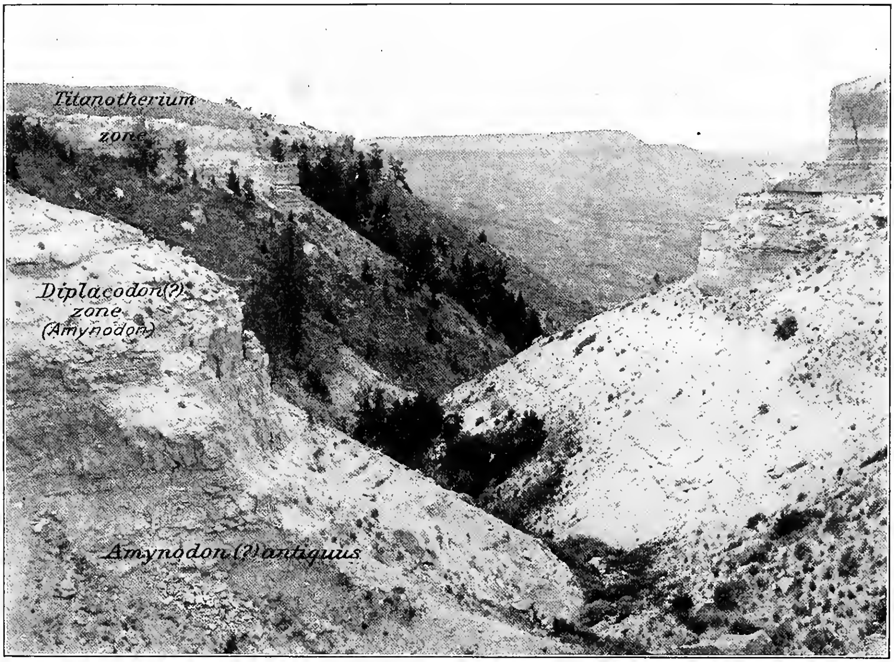
A. NORTHERN BOUNDARY OF COYOTE BASIN, UINTA BASIN, UTAH

Showing greenish clays of the *Eobasileus-Dolichorhinus* zone (level Uinta B 2) capped by "*Amynodon* sandstone." These clays have yielded most of the smaller mammalian fauna of this middle horizon of Uinta Basin. (After Riggs, 1912.1.) Field Mus. negative

B. DIVIDE BETWEEN WHITE RIVER CANYON AND COYOTE BASIN, UINTA BASIN, UTAH

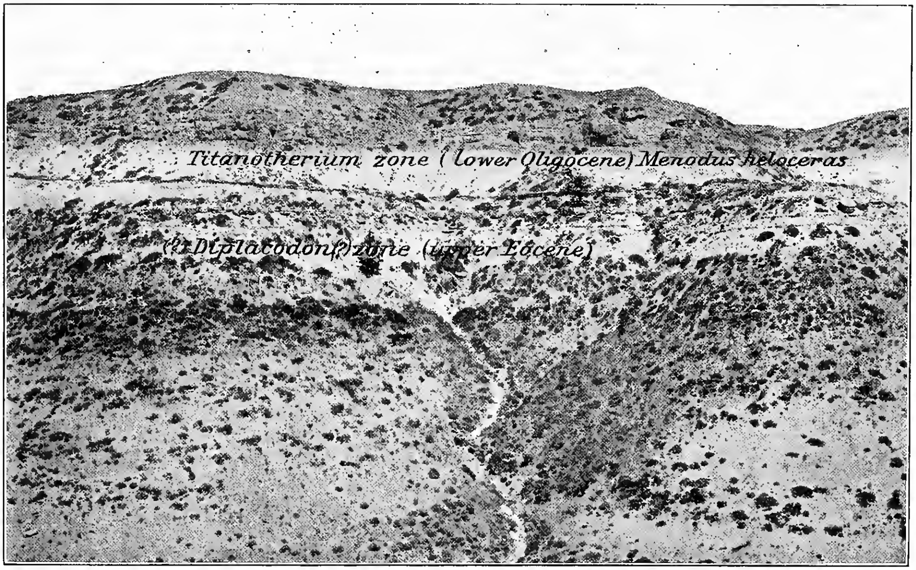
Showing fossil-bearing sandstone of the *Metarhinus* zone (level Uinta B 1). (After Riggs, 1912.1.) Field Mus. negative

UPPER EOCENE OF NORTHERN UTAH (LEVEL UINTA B)



A. NORTH FACE OF BEAVER DIVIDE, WIND RIVER BASIN, WYO.

View westward from point near Wagonbed Spring, showing lower Oligocene beds (*Titanotherium* zone), with *Menodus heloceras* (level Chadron A), resting on upper Eocene (*Diplacodon* zone?). Skull provisionally referred to *Amynodon antiquus* was taken from left foreground. (After Granger, 1910.1.) Am. Mus. negative 18388



B. EXPOSURES AT WAGONBED SPRING, BEAVER DIVIDE, FREMONT COUNTY, WYO.

Showing contact between upper Eocene and lower Oligocene. The skull of *Menodus heloceras* came from the draw just to the right of this view. Am. Mus. negative 18391

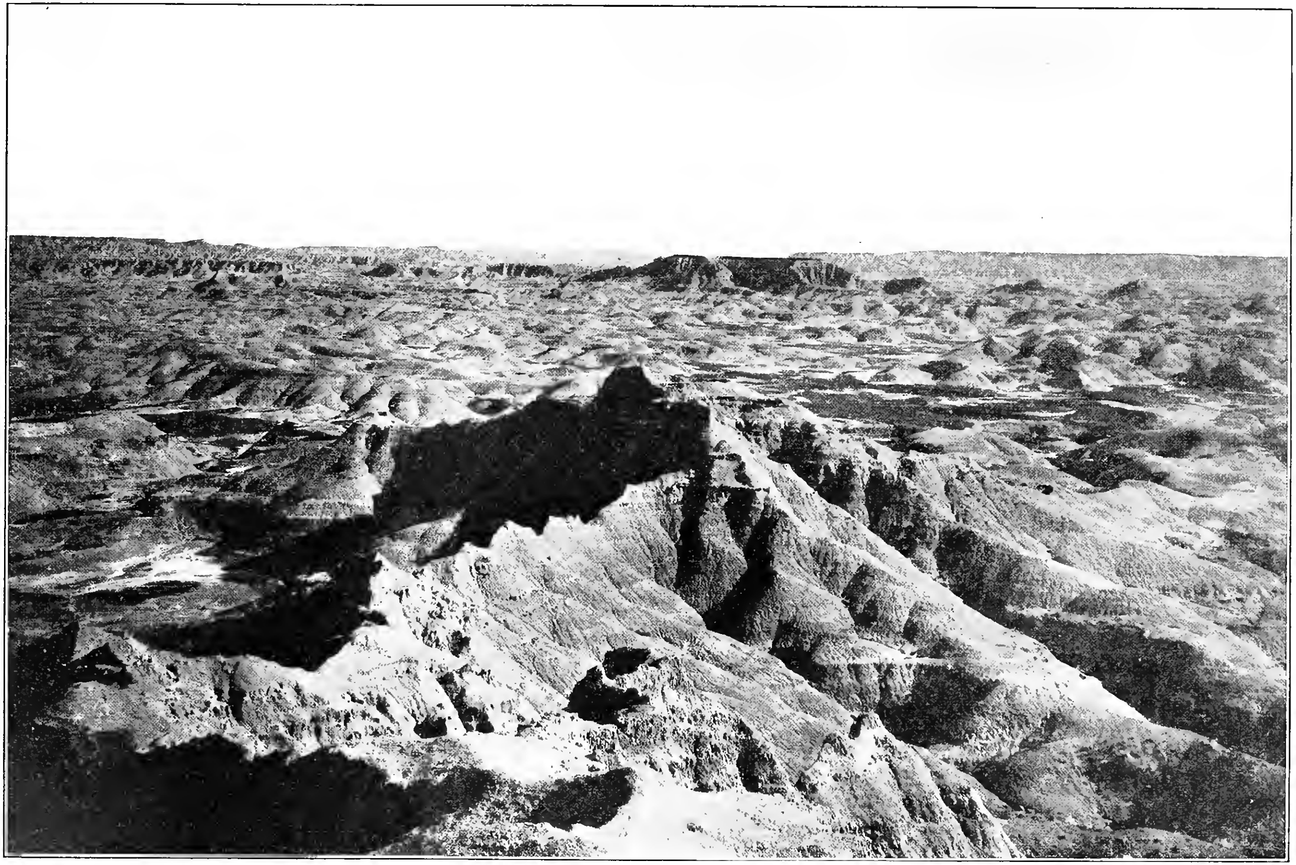
LOWER OLIGOCENE OVERLYING UPPER EOCENE OF CENTRAL WYOMING

A. CONTACT BETWEEN TITANOTHERIUM ZONE (LOWER OLIGOCENE) AND PIERRE SHALE (CRETACEOUS), NEAR MOUTH OF CEDAR CREEK, BIG BADLANDS, S. DAK.

Oreodon zone in the distance to the right. Am. Mus. negative 35997

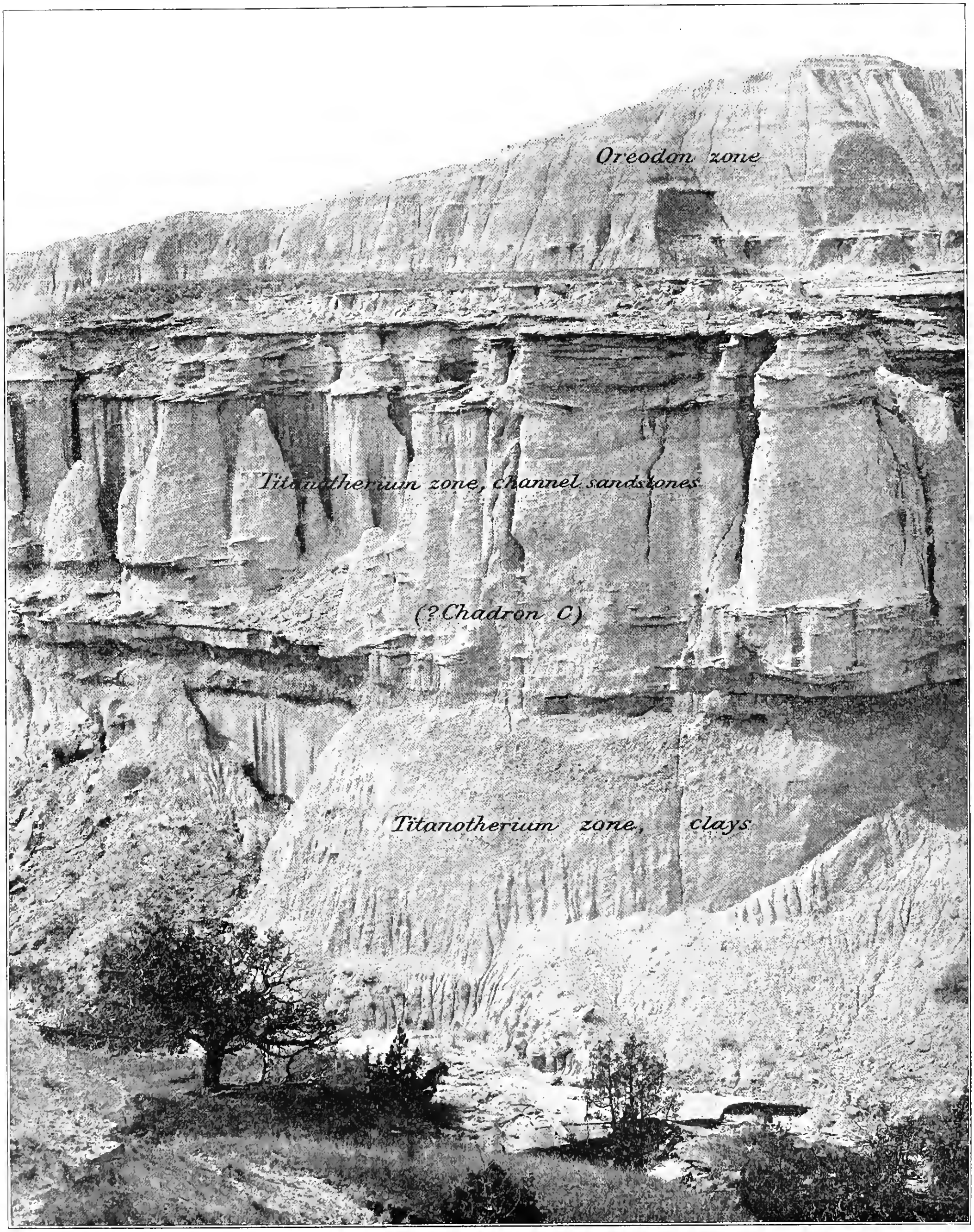
B. BADLANDS SOUTH OF WHITE RIVER, UTAH

Showing *Diplacodon* zone (level Uinta C 1, upper Eocene) in foreground and level Uinta C 2 in distance. (Compare fig. 66.) Am. Mus. negative 17665



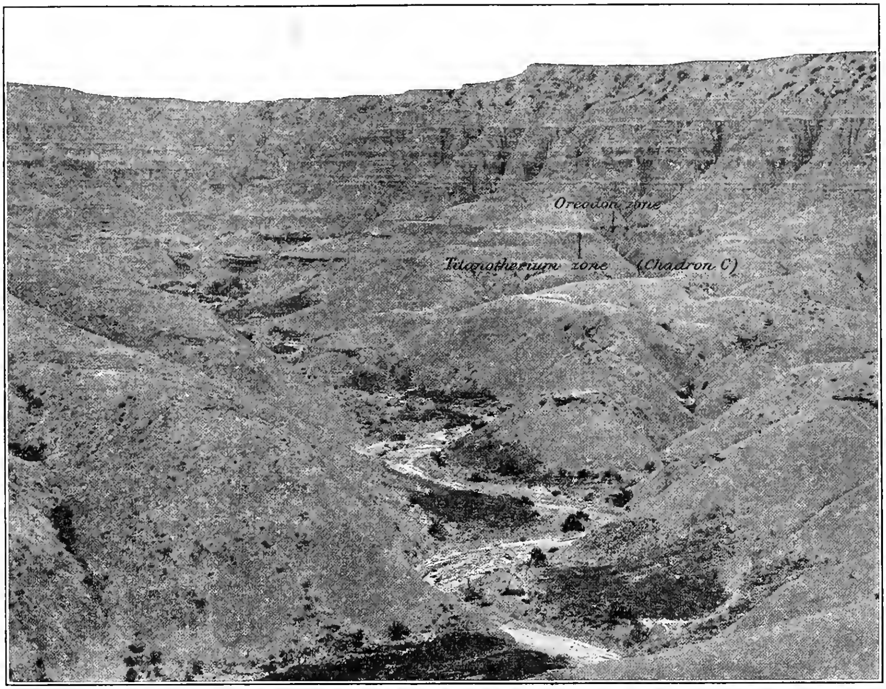
"MAUVAISES TERRES" OR BIG BADLANDS OF SOUTH DAKOTA

The rounded surfaces in the middle distance are the Chadron formation (the "*Titanotherium* beds" of Hayden). The pointed buttes in the foreground and distance represent the Brule formation of Darton (the "*Oreodon* beds" of the paleontologists). Photograph by N. H. Darton. U. S. Geol. Survey negative 640

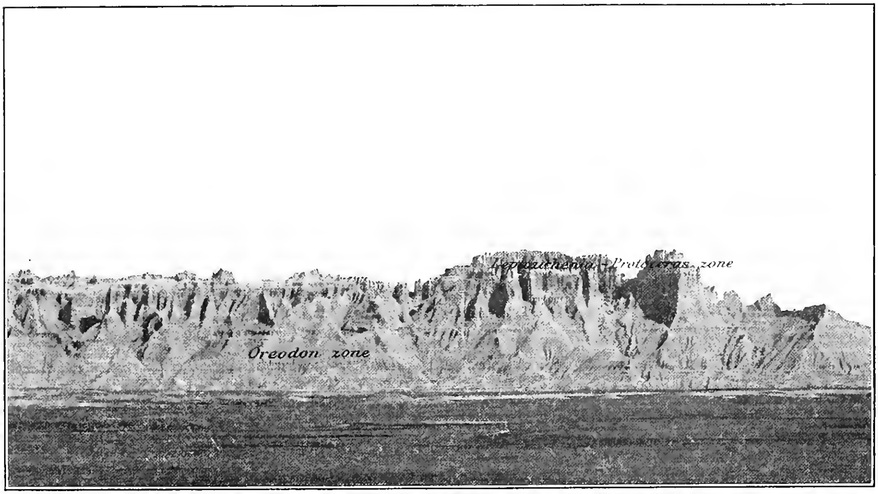


EXPOSURES AT QUINN DRAW, BIG BADLANDS, S. DAK.

Showing summit of lower Oligocene Chadron formation (*Titanotherium* zone) and, at the top, base of younger Brule formation (*Oreodon* zone). The sandstone columns in the center indicate a river channel between underlying and overlying clays. Am. Mus. negative 36012



A. SOUTH END OF SHEEP MOUNTAIN, NEAR HEAD OF CORRAL DRAW, BIG BADLANDS, S. DAK.
Showing *Oreodon* zone (Brule formation). Am. Mus. negative 36006



B. CEDAR CREEK, BIG BADLANDS, S. DAK.
Showing *Oreodon* zone (Brule formation) overlying *Titanotherium* zone (Chadron formation). Am. Mus. negative 36013

BRULE AND CHADRON FORMATIONS OF SOUTH DAKOTA

CHAPTER III

DISCOVERY OF THE TITANOTHERES AND ORIGINAL DESCRIPTIONS OF THE TYPES

SECTION I. HISTORY OF DISCOVERY

Full descriptions of the geologic and geographic positions of the several types and kinds of titanotheres are given in Chapter II. The present chapter relates the history of the explorations and of the gradual discovery of the character and relations of the titanotheres.

THE OLIGOCENE TITANOTHERES

THE PIONEER PERIOD: PROUT, OWEN, EVANS, LEIDY (1846–1873)

The Big Badlands of South Dakota and northwestern Nebraska are even now practically unknown to most Americans. As these lands lie in an arid region far from navigable rivers—a region that was formerly occupied by hostile Indians and that offers little attraction to either the prospector or the settler—it is not surprising that their fossil wonders long lay hidden from the world. The fossil remains of the great animals described in this monograph were known to the Indians and referred to in their mythology as "thunder horses." (See Preface, p. xxi.)

In 1846 Dr. Hiram A. Prout, of St. Louis, sent to Professors Dana and Silliman of Yale College a cast of a remarkable fossil that he had received from "a friend residing at one of the trading posts of the St. Louis Fur Co. on the Missouri River." Prout's brief notes, together with a crude sketch of one of the lower molars, were accordingly published in the American Journal of Science and Arts. (Prout, 1846.1, pp. 288, 289.) In a later communication Prout (1847.1) stated that this fossil (fig. 85) was discovered in the "Mauvais Terre, on the White River, one of the western confluents of the Missouri." This was the famous specimen described by Prout as a "gigantic *Palaeotherium*," which Leidy tells us (1852.1, p. 551) was "the first of the many mammalian remains which have been brought to the notice of the scientific world from the vast Eocene cemetery of Nebraska." It thus gave the first hint to scientists that "the region of Nebraska Territory of the United States appears to be as rich in the remains of Mammalia and Chelonia of the Eocene period as the deposits of the same age of the Paris Basin." (Leidy, 1852.1, p. 539.)

The fossil jaw described by Prout represented an animal of great size. "The entire jawbone," he says, "must have been at least 30 inches long, which far exceeds in size the *Palaeotherium magnum*." The reference to Cuvier's *Palaeotherium* was, under the circumstances, very natural, because the lower molars of Prout's specimen were surmounted by crescentic cutting surfaces somewhat like those of *Palaeotherium*.

This discovery evidently attracted attention abroad, for in 1849 the French paleontologist Pomel (1849.1, pp. 73–75), after carefully considering Prout's description and figures, stated that the fossil represented a new subgenus of paleotheres, for which he proposed the name *Menodus giganteus*, the generic name referring to the crescents of the lower molars, the specific name to the great size of the animal.

Meanwhile (in 1839, 1840–1849) the United States Government geologist, Dr. David Dale Owen, was making his extensive geologic reconnaissance of Wisconsin, Iowa, and adjacent States. In his final report (Owen, 1852.1, p. 194) he tells us that he was "desirous, if possible, to connect the geology of the Mississippi Valley, through Iowa, with the Cretaceous and Tertiary formations of the upper Missouri, a matter very important to the proper understanding of the formations of the intervening country, which it had been made my particular duty to explore." Finding it impracticable to explore the Missouri region himself he detailed to this work one of his assistants, Mr. John Evans. Late in the field season of 1849 Evans "finally reached that most curious unexplored region, the corner of the 'Badlands' (Mauvaises Terres), lying high up on White River, a locality which seemed likely, above all others, to furnish satisfactory information regarding the precise character and age of the Tertiary deposits of the upper Missouri country." (Owen, 1852.1, p. 195.)

From Evans's report (p. 197) Owen gives the following description of the Mauvaises Terres of White River:

> To the surrounding country, however, the Mauvaises Terres present the most striking contrast. From the uniform, monotonous open prairie, the traveler suddenly descends, one or two hundred feet, into a valley that looks as if it had sunk away from the surrounding world, leaving standing, all over it, thousands of abrupt, irregular, prismatic, and columnar masses, frequently capped with irregular pyramids and stretching up to a height of from one to two hundred feet or more.
>
> So thickly are these natural towers studded over the surface of this extraordinary region that the traveler threads his way through deep, confined, labyrinthine passages, not unlike the narrow, irregular streets and lanes of some quaint old town of the European continent. Viewed in the distance, indeed, these rocky piles, in their endless succession, assume the appearance of massive artificial structures, decked out with all the accessories of buttress and turret, arched doorway and clustered shaft, pinnacle and finial, and tapering spire.
>
> One might almost imagine oneself approaching some magnificent city of the dead, where the labor and the genius of forgotten nations had left behind them a multitude of monuments of art and skill.
>
> On descending from the heights, however, and proceeding to thread this vast labyrinth and inspect, in detail, its deep, intricate recesses, the realities of the scene soon dissipate the

delusions of the distance. The castellated forms which fancy had conjured up have vanished, and around one, on every side, is bleak and barren desolation.

Then, too, if the exploration be made in midsummer, the scorching rays of the sun, pouring down in the hundred defiles that conduct the wayfarer through this pathless waste, are reflected back from the white or ash-colored walls that rise around, unmitigated by a breath of air or the shelter of a solitary shrub.

The drooping spirits of the scorched geologist are not permitted, however, to flag. The fossil treasures of the way well repay its sultriness and fatigue. At every step objects of the highest interest present themselves. Embedded in the débris lie strewn, in the greatest profusion, organic relics of extinct animals. All speak of a vast fresh-water deposit of the early Tertiary period and disclose the former existence of most remarkable races that roamed about in bygone ages high up in the valley of the Missouri, toward the sources of its western tributaries, where now pastures the big-horned *Ovis montana*, the shaggy buffalo or American bison, and the elegant and slenderly constructed antelope.

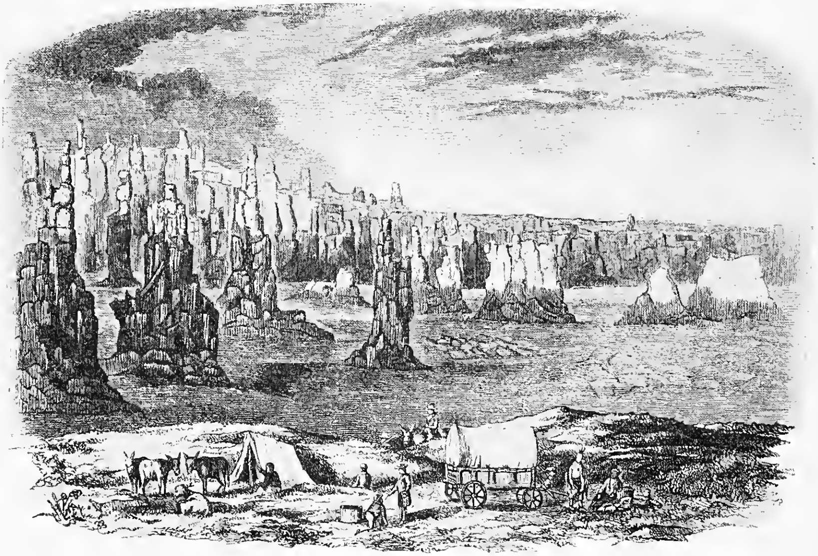


FIGURE 83.—Mauvaises Terres, Nebraska. After David Dale Owen, 1851

Owen continues (p. 198) with a popular description of the extinct animals found:

Every specimen as yet brought from the Badlands proves to be of species that became exterminated before the mammoth and mastodon lived and differ in their specific character, not alone from all living animals, but also from all fossils obtained even from cotemporaneous geological formations elsewhere.

Along with a single existing genus, the *Rhinoceros*, many new genera never before known to science have been discovered, and some, to us at this day, anomalous families, which combine in their anatomy structures now found only in different orders. They form, indeed, connecting links between the pachyderms, plantigrades, and digitigrades. For example, in one of the specimens from this strange locality, described by Dr. Leidy under the name *Archiotherium*, we find united characters belonging now to the above three orders; for the molar teeth are constructed after the model of those of the hog, peccary, and babyroussa; the canines as in the bear; while the upper part of the skull, the cheek bones, and the temporal fossa assume the form and dimensions which belong to the cat tribe. Another, the *Oreodon* of Leidy, has grinding teeth like the elk and deer, with canines resembling the omnivorous thick-skinned animals, being, in fact, a race which lived both on flesh and vegetables and yet chewed the cud like our cloven-footed grazers.

Associated with these extinct races we behold also, in the Mauvaises Terres, abundant remains of fossil Pachydermata of gigantic dimensions and allied in their anatomy to that singular family of proboscidate animals of which the tapir may be taken as a living type. These form a connecting link between the tapir and the rhinoceros; while, in the structure of their grinders, they are intermediate between the daman and rhinoceros; by their canines and incisors, they connect the tapir with the horse, on the one hand, and with the peccary and hog on the other. They belong to the same genus of which the labors of the great Cuvier first disclosed the history, under the name of *Palaeotherium*, in publishing his description of the fossil bones exhumed from the gypsum quarries of Montmartre, near Paris, but are of distinct species; and one at least, of this genus, discovered in the Badlands (*Palaeotherium proutii*), must have attained a much larger size than any which the Paris Basin afforded. In a green, argillo-calcareous, indurated stratum, situated within 10 feet of the base of the section, a jaw of this species was found, measuring, as it lay in its matrix, 5 feet along the range of the teeth, but in such a friable condition, that only a portion of it could be dislodged; and this, notwithstanding all the precautions used in packing and transportation, fell to pieces before reaching Indiana.

A nearly entire skeleton of the same animal was discovered, in a similar position, which measured, as it lay embedded, 18 feet in length, and 9 feet in height. But here, as in the former case, the crumbling condition of the bones rendered it impossible to disinter them whole; and the means of transportation to the Missouri were insufficient, even if these interesting remains could have been extracted in good condition.

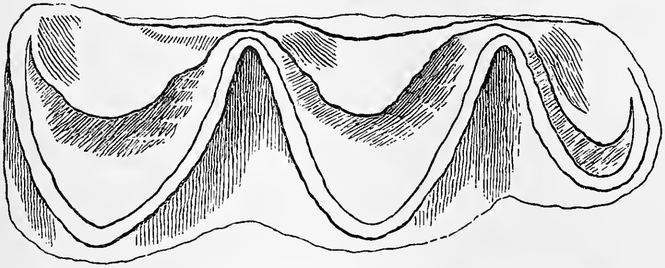


FIGURE 84.—"Vertical view of the posterior tooth belonging to the lower jaw of Mr. Prout's *Palaeotherium;* natural size." After Prout, 1846

Owen also gives (1852.1, p. 200) a tabular "Section of beds constituting the early Tertiary (Eocene) of the Badlands." This section, reproduced below, was doubtless taken by Evans.

Section of beds constituting the early Tertiary (Eocene) of the Badlands (Mauvaises Terres)

[Numbered in descending order]

		Ft.	in.
1.	Ash-colored clay, cracking in the sun; containing siliceous concretions	30	
2.	Compact white limestone	3	
3.	Light-gray marly limestone	8	
4.	Light-gray indurated siliceous clay (not effervescent)	30	
5.	Aggregate of small angular grains of quartz, or conglomerate, cemented by calcareous earth; slightly effervescent	8	
6.	Layer of quartz and chalcedony (probably only partial)		1
7.	Light-gray indurated siliceous clay, similar to No. 4 but more calcareous, passing downward into pale flesh-colored indurated siliceous marly limestone (effervescent); turtle and bone bed	25	
8.	White and light-gray calcareous grit; slightly effervescent	15	
9.	Similar aggregate to No. 5 but coarser	8	
10.	Light-green indurated argillaceous stratum (slightly effervescent); "palaeotherian bed"	20	

Some of the specimens brought back by Evans were referred to in a brief notice published by Owen, Norwood, and Evans (1850.1), in which the name "*Palaeotherium proutii*" was proposed "in compliment to Dr. Prout, of St. Louis."

The next year (1850) after Evans's journey Mr. Thaddeus A. Culbertson visited, under the auspices of the Smithsonian Institution, the same region (Leidy, 1854.1, p. 12) and "made a good collection of its animal remains," including skulls of *Oreodon culbertsoni* and the titanothere upper premolars which Leidy afterward described (1852.2, p. 2) under the names *Rhinoceros americanus* and *Eotherium americanus.* The locality was Bear Creek, a dry tributary of Cheyenne River. (See Chap. II, p. 104.)

The detailed description of the mammalian and chelonian fossils collected by Owen, Evans, and others was intrusted to Dr. Joseph Leidy, of Philadelphia, and was published in Owen's report of 1852 (1852.1, pp. 551, 552), already cited. In this publication Leidy describes Prout's original specimen and gives a poor figure of Evans's principal specimen, an imperfect lower jaw of a titanothere. He adopts provisionally the name *Palaeotherium? proutii* Owen, Norwood, and Evans but concludes his description of these fossils with the following significant remark:

> All the preceding specimens, except, probably, the latter two (fragments of upper molars), I suspect belong to a different genus from either *Palaeotherium* or *Anchitherium,* and should the suspicion prove correct, *Titanotherium* would be a good name for the animal, as expressive of its very great size.

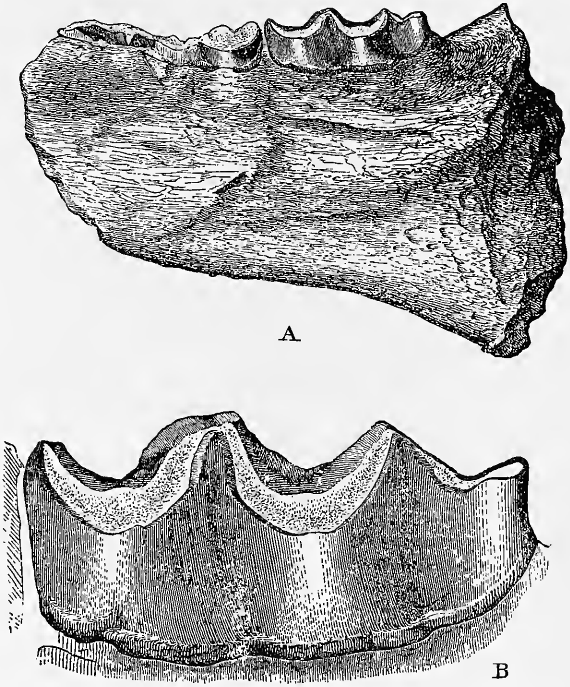


FIGURE 85.—Original figures of Prout's "gigantic *Palaeotherium,*" the first titanothere discovered. After Prout, 1847

A, "Fragment of the inferior maxillary of the left side," one-fourth natural size; B, last lower molar, left side, four-fifths natural size.

Thus was proposed the name *Titanotherium,* which has figured so largely in the literature of American paleontology and was consequently chosen as the basis for the title of this monograph.

Two years later Leidy (1854.1) gave a revised and extended description of the available remains of titanotheres, which was accompanied by excellent lithographs of Prout's and other fragmentary specimens. At this stage of knowledge the only parts figured under the name *Titanotherium proutii* included the lower molars, a lower premolar, a lower canine, a fragmentary upper molar, and two upper premolars (Leidy's types of *Rhinoceros americanus*). Fragments of large upper molars were named *Palaeotherium giganteum*.

The "palaeotherian bed" of Owen and Evans is referred to by Leidy (op. cit., p. 13) as the "*Titanotherium* bed." This appears to be the first use of this term, which was afterward, in the form "*Titanotherium* beds" (now *Titanotherium* zone), so widely used by geologists and paleontologists.

An interval of 15 years in the literature of the subject, from 1854 to 1869, is broken only by Prout's brief notice of an indeterminate molar (now lost) of a titanothere, which he named *Leidyotherium*. But during this seemingly barren interval Meek and Hayden were making their historical explorations (Merrill, 1906.1, pp. 585–592), which resulted in notable advances in our knowledge of the relations of the geologic deposits of the Rocky Mountains and Great Plains. They also brought back many vertebrate fossils, including specimens of *Titanotherium*.

One of the specimens of titanotheres collected by Meek and Hayden included a nearly complete series of upper teeth. This specimen, which belonged to Prof. James Hall and is now No. 433 of the Hall collection of the American Museum of Natural History, was described and figured by Leidy in his memoir of 1869 (1869.1, pp. 206, 207, pl. 24) and was by far the best specimen that had been described up to that time. Leidy referred it to his species *Titanotherium proutii*, but it probably belongs in the genus that Marsh afterward named *Brontotherium*. This specimen misled Leidy into assigning *Titanotherium* to the Artiodactyla. "From the form of its lower true molars, which were first discovered," he says, "it was supposed to be more nearly allied with the *Palaeotherium* and was hence placed among the uneven-toed pachyderms, or Perissodactyla, but the nearly complete dentition of both jaws, since discovered, appears to indicate its position to be as above stated"—that is, it appeared to be "nearly allied with *Chalicotherium*, and, like it, approximates the even-toed pachyderms, or Artiodactyla * * * with the Ruminantia."

In 1870 Leidy (1870.1, pp. 1, 2) described a fragmentary fossil from Colorado that had been submitted to him by Doctor Hayden. We now know that this specimen consists of the horn cores and attached coossified nasal bones of a titanothere of some sort, but to Leidy, who knew practically nothing of the skull of the titanothere, it proved "singularly puzzling in character." He at first thought it might pertain to *Titanotherium*, "but in the state of extreme uncertainty as to its collocation, it may with equal probability be referred to other genera, perhaps to *Megalomeryx*, or it may have been an American species of *Sivatherium*. Under the circumstances it may be referred to a new genus, with the name of *Megacerops coloradensis*."

This problematical fossil was redescribed and figured by Leidy in his memoir of 1873 (1873.1, p. 239). He states that the specimen "appears to correspond with that portion of the face * * * [of *Sivatherium*] which comprises the upper part of the nose, together with the forehead and the anterior horn cores." He compares the specimen with the corresponding parts of the *Sivatherium*, the rhinoceros, the tapir, and the mastodon. He decides that the fragmentary horn core formerly attributed to *Titanotherium* may perhaps belong to another species of *Megacerops*.

This erroneous determination, together with the previous assignment of *Titanotherium* to the Artiodactyla, shows how greatly Leidy, even with all his skill and caution, was deceived by the lack of well-preserved and definitely associated feet and skulls, a lack which is felt to some extent even at the present time.

Leidy's description of *Megacerops* may be regarded as marking the close of the first or pioneer period in the study of the titanotheres, a period characterized by (1) the chance discovery of "Prout's specimen," (2) the exploration of the White River badlands by Evans, Hayden, and others and the resulting knowledge of the general geologic age of the beds, (3) the description of fragmentary remains of titanotheres, chiefly teeth, by Prout, by Pomel, and by Leidy in successive publications, together with the beginnings of the systematic nomenclature, (4) the erroneous reference of *Titanotherium* to the Anoplotheriidae among the Artiodactyla.

TAXONOMIC ARRANGEMENT AND COMPARISON

WORK OF MARSH AND COPE (1870–1887)

The second period in the study of titanotheres, which may be called the period of systematic description, really began before the first period had closed (1873).

From 1873 to 1891, inclusive, the literature of the Oligocene titanotheres is dominated almost exclusively by the explorations and systematic contributions of Marsh and Cope. During this time Marsh described eight genera and fourteen species as new, and Cope described three genera and twelve species as new. The solution of the exact systematic and phylogenetic interrelations of these genera and species is one of the principal themes of Chapters IV to VII of the present monograph.

In 1870 Prof. Othniel C. Marsh (1870.1) headed an expedition sent from Yale College to northern Colorado, where he not only discovered and explored "an extensive outcrop of the true Mauvaises Terres, or White River formation," but also procured some magnificent specimens of titanotheres (including the types of *Brontotherium gigas* and *B. ingens*), which he described and figured three years later. Marsh was also able to solve the problem of the ordinal relationships of the titanotheres (1873.1, p. 486), showing that his *Brontotherium gigas* was a "true perissodactyl with limb bones resembling those of *Rhinoceros*. The genus is related to *Titanotherium*, and the two appear to form a distinct family, which may be called Brontotheridae." He was able in a very few words to throw a flood of light upon the characters of the skeleton, hitherto known chiefly from fragments:

> It closely resembles that in recent perissodactyls but shows some approach to the Proboscidea. The femur has a third trochanter, and its head a pit for the round ligament. The fibula is entire and slender. The astragalus is remarkably short. It has a deep groove on its upper surface, and the articular facets for the navicular and cuboid are nearly equal. In the manus there are four toes of nearly equal size, the first digits being rudimentary or wanting. There were three digits only in the pes, the first and fifth being entirely wanting. The toes were short and thick, as in proboscidians. The metacarpals and metatarsals are longer than in the elephant, and the phalanges shorter. The foot was also more inclined. The carpal and tarsal bones are very short and form interlocking series. The tail was long and slender.

An important point not touched upon in this communication was the presence or absence of horns.

Prof. Edward D. Cope was not far behind Marsh in contributions to the literature of the titanotheres. Two years after Marsh had made his explorations in Colorado, Cope, in 1872, discovered a number of remarkable skulls (now in the Cope collection of the American Museum of Natural History) which, in bulletins published in 1873 and 1874, he made the types of *Symborodon torvus, Megaceratops acer, M. heloceras, Symborodon bucco, S. altirostris, S. trigonoceras.* He states (1873.2, pp. 2, 3) that "Leidy and Marsh have described two genera of this group, viz, *Titanotherium* and *Brontotherium*, but without certain indications of their possession of horns." He regards them as "all true perissodactyls and allied to the *Rhinoceros* and *Palaeotherium*." His genus *Symborodon*, like *Menodus, Titanotherium*, and *Brontotherium*, was "established on mandibular rami only, which can not be certainly associated with crania," the last phrase suggesting one of the most troublesome and obdurate of titanothere problems, which from the first has caused confusion in the systematic nomenclature. Cope regarded the absence of incisors as one of the generic characters that separated *Symborodon* from *Titanotherium* and *Brontotherium*, thus first raising the problem how far differences in the number of incisors may correspond to true generic differences. The discovery of so many more or less complete skulls enabled Cope to infer specific and generic characters from the variations in form of the horn cores, skull top, nasals, and zygomatic arches. Thus the discoveries of Cope and Marsh, although they settled the ordinal relationships of the titanotheres, began to complicate the problem of their interrelationships.

SUMMARY OF MARSH'S CONTRIBUTIONS

In Marsh's paper "On the structure and affinities of the Brontotheridae" (1874.1) he developed further the family characters of the group, separating them from the Rhinocerotidae, "apparently their near allies," establishing the number of digits in the fore and hind feet and the general characters of the skull, lower jaw, vertebrae, and limbs. This paper is accompanied by the first of a series of excellent lithographic plates, illustrating some of Professor Marsh's superb specimens of titanotheres from Colorado. Marsh contributed another short but pregnant article on the "Principal characters of the Brontotheridae" in 1876 (1876.1), and after that he published at intervals brief descriptions of supposedly new genera and species, not all of them accompanied by illustrations, until September, 1891, the date of his last published contribution to the subject.

Marsh's most valuable contributions to our knowledge of the titanotheres may be summarized as follows: (1) He and his party explored the White River formation in Colorado and collected from it many remarkably fine specimens; (2) he demonstrated the ordinal position of the group, classifying its members as perissodactyls; (3) he recognized the fact that the titanotheres constitute a distinct family, which he named the Brontotheridae; (4) he made the illuminating observation that his upper Eocene genus *Diplacodon* served to connect the Oligocene Brontotheridae with the Eocene "Limnohyidae"; (5) he published many excellent lithographs and woodcuts, showing chiefly the skulls and dentition of titanotheres, but including also (1889) an excellent restoration of *Brontops robustus;* (6) he supervised the preparation of a fine series of lithographic plates for the present work; (7) under the auspices of the United States Geological Survey he founded the present series of monographs on fossil vertebrates; (8) he began the preparation of the present monograph, although he left no manuscript for it; (9) he obtained for the National and Yale Museums their superb specimens of titanotheres, most of which were collected by his field assistant J. B. Hatcher, who in turn also made valuable scientific contributions to our knowledge of these animals.

Marsh's detailed systematic work on the titanotheres was less fortunate than his broader contributions, owing chiefly to confusion in regard to features of the skull and jaw. After founding the genus and species *Brontotherium gigas* upon a lower jaw, he referred to the same genus as the type of *B. ingens*, a skull that certainly belongs to another genus (*Menodus*). In consequence of this initial confusion he erected a new genus (*Titanops*) for skulls that should have been referred to *Brontotherium.* Many of his conceptions of the interrelations of the genera and species proposed by him were erroneous. Although recognizing the fact that the genera *Brontops, Allops*, and *Teleodus* were all allied to "*Brontotherium*"—that is, as represented by the skull of "*Brontotherium* [*Menodus*] *ingens*"—he nevertheless thought that *Diploclonus* was related to *Titanops* (the true *Brontotherium*), and he referred to *Menops* (a near ally of his "*Brontotherium*" *ingens*) a well-preserved skull that is now known to belong to *Brontotherium* proper. In fact, in common with Cope and others, Marsh apparently failed to recognize the comparatively wide phyletic gap between the true *Brontotherium* (his *Titanops*) and Cope's *Symborodon* on the one hand and the supposed genera *Brontops, Allops, Menops*, and *Menodus* (his "*Brontotherium ingens*") on the other. Consequently his generic definitions are unsatisfactory, and he was certainly not overconservative in proposing new generic and specific terms.

SUMMARY OF COPE'S CONTRIBUTIONS

The next year (1874) after publishing his preliminary descriptions of the several species of *Symborodon* and allied genera Cope (1874.2) gave full descriptions of these forms in his "Report on the vertebrate paleontology of Colorado," which was accompanied by eight lithographic plates. He presented a careful review of the general morphology of the skull, including the brain case and cranial antra, which was followed by a review of the work of preceding authors and by a tabular analysis and detailed description of the species of *Symborodon.* He recorded many interesting facts, such as the similarity of the dentition of *Symborodon* to that of *Palaeosyops* and of *Chalicotherium* and the mingling of proboscidian and rhinoceros analogies in the limbs. He considered the indications that *Symborodon* possessed a short proboscis. In his tabular analysis of species he indicated the differences in the shape of the horns and noted that in *S. trigonoceras* and *S. hypoceras* the upper premolars have a strong internal basal cingulum, whereas in *S. bucco* and *S. altirostris* the premolars are "without inner basal cingulum."

Cope, like Marsh, failed to distinguish the sexes as well as the separate groups or phyla of titanotheres. His "*S.*" *trigonoceras*, for example, is a *Menodus*, a member of an altogether different group from his "*S.*" *hypoceras*, which is a *Brontotherium.*

After an interval of 12 years, in 1886, Cope (1886.1) described the first Canadian species, *Menodus angustigenis*, basing it upon fragments discovered by McConnell and Weston for the Geological and Natural History Survey of Canada. Three years later (1889.1, p. 153) he referred this form to a new genus, *Haplacodon*, and in the same year (1889.2, pp. 628, 629) he described two other Canadian species. His review (1891.2, p. 17) of these forms and attempted revision of the nomenclature were involved and unsatisfactory. He recognized only two genera, *Menodus* and *Symborodon.* The last species of titanothere described by him was his *Menodus peltoceras* (1891.1), which is probably a female of Marsh's *Brontotherium curtum.*

REINTERPRETATION AND PHYLOGENETIC STUDY (OSBORN, 1887–1919)

STUDY OF CERTAIN FEATURES

Before Marsh and Cope had ceased naming new or supposedly new genera of titanotheres a turn was given to the trend of study by a paper by Scott and Osborn (1887.1, pp. 157, 158), entitled "Preliminary account of the fossil mammals from the White River formation contained in the Museum of Comparative Zoology." This paper, which was a description of the interesting collection made by Mr. Samuel Garman under the auspices of Prof. Alexander Agassiz, reacted from the polynomial systems of Marsh and Cope and tended toward a mononomial system. In this paper the Perissodactyla were described by Osborn, the Artiodactyla and Carnivora by Scott. Before describing the new titanothere material the authors noted the difficulty in deciding where to draw generic lines, a difficulty that is increased by the fact that the mandibles are seldom found with the skulls.

> As in *Uintatherium*, the variability in the various portions of the skull, especially in the region of the horns, is so extreme that no two skulls are found which are exactly alike. But the dentition, which is constant among the Dinocerata, here greatly complicates the problems of classification. The premolars vary in number, and the incisors, always of relatively small size and fairly constant in number in the upper jaw, vary from three to none in the lower jaw.[14] In all the lower jaws found in Professor Cope's collection of Menodontidae from northern Colorado there are no incisors, and the mandibular symphysis is extremely narrow. In the lower jaws of the Cambridge and Princeton collections, which are all from the Nebraska and Dakota exposures, the symphysis is broad, and the incisors, where preserved, are two in number, while in one of the Cambridge specimens no less than three incisor alveoli may be counted upon one side of the symphysis.
>
> We might infer from this that *Symborodon* can be clearly separated from *Menodus* by the absence of the lower incisors, accompanied by a narrowing of the symphysis; but Professor Cope has recently described a new species, *M. angustigenis*, from the Swift Current Creek region (Cope, 1886.1, p. 81c), which combines the narrow type of symphysis with the presence of two incisors. The separation of these genera is rendered still more improbable by the parallelism which exists between the skulls from the Nebraska and Colorado localities, especially in respect to the conformation of the nasal bones and the horns. The genus *Symborodon* is, however, provisionally adopted at present to include the species with a narrow mandibular symphysis and no lower incisors.
>
> The genus *Brontotherium* Marsh (that is, Marsh's "*Brontotherium*" *ingens*, not the true *Brontotherium*) can not be distinguished from *Menodus.* It rests in part upon the premolar

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[14] One of the Cambridge skulls, *M. coloradensis*, has but a single upper incisor.

> formula $\frac{4-4}{3-3}$, in the synopsis given by Professor Marsh (1876.1, p. 339), as distinguished from *Menodus*, with ?pm $\frac{4-4}{4-4}$. One of the lower jaws of the Princeton collection, however, has the premolar formula $\frac{}{3-4}$, demonstrating that the first lower premolar is a variable tooth and can not in this case be used in classification. The same rule applies to the second cone upon the last upper molar, the supposed generic character of *Diconodon* Marsh. This is found in different species in all degrees of development, from a small prominence upon the basal cingulum to a well-developed cone (*M. proutii*).

From this evidence Osborn draws the following partly erroneous conclusion:

> Such characters as the invariable absence of lower incisors may subsequently be found to separate one genus of the Menodontidae from another; but our present evidence goes to show that they simply characterize the extremes of a closely related series of animals, from the same horizon, of which the intermediate forms are represented by numerous species. The safest basis of specific determination seems to be the correlation between the development and proportion of the horns and of the nasals, the rule being that where the horns are long the nasals are short, and conversely. The number of the teeth does not at present seem to be absolutely constant, even within the limits of the species.
>
> The following determination of the species in the Cambridge collection is, for the above and other obvious reasons, provisional. The classification can be finally settled only when the lower jaws and skulls are found in association.

Thus the validity of the several genera recognized by Marsh and Cope and of the chief criteria used by them as generic characters was called in question. The species are treated as belonging mainly to the single genus *Menodus*. Taking up the description of the new material, the authors mistakenly refer to Leidy's *Megacerops coloradensis*, a well-preserved skull, which at present is referred to *Allops marshi*. They then describe two new species—"*Menodus*" *tichoceras*, based on a skull, and "*Menodus*" *platyceras*, based on a pair of bony horns. Both these species are at present referred to the true *Brontotherium* or flat-horned genus. The authors conclude their discussion of the "Menodontidae" by presenting the first published restoration of the skeleton, made up of material in several museums, forming a composite animal representing *Menodus proutii*. In connection with a table of measurements arranged to show progressive and correlated changes in the horns and nasals, they make the following remarks (op. cit., p. 16):

> The above measurements bring out very clearly the decrease in the proportions of the nasals pari passu with the gradual elongation of the horns. Another very interesting fact is brought out by the comparison of the transverse and longitudinal diameters of the horns at the base. As we pass from the short to the long horned types, through *M. coloradensis*, *tichoceras*, *dolichoceras*, and *platyceras*, there is a gradual rotation of the longer axis of the horn section from a fore and aft to a transverse plane, the species last named representing the extreme of the transverse type.

The fuller development and more or less radical modification of the hypotheses put forward in this paper have been the subject of successive contributions by Osborn, culminating in the present work.

GEOLOGIC LEVELS AND SUCCESSION OF TYPES (HATCHER, 1886-1893)

The work of Marsh and Cope had been exclusively descriptive and systematic. Osborn's observation of the correlated progressive reduction of the nasals and the enlargement and flattening of the horns seems to have been the first important application of evolutionary principles to the study of the Oligocene titanotheres. But materials for an exact knowledge of the phyletic succession, resting securely upon a knowledge of the precise geologic levels of a large series of specimens, had hitherto been entirely lacking. This all-important element of the time relations of the different species was largely supplied by the labors and study of J. B. Hatcher. In 1886, 1887, and 1888 Hatcher spent 15 months in the White River beds of South Dakota and Nebraska, collecting material for Professor Marsh's monograph on the Titanotheridae. In an interesting article in the American Naturalist for March, 1893, Hatcher (1893.1, pp. 214, 215) tells us that he collected or purchased "nearly 200 complete skulls and many more or less complete skeletons," a part of which are now on exhibition in the National and Yale Museums. The superb Hatcher collection in the United States National Museum contains skulls and jaws of 157 individuals; as completely listed in the generic sections of this monograph, it furnishes the classic standard of reference. Hatcher writes:

> Early in the season of 1886 it became apparent that certain forms of skulls were characteristic of certain horizons in the beds. This fact showed the importance of keeping, so far as possible, an exact record of the horizon from which each skull or skeleton was taken. From actual measurement the vertical range of the Titanotheridae was found to be about 180 feet. For convenience in keeping a record of horizons the beds were divided into three divisions of 60 feet each, and each of these three divisions was subdivided into three divisions of 20 feet each. The different skulls and skeletons, when dug out, were each given a separate letter or number, and this letter or number was placed in that subdivision of the beds from which the skull or skeleton was taken.
>
> At present about 60 of these skulls and several more or less complete skeletons have been freed from their matrix. When studied in connection with the horizons from which they were taken, these remains show that a regular and systematic development took place in these animals from the base to the top of the beds. The most noticeable change which took place in the Titanotheridae was a gradual and decided increase in their size from the lowest to the uppermost beds, as is shown by the increase in the size of the skulls, fore and hind limbs, and other portions of the skeleton. Individuals found near the bottom of the beds are little, if any, larger than the living rhinoceros. From this they gradually increase in size as we go up until at the top we find a type described by Professor Marsh as *Titanops*, rivaling the modern elephant in size.
>
> This increase in size from the base to the summit of the beds was attended by a very marked development in certain portions of the skeleton, noticeable among which are the following: A variation in shape and an increase in the size and length of the horn cores as compared with the size of the skulls, attended, near the summit of the beds at least, by a decided shortening of the nasals.

Hatcher was less fortunate in his observations on the evolutionary changes in the dentition, stating that "the number of incisors, though probably never constant, even in the same species, shows a tendency to decrease in skulls found near the summit of the beds," and concluding that "the number of incisors can hardly be considered as of either generic or specific importance in the Titanotheridae, where they are no longer functional and vary with individuals in the same species and with age in the same individual. The same may be said of the presence or absence of the first premolar."

After noting certain other changes rightly believed by him to be progressive, such as (1) the loss of the trapezium, (2) the development of a postero-internal cone on the third upper molar, and (3) the flattening of the horns, Hatcher concludes his paper by giving a tabular paleontologic section of the "*Titanotherium* beds," with a general description of the forms characterizing the three ascending divisions. As to the number of genera, he gives the impression that he regards all the various species ascribed by Marsh and Cope to different genera (except *Teleodus avus* Marsh) as referable to the single highly variable genus *Titanotherium* Leidy.

FIRST EUROPEAN NOTICE (TOULA, 1892)

The next important event is the discovery of a titanothere of Oligocene type in Europe, described as *Menodus rumelicus* by Toula (1892.1). This discovery, in connection with that of the Transylvanian *Brachydiastematherium*, described by Böckh and Maty in 1876 (1876.1), extended the known range of the titanotheres to the Old World.

DISTINCTIONS OF SEX (OSBORN AND WORTMAN, 1895)

In 1895 Osborn and J. L. Wortman (1895.105) published a corrected restoration of *Titanotherium* based upon the fine skeletal material secured by the American Museum field parties in 1892 and 1894. They ventured the conclusion that "it is probable that certain wide differences in the development of the horns, which have been assigned a generic value, are merely sexual characters."

MONOPHYLETIC INTERPRETATION (OSBORN, 1896)

The extreme development of the erroneous theory that all the various species of Oligocene titanotheres belonged to the single genus *Titanotherium* and were practically monophyletic is worked out in a very elaborate way in Osborn's paper "The cranial evolution of *Titanotherium*," published in 1896. This was the most comprehensive review of the subject that had hitherto appeared and was illustrated by numerous text figures and several folded plates. The direct observations were based chiefly on the large collection of titanotheres in the American Museum and to a less extent upon figures and descriptions previously published. Part I, the systematic introduction, includes a chronologic list of generic and specific terms, with references and a brief history of the progressive complication of the nomenclature, after which the author says (Osborn, 1896.110, p. 162):

> It is obvious that the only method of clearing up this heterogeneous list [of nominal genera and species] is first to establish certain laws of cranial development, and second to apply these laws to the distinction of genera and species in chronological order. Examined in this way, the vast array of genera and species is resolved into one or possibly two genera and about fourteen definable species.

Accordingly in Part II, "Principles of cranial and dental evolution," we find a study of the differences in size of skull, shape of horns, nasals, zygomatic arches, auditory meatus, cingula on grinding teeth, incisors, canines, second internal cone of last molar, etc., all considered as indicating either specific or sexual or individual differences within the limits of a single genus, *Titanotherium*. This is followed by the "Revision and definition of species," in which some 27 species, including the new *T. ramosum*, are discussed. The known species from the lower, middle, and upper beds are arranged in a single or monophyletic series, beginning with the *T. heloceras-trigonoceras ingens* series, continuing with *torvum*, *robustum*, *dolichoceras*, *elatum*, *amplum*, *acer*, and culminating with *ramosum* and *platyceras*.

This analysis, although wholly wrong in treating all the species as members of a monophyletic series, not only laid the foundation for the present evolutionary and phylogenetic treatment of the group but established, as it were, the technique of investigation

POLYPHYLETIC INTERPRETATION (OSBORN, 1902–1919)

The reaction against the monophyletic theory was felt by the same author as a result of more extended research. In his paper of 1902 on "The four phyla of Oligocene titanotheres," after acknowledging the services of the late Professor Marsh and admitting the incorrectness of the monophyletic theory, Osborn says (1902.208, p. 91):

> This second review is an abstract of a portion of the results obtained for the United States Geological Survey monograph "The titanotheres," now in preparation. It covers practically all the type material in the Yale, National, American, and Harvard Museums, and advantage has been taken of the invaluable field observations by Hatcher of the levels on which the different skulls in the National Museum collection were discovered. The section method also has been very greatly extended and, taken in connection with the teeth and the detailed structure of the skull, has proved to be a sure criterion of specific and phyletic character.

Four important considerations had led Osborn to give up the monophyletic theory: First, from his phylogenetic studies on the rhinoceroses of Europe and America (Osborn, 1898.143; 1900.192) he had concluded that, contrary to earlier opinions, this group was in a high degree polyphletic, embracing many parallel phyla and having a wide adaptive radiation; second, the principle of dolichocephaly and brachycephaly (Osborn, 1902.207), as interpreted by him in the rhinoceroses and other groups, raised the presumption that similar differences would be found to distinguish genera and phyla among the titanotheres; third, he had learned to realize that the extent to which parallel and convergent evolution had operated in many allied phyla had been but little appreciated by earlier writers, who had largely failed also to distinguish between persistent, progressive, and retrogressive characters; fourth, an examination of the titanothere skulls collected by Hatcher and now in the National Museum, which Hatcher had recorded exactly as to level, enabled him, with the aid of principles just stated, to distinguish several distinct phyla and to follow them from the lower part through the middle and into the very top of the "*Titanotherium* beds." The characters of these phyla were summarized by Osborn as follows (1902.208, pp. 92–94):

THE FOUR GENERA

Titanotherium Leidy applies to long-limbed animals with long skulls, persistently long and broad nasals, short triangular horns placed slightly in front of the eyes, vestigial incisors $\frac{2-0}{2-0}$, large canine teeth. Known from the base to the summit of the [lower] Oligocene.

Megacerops Leidy applies to titanotheres with broad skulls, nasals progressively shortening, short horns rounded or oval in section, shifting anteriorly, one or two pairs of incisor teeth, $\frac{2-1}{2-1}$, medium-sized canine teeth. Known from the base to the summit of the [lower] Oligocene.

Probably related to this are the subgenera of the types named *Allops* and *Diploclonus* by Marsh, differing from the above in horn characters. Known chiefly from the upper beds.

Symborodon Cope includes titanotheres with skulls of varying proportion, nasals slender and progressively shortening, horns elongate and peculiar in being placed above the eyes instead of shifting forward, incisors vestigial $\frac{2-0}{2-0}$, canines small, approximated. Known only from the middle and upper beds.

Brontotherium Marsh embraces the largest titanotheres, with very broad zygomatic arches, nasals shortening while horns elongate and shift forward; incisors persistent, $\frac{2}{2}$ in the males, canines stout and obtuse.

Representatives of *Titanotherium* and *Megacerops* can be now continuously traced from the base to the summit of the [lower] Oligocene. Primitive species of *Brontotherium* also appear at the base, although the phyletic sequence through the middle to the upper beds is not so clear. *Symborodon* suddenly appears in the middle beds.

Viewed in the light of the foregoing principles, the variations in the horns, nasals, incisors, cingula, etc., took on new meanings—biologic, phylogenetic, and systematic; so that, after more than half a century of research (1846–1902) the systematic problem presented by the Oligocene titanotheres appeared in its main features to be solved. Subsequent research, however, has led to certain regrettable but apparently necessary changes in nomenclature: (*a*) The name "*Megacerops*" Leidy, as defined above, has been set aside for *Brontops* Marsh, for the reasons given below; (*b*) the name *Titanotherium* Leidy has been abandoned for the prior name *Menodus* Pomel; (*c*) the name *Symborodon* Cope has been replaced by the prior name *Megacerops* Leidy.

RECENT DISCOVERIES BY LULL, LAMBE, AND OTHERS

There remain to be recorded the following contributions: (1) The description of *Megacerops tyleri* by Lull (1905.1), based upon a fine skull and lower jaws with associated limbs, discovered by the Amherst College paleontologic expedition of 1903; (2) the description of *Brontotherium hatcheri* and *Symborodon copei* by Osborn in 1908 (1908.318), based on skulls in the National Museum; (3) the description of *Megacerops primitivus* and *M. assiniboiensis*, based on fragments obtained from Saskatchewan, Canada, by Lambe in 1908 (1908.1); (4) W. K. Gregory observed (*a*) that there is an alliance between *Brontops*, *Allops*, and *Menodus* as these terms are now used by Osborn, indicated by certain intermediate forms between the extremely brachycephalic *Brontops robustus* and the dolichocephalic *Menodus giganteus*, (*b*) that there is also an alliance between *Brontotherium* and *Megacerops* (*Symborodon*) in spite of the differences in the incisors. Hence the former group—*Brontops*, *Allops*, *Menodus*—has been called the menodontine group, and the latter group—*Brontotherium*, *Megacerops*—has been called the brontotheriine group.

Possibly the most valuable general result of the study of the titanotheres has been the fact that it has made possible the close examination of an extensive evolutionary history, stretching from the lower Eocene to the summit of the lower Oligocene. Many observations have been made on the precise modes of evolution, especially with regard to the way in which characters first appear and subsequently develop. The results of this evolutionary study are set forth in Chapters V, VI, VII, and XI of the present work.

THE EOCENE TITANOTHERES

PIONEER DISCOVERIES

WORK IN THE BRIDGER, WASHAKIE, AND UINTA BASINS BY LEIDY, MARSH, COPE, SCOTT, OSBORN, AND OTHERS (1870–1889)

Prof. F. V. Hayden, in the course of his historic explorations in the fossiliferous beds of the Rocky Mountains and Great Plains, obtained at Church Buttes, near Fort Bridger, Wyo., a number of isolated teeth, which were described by Leidy (1870.2) under the name *Palaeosyops paludosus*. This was the first Eocene titanothere made known to science, 24 years after the discovery of Prout's "gigantic *Palaeotherium*" (*Titanotherium*) in South Dakota. Although Leidy noted that the lower molar of *Palaeosyops* "resembles in its constitution those of *Palaeotherium, Chalicotherium*, and *Titanotherium*," he did not classify the new genus with the titanotheres, for the reason that at that time he thought *Titanotherium* and *Chalicotherium* were allied to the Artiodactyla. (See p. 247.) Soon afterward Leidy (1873.1, p. 27) described a skull, some teeth, and parts of the limb bones of *Palaeosyops* and, noting the similarities of this species to its supposed allies *Tapirus* and *Palaeotherium*, correctly referred it to the perissodactyls—the odd-toed pachyderms. Three other species (*P. major, P. humilis, P. junius*) were also described by him from the Bridger beds upon very fragmentary material.

In developing our knowledge of the Eocene titanotheres of the Bridger Basin, as in developing that of the Oligocene titanotheres, Marsh and Cope were not far behind Leidy. The first specimen of an Eocene titanothere described by Marsh, however (1871.2), was not recognized as such by him, as he mistook the isolated second lower premolar of a Bridger *Palaeosyops* for the fourth upper premolar of a dog and named it "*Canis montanus*." The next year (1872.1) he described some well-preserved remains under the name *Palaeosyops laticeps* and also founded the genus *Telmatherium.* Marsh's subsequent contributions to our knowledge of middle Eocene titanotheres were not especially significant, but in 1875 he described the very important genus *Diplacodon* from the upper Eocene Uinta beds of Utah and recognized its intermediate position both in time and in structural characters between his "Limnohyidae" (Palaeosyopinae) and *Brontotherium.*

Cope's explorations of the Bitter Creek or Washakie Basin (middle Eocene) of Wyoming in 1872 led to his describing the species "*Palaeosyops*" *vallidens* and "*Limnohyus*" *laevidens*, both represented by imperfect remains. The former is now known to belong to the long-headed genus *Dolichorhinus.*

The next year, 1873, Cope (1873.5) described the species *Limnohyus* (=*Palaeosyops*) *fontinalis* from the lower levels of the Bridger formation (supposed Bridger A), which is the oldest middle Eocene titanothere yet discovered. His *Palaeosyops diaconus*, from the upper levels of the Bridger Basin, is probably a synonym of *Palaeosyops robustus* (Marsh).

DISCOVERY IN HUNGARY

Shortly after these pioneer discoveries in America Böckh and Maty (1876.1) described a large lower jaw from Eocene deposits in Transylvania, in Hungary. The animal was supposed to be allied to *Palaeotherium* and was named *Brachydiastematherium transilvanicum.* Its affinities with the *Palaeosyops* group long remained unnoted, and even to this day it is the only known specimen of its kind in Europe.

PRINCETON AND COPE-WORTMAN EXPEDITIONS

The Princeton expeditions sent to the Bridger and Washakie Basins in 1877 and 1878 under Scott, Osborn, and Speir brought to light much valuable material of *Palaeosyops* and allied genera, especially the types of "*Leurocephalus*" *cultridens* and the peculiar form which was later described by Earle as *Palaeosyops megarhinus.* Thus by the end of 1878 remains of the genus *Palaeosyops* and its allies had been discovered in the middle Eocene Bridger and Washakie Basins and in the upper Eocene Uinta Basin.

The next year (1879) Dr. J. L. Wortman, who was collecting for Cope, extended the known range of the group into the lower Eocene Wind River formation of Wyoming, where he discovered the very primitive form which Cope in 1880 named *Palaeosyops borealis* and which is now recognized as approximately ancestral to the middle Eocene titanotheres. Wortman also discovered a very small form, which was described by Cope in 1880 (1880.1) as *Lambdotherium popoagicum* and recognized as more or less closely allied to the *Palaeosyops* group.

The next important expedition was that made by a Princeton party under Scott and Speir in 1886 into the Uinta Basin (upper Eocene). They collected skeletal material, referred at that time to *Diplacodon*, which was described by Osborn in 1890 (1890.51) and which demonstrated the intermediate characters of "*Diplacodon*" (*Protitanotherium*) between the Oligocene and middle Eocene titanotheres. In the same publication Osborn also described "*Palaeosyops*" *hyognathus*, a species based on a jaw that is now known to represent the long-skulled genus *Dolichorhinus.*

FIRST SYSTEMATIC AND EVOLUTIONARY REVISION (EARLE, 1889–1891)

Although Cope in 1884 (1885.1) had republished and partly extended the original descriptions of his own species, with lithographic figures, no satisfactory revision of the *Palaeosyops* group was possible at that time or for many years later.

In 1889 Charles Earle, at the invitation of Prof. H. F. Osborn, began a careful study of the material in the Princeton Museum and other collections, and in 1892 he published a memoir "On the genus *Palaeosyops* Leidy and its allies" (1892.1). Earle gave a very detailed description of the osteology of *Palaeosyops* and of the first attempted reconstruction of the skeleton of an Eocene titanothere by Osborn. (See fig. 86.) Owing in part to the lack of sufficient well-associated material, in part to the confusing practice of the earlier writers in designating and founding species upon several specimens of doubtful specific association, Earle's revision of the species and genera was, as he himself recognized, by no means final. He rightly regarded as distinct the genera *Lambdotherium, Limnohyops, Palaeosyops*, and "*Telmatotherium*," but as he showed in his tentative phylogenetic scheme, he, like other paleontologists at that time, did not appreciate the polyphyletic character of groups and consequently referred to a single main line of descent a number of forms that belong to widely separated phyla.

AMERICAN MUSEUM AND OTHER EXPLORATIONS OF THE EOCENE BASINS (1891–1895)

The problems relating to *Palaeosyops* and its allies, which had been barely made evident by the pioneer discoveries and had now been partly formulated by Earle, were of course only particular results of the general explorations of the fossil-bearing formations of the West. The early explorations had been in part reconnaissances, and their results were accordingly incomplete as regards both the nature of the material and the records of the stratigraphic levels at which the specimens were found, both absolutely prerequisite to a detailed knowledge of the phylogeny.

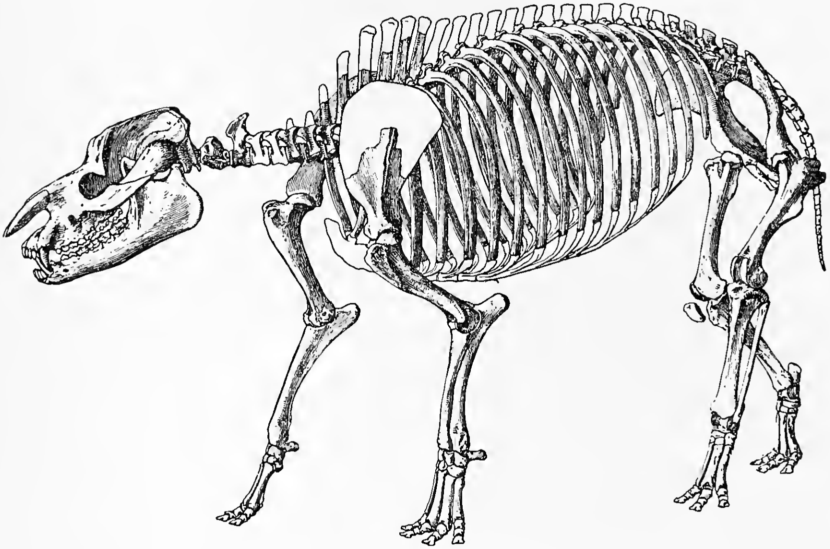

FIGURE 86.—Osborn's first restoration of *Palaeosyops paludosus* Leidy

This restoration is a composite one—the skull from the fine specimens in the Academy of Natural Sciences of Philadelphia, and the axial skeleton from the material in the Princeton Museum. The fore feet were afterward referred to *Mesatirhinus petersoni*. About one-twelfth natural size.

The founding (in 1890) of the department of vertebrate paleontology in the American Museum of Natural History by Prof. Henry Fairfield Osborn and the consequent establishment of continuous and systematic exploration began a new era of exact investigation not only of the titanotheres but of the whole series of vertebrate remains to be found in the Rocky Mountains and Great Plains regions, as well as the stratigraphic horizons at which they occur.

The first of these expeditions, led by Dr. J. L. Wortman, procured some important skeletal material of "*Palaeosyops*" *borealis* from the Wind River formation. Another expedition, sent out under Doctor Wortman in 1893, procured from the Bridger and Washakie Basins extensive material of the true *Palaeosyops*, enabling the American Museum to exhibit a mounted composite skeleton of this animal. Much other material was also collected by the same party. All this material has been used profitably in the present monograph, especially the specimens representing the "prophet-horn stage," to which Doctor Wortman in a letter from the field applied the name *Manteoceras*.

Another American Museum expedition, under Mr. O. A. Peterson, went into the Uinta Basin in 1894 and examined two hitherto unexplored horizons (Uinta B 2 and Uinta B 1 of this monograph), which underlie the true Uinta (Uinta C). This expedition collected many new forms and worked out the faunal sequence of the three horizons indicated. Among the results of this expedition, as reported in 1895, were the discussion by Osborn and Peterson (Osborn, 1895.98) of the three faunal levels (Uinta B 1, B 2, and C) and the description by Osborn of the specialized and interesting titanotheres named "*Telmatotherium*" *diploconum* and *T. cornutum*. Wortman's "prophet-horn" skulls were referred to "*Telmatotherium vallidens*," so that animals showing a wide range of form were here erroneously included under a single genus. The very aberrant form *Sphenocoelus* was also described, but its ordinal and family positions were left "Incertae sedis," on account of the lack of the teeth in the type and the peculiar characters of the base of the skull.

In the same year (1894) Mr. J. B. Hatcher, of the Princeton Museum, also went into the true Uinta area and discovered specimens representing the very advanced stage which in 1895 (1895.1) he described as *Diplacodon emarginatus*. In a brief postscript to this description he noted the wide range of forms that had been erroneously grouped by Osborn under the genus "*Telmatotherium*," and he formally proposed the generic names *Manteoceras* for the "prophet-horn" and *Dolichorhinus* for the long-skulled form. Both these terms, as well as the name *Protitanotherium* of Hatcher, have proved to be valid. Hatcher's separation of these genera was a very important move toward a correct understanding of their phylogenetic relations. He also figured a series of four stages ranging from the middle Eocene to the lower Oligocene, inclusive, showing the origin of the "horns." (See fig. 87.)

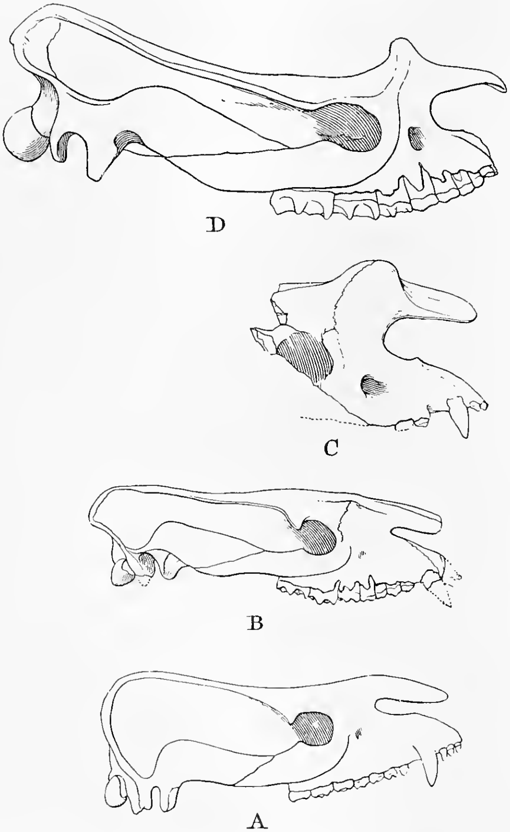

FIGURE 87.—Four stages in the origin and evolution of the horns in titanotheres

After Hatcher's original plate (1895). A, *Palaeosyops laticeps* (=*Limnohyops laticeps*), after Earle; B, *Telmatotherium vallidens* (=*Manteoceras manteoceras*), after Osborn; C, *Diplacodon emarginatus* (=*Protitanotherium emarginatum*), after Hatcher; D, *Titanotherium varians* (=*Brontotherium leidyi*), after Marsh. One-eighth natural size.

INVESTIGATIONS AND EXPLORATIONS MADE IN PREPARATION FOR THE PRESENT MONOGRAPH (1900–1919)

Between 1895 and 1900 no very important work on the Eocene titanotheres was done. By the end of the nineteenth century some 12 nominal genera and 25 nominal species of the titanotheres had been proposed, but many of the real generic limits and phylogenetic relations were still obscure except for the pregnant suggestions of Hatcher. In 1900 Professor Osborn, at the invitation of Director Charles D. Walcott, undertook to revise and monograph the Eocene titanotheres in connection with the United States Geological Survey monograph on the Oligocene titanotheres that had been begun by Professor Marsh. The work on the Eocene titanotheres has proved to be by far the most difficult and most extensive part of this task. During the last 28 years Professor Osborn, with the assistance of Dr. W. K. Gregory, has studied the great and growing collection in the American Museum of Natural History and in other institutions and has set forth the results in several preliminary articles and more fully in the present work.

A long series of parties of exploration, beginning in 1903, sent out from the American Museum by Osborn (1909.321) and conducted chiefly by Mr. Walter Granger, have carefully examined the various lower, middle, and upper Eocene basins of the West with special reference to the exact succession of species. This very precise work has shown that the Bridger and other formations are divided into a succession of zonal levels characterized by the remains of titanotheres and other mammals in different generic and specific stages of evolution. The stratigraphic relations of the Eocene to the Oligocene deposits have also been in part explored. The results are fully set forth in this monograph. Although this work in the Eocene basins has been carried on chiefly by the American Museum of Natural History, the Carnegie and Field Museums have sent expeditions into the Uinta Basin under Douglass (1909.1) and under Riggs (1912.1), which have yielded similar results as to specific and generic succession.

The distinction of numerous independent Eocene phyla by Osborn has followed the discovery of the Oligocene phyla, some of which arise from those of the Eocene.

Thus have been established secure bases of fact, first, for a general history of the early Tertiary faunas of the West; second, for a demonstration of the evolution of certain phyla of titanotheres through long periods of time; and, third, for a consideration of the modes and factors of evolution of titanotheres in particular and of mammals in general.

SECTION 2. ORIGINAL DESCRIPTIONS OF EOCENE TITANOTHERES

FIVE RULES FOR DETERMINING THE NAMES OF TITANOTHERES

The systematic revision of the Eocene and Oligocene titanotheres was begun in 1900 by the author with the cooperation of W. K. Gregory and has been continued up to the day of the delivery of the manuscript of this volume to the Geological Survey. The great difficulties and the labor involved in determining the correct prior names for the genera and species have been due to the imperfection of the fossil types, to loose methods of description and comparison, and to the mingling as cotypes of animals belonging to different species or even to different genera.

Experience has shown that the following five rules are absolutely necessary for future vertebrate paleontologic work.

Rule 1. Accept the "law of priority," as defined by the International Committee on Nomenclature.

In this revision the author has accepted as authoritative the rules of nomenclature based upon the "law of priority," as defined by the "Code" of the American Ornithologists' Union and by the recommendations of the committee on nomenclature of the Twelfth International Congress of Zoology. Special acknowlegments are due to the eminent authority Dr. J. A. Allen for frequent aid in deciding troublesome problems of nomenclature.

Rule 2. Determine the geologic level and characters of the type, as the starting point of monographic inquiry.

Experience teaches that the characters of the holotype specimen and the geologic level on which it was found afford the permanent facts to which all questions of nomenclature must be referred as the basis of monographic investigation.

Rule 3. Avoid confusion of characters of the type and cotype or paratype.

All the early systematic work on the titanotheres was done without regard to precise discrimination between the certain or permanent nomenclatural value of the holotype specimen and the uncertain value of "specific" characters based on cotype, paratype, and neotype specimens.

For example, take the case of the classic species *Palaeosyops paludosus* Leidy. Leidy used as types the very fragmentary teeth from the lower levels of Bridger B, which first came into his hands; he later erroneously associated with these fragments, practically as cotypes, other more complete specimens, which are now known to belong to two or three different species from higher geologic levels. Subsequently Leidy himself, Cope, Marsh, Scott, Osborn, and Earle all accepted Leidy's erroneous associations, and *P. paludosus* came to be known by certain of its falsely associated cotype and paratype characters instead of by its true type characters.

Thus the entire nomenclature of the subject became a mass of confusion, and the difficulties encountered in clearing it up have been almost insuperable.

The rule is that specific definitions must be based on holotypes only, unless there is absolutely no possibility of doubt that the associated types are from the same geologic level and belong to the same species.

Rule 4. Distinguish the different values and kinds of types.

The use of the terms type (or holotype), cotype, paratype, lectotype, hypotype, neotype has been discussed critically by Oldfield Thomas (1893.1, p. 241), by Schuchert (1905.1, pp. 9–14), and by Osborn (1918.473). The distinctions indicated below should be noted.

Type, individual, or holotype.—A holotype is a particular individual specimen "deliberately selected by the author of a species; or it may be the only example of a species known at the time of original publication. A holotype, therefore, is always a single individual but may embrace one or more parts, as the skin, skeleton, or other portions." (Schuchert, op. cit.) The holotype must usually be determined from the original description.

Cotype, coordinate or equivalent type.—The term cotype is applied to specimens when an author's type description refers to remains of two or more individuals without selecting or distinguishing one as the holotype, so that all appear to be equally identified with the specific name given.

Lectotype.—"Where the original diagnosis is without illustrations or is accompanied by figures based on two or more specimens, the first subsequent author is at liberty to select from these cotypes a type for the old species, adhering, so far as can be ascertained, to the intention of the original author. Such a type specimen is to be designated a lectotype (=a chosen type)." (Schuchert, idem.) The practice of Osborn as to lectotypes in paleontology is either (*a*) to select the first individual specimen named by the original author, because the second individual specimen may belong to a distinct species, or (*b*) to select the specimen to which the specific name obviously refers—for example, Cope's *Menodus angustigenis.*

Hypotype and plesiotype.—As shown by Schuchert (idem), the terms hypotype and plesiotype have been used in two different senses to cover "supplementary types." They may well be dropped.

Neotype.—A neotype is defined by Schuchert (idem) as a [new] "supplementary type selected by an [a subsequent] author, on which a species is to rest because of the loss of the original type, or where the original material still extant is so poor or fragmentary that from it the characters of the species can not be determined with certainty." Great care must be taken that the neotype comes from the same geologic level as the type.

Summary.—The usage adopted in this monograph is as follows:

Holotype (of original author): The original individual type specimen selected by the author.

Cotypes: Different individual specimens rightly or wrongly put together by the author as "types."

Paratype (of original author): Additional individual specimen or specimens noted by the author in the original description and used by him in defining the species.

Lectotype (of subsequent author): The specimen selected by a subsequent author, from among the "cotypes," for purposes of subsequent description or redefinition. This may be (*a*) the specimen first mentioned by the author, or (*b*) the specimen to which the specific name obviously applies.

Neotype (of second or subsequent author): A new specimen selected in a subsequent description because of the loss or imperfection of the holotype or type.

These five terms are all that are necessary in vertebrate paleontology. The terms plesiotype and hypotype are discarded in this monograph because they are too indefinite.

Monographic revision in the use of above terms.—Leidy founded the species *Palaeosyops paludosus* upon some isolated teeth from the low levels of Church Buttes. In the original description these teeth, which probably represent more than one individual, were treated as coordinate or equivalent types or "cotypes." Out of this lot the second lower molar (m_2), which was the first specimen mentioned and described by Leidy, has been selected by Osborn in the present volume as the final standard, or "lectotype," of the species.

In the same original description by Leidy of *P. paludosus* a second lot of teeth, from the high levels of Henrys Fork, were mentioned, and the characters, of these teeth entered into Leidy's original conception of the species. These teeth are now called "paratypes."

In the present revision, since there is little doubt that Leidy's paratypes are not really conspecific with the specimen first mentioned (lectotype), Osborn has selected from the same geologic level, Church Buttes, a lower jaw in which m_2 agrees most clearly with the lectotype m_2 and which is to serve as a secondary type, or "neotype."

It will be seen that cotypes, paratypes, or neotypes may sometimes be wrongly associated specifically with the holotype, in which case the specific name must cling to the holotype and lectotype as the ultimate standard means of identification.

The first step toward permanence, therefore, is the settlement of the holotype characters, which is sometimes an almost impossible task, owing to the poor quality of the holotype selected—for example, the holotype of *Palaeosyops major* Leidy, a jaw fragment without teeth; the holotype of *P. humilis* Leidy, a single deciduous premolar.

Rule 5. Avoid mingling as types and cotypes specimens from different geologic levels.

The mingling of types and cotypes from different geologic levels has been the second chief source of confusion. To cite a prominent instance, Cope's cotypes of *Palaeosyops laevidens* were two skulls collected at widely separated localities, and in his original description no regard was shown for their possible difference of geologic age. It appears almost certain that the lectotype belongs to a lower level and is perhaps some thousands of years more ancient than the paratype. Similarly we have shown that the lectotype of Leidy's *P. paludosus* is from Bridger level B 1 or B 2; the paratypes are from level C 2 or C 3, a difference of geologic level representing a very long period of time, in which it is now certain that a very marked progressive evolution took place in teeth, skull, and skeleton.

Our geologic leveling of the Bridger formation, described in Chapter II, has therefore not only afforded us the means of determining the evolutionary succession of the species of titanotheres but, if the localities of the types were properly recorded by the authors, it has enabled us to separate many erroneously associated type specimens. The geologic levels of the materials recently acquired by the American Museum have been ascertained precisely; on the whole, the successive species correspond very closely with the successive levels—that is, in no case have different species in the same line of descent been found at the same level, although species in different lines of descent (that is, in different genera) are found in analogous stages of evolution.

THE GENERA AND SPECIES OF EOCENE TITANOTHERES

The accompanying list shows, in chronologic order, the names assigned to Eocene titanotheres. The numbers in the first column indicate the chronologic order or rank of the systematic names, the roman numerals indicating generic names, the arabic numerals specific names.

Chronologic list of original descriptions of Eocene titanotheres

[Generic names accepted in this work as valid are printed in small capitals; abandoned names are inclosed in brackets]

Rank	Date	Genus	Species	Author	Present determination
I	1870	PALAEOSYOPS		Leidy	Palaeosyops Leidy.
1	1870	Palaeosyops	paludosus	do	Palaeosyops paludosus Leidy.
2	1871	Palaeosyops	major	do	Palaeosyops major Leidy.
3	1871	[Canis]	[montanus]	Marsh	Palaeosyops major? Leidy.
4	1872	Palaeosyops	[humilis]	Leidy	Palaeosyops sp.
5	1872	[Palaeosyops]	junius	do	Mesatirhinus junius (Leidy).
6	1872	[Palaeosyops]	laticeps	Marsh	Limnohyops laticeps (Marsh).
II	1872	TELMATHERIUM		do	Telmatherium Marsh.
7	1872	Telmatherium	validus	do	Telmatherium validum Marsh.
IIIa	1872	[Limnohyus]		do	Palaeosyops Leidy.
8	1872	[Limnohyus]	robustus	do	Palaeosyops robustus (Marsh).
9	1872	[Palaeosyops]	vallidens	Cope	Dolichorhinus vallidens (Cope).
IIIb	1872	[Limnohyus]		Leidy (not Marsh)	(Preoccupied.)
10	1873	[Limnohyus]	laevidens	Cope	Limnohyops laevidens (Cope).
11	1873	[Limnohyus]	fontinalis	do	?Palaeosyops fontinalis (Cope).
12	1873	Palaeosyops	[diaconus]	do	Palaeosyops robustus (Marsh).
IV	1875	DIPLACODON		Marsh	Diplacodon Marsh.
13	1875	Diplacodon	elatus	do	Diplacodon elatus Marsh.
V	1876	BRACHYDIASTEMATHERIUM		Böckh and Maty	Brachydiastematherium Böckh and Maty.
14	1876	Brachydiastematherium	transilvanicum	do	Brachydiastematherium transilvanicum Böckh and Maty.
VI	1878	[Leurocephalus]		Osborn, Scott, and Speir.	Telmatherium Marsh.
15	1878	[Leurocephalus]	cultridens	do	Telmatherium cultridens (Osborn, Scott, and Speir).
16	1880	[Palaeosyops]	borealis	Cope	Eotitanops borealis (Cope).
VII	1880	LAMBDOTHERIUM		do	Lambdotherium Cope.
17	1880	Lambdotherium	popoagicum	do	Lambdotherium popoagicum Cope.
18	1881	[Lambdotherium]	brownianum	do	Eotitanops brownianus (Cope).
19	1889	[Palaeosyops]	hyognathus	Osborn	Dolichorhinus hyognathus (Osborn).
VIII	1890	LIMNOHYOPS		Marsh	Limnohyops Marsh.
20	1891	[Palaeosyops]	megarhinus	Earle	Mesatirhinus megarhinus (Earle).
21	1891	[Palaeosyops]	[minor]	do	Palaeosyops paludosus Leidy.
22	1892	Palaeosyops	longirostris	do	Palaeosyops longirostris Earle.
23	1895	[Telmatotherium]	diploconum	Osborn	Rhadinorhinus diploconus (Osborn).
24	1895	[Telmatotherium]	[cornutum]	do	Dolichorhinus hyognathus (Osborn).
IX	1895	SPHENOCOELUS		do	Sphenocoelus Osborn.
25	1895	Sphenocoelus	uintensis	do	Sphenocoelus uintensis Osborn.
X.	1895	PROTITANOTHERIUM		Hatcher	Protitanotherium Hatcher.
26	1895	[Diplacodon]	emarginatus	do	Protitanotherium emarginatum Hatcher.
XI	1895	MANTEOCERAS		do	Manteoceras Hatcher.
XII	1895	DOLICHORHINUS		do	Dolichorhinus Hatcher.
27	1897	[Palaeosyops]	ultimus	Matthew	Telmatherium ultimum Osborn.
28	1899	[Palaeosyops]	manteoceras	do	Manteoceras manteoceras Hay.
29	1899	[Telmatotherium]	[diploconum var. minus.	do	Metarhinus fluviatilis Osborn.
30	1899	[Canis?]	[marshii]	Hay	Palaeosyops major? Leidy.
31	1902	Manteoceras	manteoceras	do	Manteoceras manteoceras Hay.
XIII	1907	EOTITANOPS		Osborn	Eotitanops Osborn.
32	1907	Lambdotherium	primaevum	Loomis	Lambdotherium primaevum Loomis.
33	1908	Limnohyops	priscus	Osborn	Limnohyops priscus Osborn.
34	1908	Limnohyops	matthewi	do	Limnohyops matthewi Osborn.
35	1908	Limnohyops	monoconus	do	Limnohyops monoconus Osborn.
36	1908	Palaeosyops	leidyi	do	Palaeosyops leidyi Osborn.

Chronologic list of original descriptions of Eocene titanotheres—Continued

[Generic names accepted in this work as valid are printed in small capitals; abandoned names are inclosed in brackets]

Rank	Date	Genus	Species	Author	Present determination
37	1908	Palaeosyops	grangeri	Osborn	Palaeosyops grangeri Osborn.
38	1908	Palaeosyops	copei	do	Palaeosyops copei Osborn.
39	1908	Manteoceras	washakiensis	do	Manteoceras washakiensis Osborn.
XIV	1908	MESATIRHINUS		do	Mesatirhinus Osborn.
40	1908	Mesatirhinus	petersoni	do	Mesatirhinus petersoni Osborn.
XV	1908	METARHINUS		do	Metarhinus Osborn.
41	1908	Metarhinus	fluviatilis	do	Metarhinus fluviatilis Osborn.
42	1908	Metarhinus	earlei	do	Metarhinus earlei Osborn.
43	1908	Dolichorhinus	intermedius	do	Dolichorhinus intermedius Osborn.
44	1908	Telmatherium	ultimum	do	Telmatherium ultimum Osborn.
45	1908	Telmatherium?	altidens	do	Telmatherium altidens Osborn.
46	1908	Protitanotherium	superbum	do	Protitanotherium superbum Osborn.
47	1909	[Telmatherium?]	incisivum	Douglass	Sthenodectes incisivus (Douglass).
48	1909	Manteoceras	uintensis	do	Manteoceras uintensis Douglass.
49	1909	Dolichorhinus	heterodon	do	Dolichorhinus heterodon Douglass.
50	1909	Dolichorhinus	longiceps	do	Dolichorhinus longiceps Douglass.
XVI	1912	STHENODECTES		Gregory	Sthenodectes Gregory.
51	1912	[Mesatirhinus]	superior	Riggs	Dolichorhinus superior (Riggs).
52	1912	Metarhinus	riparius	do	Metarhinus riparius Riggs.
53	1912	Metarhinus	cristatus	do	Metarhinus cristatus Riggs.
54	1912	Dolichorhinus	fluminalis	do	Dolichorhinus fluminalis Riggs.
XVII	1912	RHADINORHINUS		do	Rhadinorhinus Riggs.
55	1912	Rhadinorhinus	abbotti	do	Rhadinorhinus abbotti Riggs.
56	1913	Eotitanops	gregoryi	Osborn	Eotitanops gregoryi Osborn.
57	1913	Eotitanops	princeps	do	Eotitanops princeps Osborn.
58	1913	Eotitanops	major	do	Eotitanops major Osborn.
59	1913	Lambdotherium	priscum	do	Lambdotherium priscum Osborn.
60	1913	Lambdotherium	progressum	do	Lambdotherium progressum Osborn.
XVIII	1914	[Diploceras]		Peterson	Eotitanotherium Peterson.
61	1914	[Diploceras]	orborni	do	Eotitanotherium osborni Peterson.
XIX	1914	[Heterotitanops]		do	?Metarhinus.
62	1914	[Heterotitanops]	parvus	do	?Metarhinus sp.
XX	1914	EOTITANOTHERIUM		do	Eotitanotherium Peterson.
63	1916	[Telmatherium?]	birmanicum	Pilgrim and Cotter	Uncertain.
64	1919	Lambdotherium	magnum	Osborn	Lambdotherium magnum Osborn.
65	1919	Eotitanops	minimus	do	Eotitanops minimus Osborn.
XXI	1919	EOMETARHINUS		do	Eometarhinus Osborn.
66	1919	Eometarhinus	huerfanensis	do	Eometarhinus huerfanensis Osborn.

ORIGINAL DESCRIPTIONS OF THE SPECIES

Palaeosyops Leidy, 1870

Cf. *Palaeosyops*, this monograph, page 312

Original reference.—Acad. Nat. Sci. Philadelphia Proc., 1870, p. 113 (Leidy, 1870.2).

Type species.—*Palaeosyops paludosus* Leidy. (See p. 319.)

Generic characters.—Leidy, in his description of the fragmentary type, very properly refrained from attempting to distinguish generic from specific characters. Generic characters are given below.

Etymology.—παλαιός, ancient; σῦς, boar; ὤψ, face (appearance). The name was probably suggested by the fact that the "upper true molars exhibit the outer part of a crown composed of a pair of lobes, exactly as in *Hyopotamus.*" (Leidy.)

Present determination.—The generic name is a valid one.

Palaeosyops paludosus Leidy, 1870

Cf. *Palaeosyops paludosus*, this monograph, page 319

Original reference.—Acad. Nat. Sci. Philadelphia Proc., 1870, p. 113 (Leidy, 1870.2).

Subsequent reference.—Leidy, Extinct vertebrate fauna of the Western Territories, p. 28, pl. 23, figs. 3–6 (fig. 5 lectotype), 1873 (Leidy, 1873.1).

Type locality and geologic horizon.—Church Buttes, near Fort Bridger, Bridger Basin, Wyo.; *Palaeosyops paludosus-Orohippus* zone (Bridger B 1 or Bridger B 2).

Leidy's cotypes.—M_2, p^4, m^2, m^3 (Nat. Mus. 759, 758, 762). (Extinct vertebrate fauna, p. 28, 1873.) "The species *Palaeosyops paludosus* * * * was founded on a number of isolated teeth * * * obtained by Professor Hayden at Church Buttes, Wyo." (Leidy.) (See fig. 88.)

Characters.—Leidy (1870.1, p. 113) writes:

> The crown of a lower true molar [m_2 of the right side, the Osborn lectotype (fig. 88)] resembles in its constitution those of *Palaeotherium*, *Chalicotherium*, and *Titanotherium*, being composed of a pair of fore and aft conjoined pyramidal lobes with crescentic summits. It measures 16 lines anteroposteriorly and 10 lines transversely. Fragments of upper true molars [m^2 left, m^3 right] exhibit the outer part of the crown composed of a pair of lobes exactly as in *Hyopotamus*. The inner portion of the crown is composed of a pair of simple cones, broad and low, the front one considerably larger than the back one. One of the specimens in the entire condition of the crown measured about 22 lines fore and aft and 18 lines transversely. The crown of an upper premolar [p^4] has its outer part composed of a pair of conjoined cones with acute summits and sides. The inner portion of the crown [p^4 of the opposite side] consists of a single broad, simple cone embraced in front and behind by a basal ridge. The anteroposterior diameter of the crown externally measures 9½ lines; the transverse diameter is an inch.

Leidy's cotypes.—The first lot of specimens from Church Buttes (Bridger B 1), upon which the species was originally established, consist of a second lower molar (m_2, Nat. Mus. 759; see Leidy, 1870.1, p. 113; 1873.1, pl. 23, fig. 5); "of an upper fourth premolar nearly unworn" (p^4, Nat. Mus. 762; see Leidy, 1873.1, pl. 5, fig. 5); of the anterior half of a second upper molar (m^2, Nat. Mus. 758; see Leidy; 1873.1, pl. 23, fig. 6); and of the inner side of a premolar (p^4) of the opposite side. This lot constitutes the cotypes, which are here refigured. Of these, the second lower molar agrees with the specimens described in this monograph as *P. paludosus.* The upper teeth do not certainly belong to the same animal; it appears necessary, therefore, to base the genus and species on the first specimen described in the original description, namely, the second lower molar, which may be taken as the lectotype.

Leidy's paratypes.—Specimens of a second lot, from Henrys Fork, belonging to a much older individual, were treated practically as paratypes of this species in the original notice; they were described in Leidy's memoir of 1873 (1873.1, pp. 29, last line, and 30), were figured in Plate 5, Figures 4, 6, 7, 8, 9, and are preserved in the United States National Museum. These are the specimens that Cope, Marsh, Osborn, Earle, and others may have taken for the types, but they are from a higher geologic level and may pertain to *P. major* or *P. leidyi.* A third lot of specimens, from Grizzly Buttes, included the "facial portion of a skull containing nearly all the molars and the canines of both sides." This specimen was treated virtually as a paratype by Leidy (1873.1, pp. 30–34, pl. 18, fig. 51, and pl. 4, fig. 3) and was described at length by him. It is probably but not certainly conspecific with the lectotype m_2.

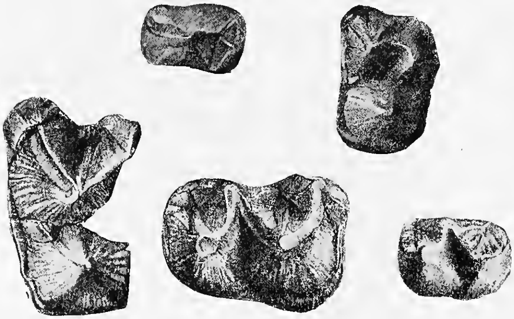

FIGURE 88.—Leidy's cotypes of *Palaeosyops paludosus*

Specimens upon which the species was originally established. Hayden's collection of 1870. After Leidy, 1873; Nat. Mus. 758, 759, 762. Natural size. The second lower molar (Nat. Mus. 759) is the lectotype.

Osborn's neotype.—The determination of *P. paludosus* therefore rests positively on the second lower molar alone. To supplement this lectotype the present author has selected as a neotype a lower jaw (Pl. LVI, *B;* fig. 268, C) with dentition, Am. Mus. 11680, in which m_2 agrees closely with the lectotype and with the measurements given by Leidy for *P. paludosus* (1873.1, p. 57 and pl. 5, figs. 10, 11). The locality

(Millersville) is about 10 miles distant from that of the holotype (Church Buttes), but the geologic level is believed to be identical, namely, Bridger B 1.

Etymology.—paludosus, marshy, dwelling in the marshes, probably because the remains were found in one of the supposed "ancient lake basins."

Present determination.—Palaeosyops paludosus Leidy is a valid species, but the "*P. paludosus*" of other authors refers to related species of more recent geologic age (*P. major*, *P. leidyi*, *P. robustus*).

Palaeosyops major Leidy, 1871

Cf. *Palaeosyops major*, this monograph, page 321

Original reference.—Acad. Nat. Sci. Philadelphia Proc., 1871, p. 229 (Leidy, 1871.1).

Subsequent reference.—Leidy, Extinct vertebrate fauna of the Western Territories, p. 45, pl. 20, fig. 8, 1873 (Leidy, 1873.1).

FIGURE 89.—Leidy's type (holotype) of *Palaeosyops major* in the collection of the Academy of Natural Sciences of Philadelphia

Part of the right ramus of a lower jaw. After Leidy, 1873. One-half natural size. "The specimen is somewhat swollen and altered from disease and is one of those upon which the species was first indicated. Discovered by Dr. Carter at Grizzly Buttes." (Leidy.)

Type locality and geologic horizon.—Grizzly Buttes, Bridger Basin, Wyo.; *Palaeosyops paludosus-Orohippus* zone (Bridger B 2 or B 3). Dr. J. Van A. Carter, collector.

Holotype.—"A jaw fragment with the retained fragments of the true molars." This type is now in the collection of the Philadelphia Academy of Natural Sciences. (See fig. 89.)

Characters (Leidy).—Size apparently "much larger than *P. paludosus*."

> The true molars occupied a space of 4½ lines. The last molar measured 1⅞ inches fore and aft and an inch transversely in front.

In his "Extinct vertebrate fauna" of 1873 (1873.1, pp. 45, 46) Leidy gives a fuller description of the very imperfect holotype and figures it on Plate 20, Figure 8. He believed the jaw specimen to be

> in some degree abnormal in form, due to inflammation or some other affection connected with the second molar tooth. * * * In its proportions the jaw, in a normal condition, would appear to be of more robust character than in *Palaeosyops paludosus*. * * * In its present state the base is more convex fore and aft than in the latter, and the alveolar border more ascending posteriorly.
>
> The remains of the molar fangs at the entrance of the alveoli appear to indicate teeth of the same form and construction as in *Palaeosyops paludosus*, for which reason the fragment was referred to the same genus. The true molars appear to have occupied a space of 4¾ inches, though this is probably somewhat exaggerated, as the interval occupied by the last intermediate molar appears proportionately somewhat too large. The crown of the last molar, which was clearly trilobate as in *Palaeosyops paludosus*, had an antero-posterior diameter of 2 inches.

Leidy's paratype, "consisting of the left ramus of the lower jaw, containing six molar teeth," was obtained by Doctor Carter "in Dry Creek Canyon, 40 miles from Fort Bridger" (Bridger Basin, Bridger C) and together with a second similar specimen from the same locality is described by Leidy (1873.1, p. 46, pl. 23, fig. 1; second specimen, fig. 2).

The holotype, it is important to note, is from the low level (probably Bridger B 2) of Grizzly Buttes, but Leidy's paratype, which has the characters of the more progressive *Palaeosyops leidyi* Osborn, is from the higher level (Bridger C) of Dry Creek. The paratype is thus certainly not conspecific with the holotype.

Osborn's neotype.—In order to supplement the characters of Leidy's imperfect holotype, the present writer has selected as a neotype a lower jaw (fig. 268, C) with dentition (Am. Mus. 12181) from Cottonwood Creek and from about the same level (B 3) as the holotype, with which it agrees closely. (See Chap. V.)

Etymology.—major, in allusion to the larger size as compared with *P. paludosus*.

Present determination.—The species *P. major* is believed to be a valid one.

Canis montanus Marsh, 1871

Cf. *Canis? marshii* Hay, below (*Palaeosyops major?*), page 178

Original reference.—Am. Jour. Sci., 3d ser., vol. 2, p. 123, August, 1871 (Marsh, 1871.2).

Type locality and geologic horizon.—Grizzly Buttes, Bridger Basin, Wyo.; *Palaeosyops paludosus-Orohippus* zone (Bridger B, probably B 2).

Marsh's cotypes.—"A last upper premolar tooth in good preservation, a canine, wanting most of the crown, and a number of the larger bones of a skeleton, all apparently of the same species, but pertaining to three individuals, differing somewhat in size" (Marsh). Of these materials the "last upper premolar" (first lower premolar) alone is described and measured, and it is also the first specimen mentioned. It should therefore be taken as the lectotype (Yale Mus. 11770).

Characters.—"The last upper premolar * * * is robust, has a short compressed crown. The principal cusp is conical, with subacute edges, the anterior being about twice the length of the posterior. Behind the main cusp there is a large triangular tubercle, with its apex exterior to the fore and aft axis of the crown." (Marsh.)

Anteroposterior diameter of last upper premolar	9 lines [19 mm.]
Greatest transverse diameter of same	4.25 lines [8 mm.]
Height of main cusp	6 lines [12.7 mm.]
Height of posterior tubercle	3.75 lines [7 mm.]

Synonym.—*Canis? marshii* Hay was proposed in place of *C. montanus* Marsh, name preoccupied by *C. montanus* Pearson (Hay, 1899.1).

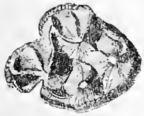

FIGURE 90.—Leidy's type of *Palaeosyops humilis*

Specimen in the collection of the Academy of Natural Sciences of Philadelphia, After Leidy, 1873. Natural size. Regarded by Leidy as "A last upper molar of the left side. * * * Found by Doctor Corson on the buttes of Dry Creek Canyon."

Etymology.—*montanus*, dwelling in the mountains—that is, from the Rocky Mountain region.

Present determination.—The type specimen of "*Canis montanus*" is a first lower premolar of some undetermined member of the genus *Palaeosyops*, possibly *Palaeosyops paludosus* or *P. major*. The reference to *Canis* was doubtless made by reason of the deceptive resemblance of one of the lower premolars to the upper carnassial tooth of a dog.

Palaeosyops humilis Leidy, 1872

Cf. *Palaeosyops major*, this monograph, page 321

Original reference.—Acad. Nat. Sci. Philadelphia Proc., 1872, p. 168 (Leidy, 1872).

Subsequent reference.—Leidy, Extinct vertebrate fauna of the Western Territories, p. 58, pl. 24, fig. 8, 1873 (Leidy, 1873.1).

Type locality and geologic horizon.—"Valley of Dry Creek 40 miles from Fort Bridger (Wyo.)." Doctor Corson, discoverer. "Buttes of Dry Creek Canyon," Bridger Basin; horizon probably Bridger C (*Uintatherium-Manteoceras-Mesatirhinus* zone).

Holotype.—"An upper molar." (See fig. 90.)

Characters (Leidy).—"An upper molar tooth of this animal measures three-fourths of an inch in diameter." In his later description Leidy recognized that the specimen belonged to the milk series.

Etymology.—*humilis*, lowly, small; in allusion to the small size in comparison with *P. paludosus*.

Present determination.—This milk tooth probably pertains to the genus *Palaeosyops*, but comparison with *P. major* and *P. leidyi* leaves the species undetermined.

Palaeosyops junius Leidy, 1872

Cf. *Mesatirhinus junius* (Leidy), this monograph, page 388

Original reference.—Acad. Nat. Sci. Philadelphia Proc., 1872, p. 277 (Leidy, 1872.3).

Subsequent reference.—Leidy, Extinct vertebrate fauna of the Western Territories, p. 57, no figure, 1873 (Leidy, 1873.1).

Type locality and geologic horizon.—Fort Bridger, Bridger Basin, Wyo.; level not recorded. Dr. J. Van A. Carter, collector.

Holotype.—"Doctor Carter recently sent the writer several small fragments of the right side of a lower jaw, together with a sketch of a larger fragment of the left side, containing the last premolar and the succeeding molars." Of this type material only p_4 (right) and the posterior half of m_3 (right) were located (1906) in the collection of the Academy of Natural Sciences of Philadelphia.

Characters.—Leidy writes:

> Intermediate in size to *P. paludosus* and *P. humilis*. Founded on portions of a lower jaw agreeing in character with the corresponding parts of *P. paludosus* but smaller. Space occupied by the last premolar and the true molars, 4 inches. Anteroposterior diameter of last premolar, 8 lines; of last molar, 17½ lines.

In the fuller description in his memoir of 1873, Leidy says:

> The specimens * * * appear to indicate a small species of *Palaeosyops*, though it is not improbable that they pertain to a small variety of *P. paludosus*.
>
> The parts agree closely with the corresponding parts of the lower jaw and teeth of the latter, except in size. They have been viewed as representatives of a species with the name of *Palaeosyops junius*.

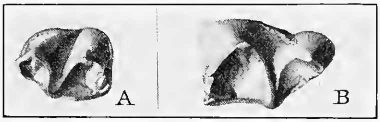

FIGURE 91.—Leidy's cotypes of *Palaeosyops junius*

Specimens in museum of Academy of Natural Sciences of Philadelphia; Bridger B(?), level doubtful. A, Right fourth lower premolar (p_4); B, posterior part of third lower molar (m_3). Natural size.

The measurements of the teeth (fig. 91) in comparison with those of *P. paludosus* are as follows:

	Palaeosyops junius		Palaeosyops paludosus	
	Lines	[Millimeters]	Lines	[Millimeters]
Space occupied by the last premolar and molars	48	[102]	55	[116]
Space occupied by the molars	39½	[94]	46	[96]
Breadth [anteroposterior] of last premolar	8	[17]	9	[19]
Thickness [transverse] of last premolar	5½	[12]	6¼	[12]
Breadth [anteroposterior] of first molar	10	[21]	12½	[38]
Breadth [anteroposterior] of second molar	12	[25]	15	[32]
Breadth [anteroposterior] of third molar	17	[10]	19	[39]
Thickness [transverse] of third molar at middle	7	[14]	9½	[19]

Etymology.—junius, younger, in allusion to its small size.

Present determination.—From the two teeth (p_4 and part of m_3) preserved it appears that this species probably pertains to the genus *Mesatirhinus*. It is smaller than *Mesatirhinus megarhinus*. No other material has been certainly identified with it. (See p. 388.)

Palaeosyops laticeps Marsh, 1872

Cf. *Limnohyops laticeps* Marsh, this monograph, page 311

Original reference.—Am. Jour. Sci., 3d ser., vol. 4, p. 122, August, 1872, dated "July 18, 1872" (Marsh, 1872.1).

Type locality and geologic horizon.—Near Marsh's Fork, about 15 miles from Fort Bridger, Wyo. A. H. Ewing, discoverer. Level not recorded.

Holotype.—"A nearly complete skeleton" (Yale Mus. 11000).

Characters.—Marsh writes:

> The teeth in this specimen have apparently the same general structure as those in the type of *P. paludosus* but differ in being nearly smooth, and this is not the result of age, as this individual was younger than the original of the larger species. The proportions, moreover, given for the molar described (Leidy, 1870.2, p. 113), "22 lines fore and aft and 18 transversely," would not apply to any of the series in the present specimen. The last upper molar of the latter has two well-developed internal cones. * * * The upper teeth form a complete series. The canine is large and broadly oval at its base. The outer incisor is the largest, and at its posterior edge the premaxillary is subtriangular in transverse section. The sagittal and occipital crests are strongly developed, and the coronoid process of the lower jaw is short and recurved.

Measurements [Marsh]

	Millimeters
Length of entire upper molar series	155
Anteroposterior extent of three true upper molars	94 [90]
Anteroposterior diameter of last upper molar	36 [33]
Transverse diameter [protocone to mesostyle]	40
Anteroposterior diameter of upper canine at base [alveolar portion 28]	29
Transverse diameter	22

Etymology.—latus, broad; *caput* (in compounds *ceps*), head; in allusion to the width across the zygomata.

Present determination.—Marsh's accurate diagnosis of this excellent type was made before the generic characters of *Palaeosyops* were fully known. The species was subsequently chosen by Marsh as the type of the genus *Limnohyops* Marsh, and both the genus and the species are valid.

Telmatherium Marsh, 1872

Cf. *Telmatherium*, this monograph, page 340

Original reference.—Am. Jour. Sci., 3d ser., vol. 4, p. 123, August, 1872 (Marsh, 1872.1).

Type species.—*Telmatherium validum* Marsh. (See pp. 160, 344 of this monograph.)

Generic characters.—See *T. validum* (p. 340).

Etymology.—τέλμα, a pool, marsh (cf. "*paludosus*"); θηρίον, beast.

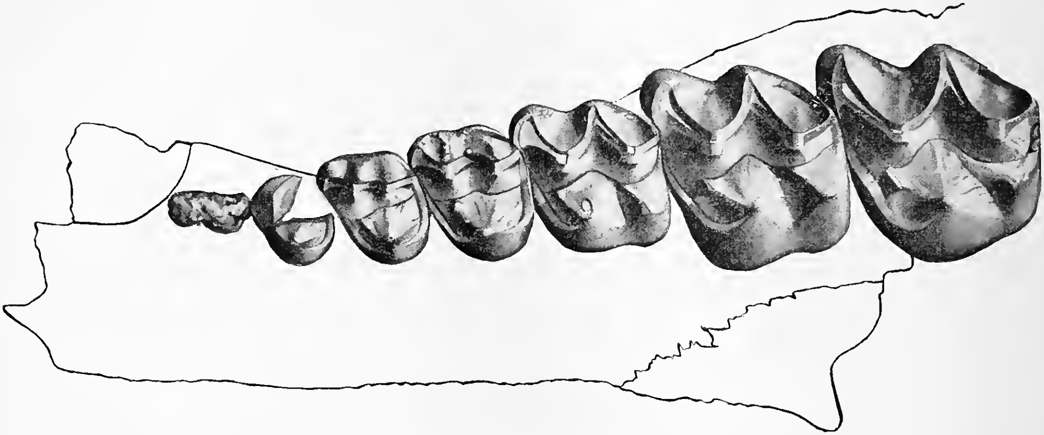

FIGURE 92.—Marsh's type of *Palaeosyops laticeps*

Natural size.

Present determination.—The generic term as redefined in the present monograph is a valid one.

Telmatherium validus Marsh, 1872

Cf. *Telmatherium validum*, this monograph, page 344

Original reference.—Am. Jour. Sci., 3d ser., vol. 4, p. 123, August, 1872; dated "July 18, 1872" (Marsh, 1872.1).

Type locality and geologic horizon.—"Near Henrys Fork of the Green River in Wyoming." (Bridger Basin, level C or D.) J. F. Quigley, discoverer.

Holotype.—"The greater portion of a skull, with teeth" (Yale Mus. 11120). (See fig. 93.)

Characters.—Marsh writes:

> The dentition of this genus, so far as known, appears to be similar to that of *Palaeosyops;* but the two may readily be distinguished by the anterior portion of the skull, which in the present genus has the premaxillaries compressed, with an elongated median suture. The zygomatic arch is also much less strongly developed, and the squamosal portion of it is comparatively slender.

The upper molar teeth have the inner cones more elevated and more pointed than in *Palaeosyops*, and the basal ridge is well developed. The last upper molar has but a single internal cone. The upper canines are large, pointed, and have strong cutting edges. The outer incisors are the largest, and all these teeth have a strong inner basal ridge. The roof of the mouth is deeply excavated between the premolars. The nasals are decurved laterally and much compressed.

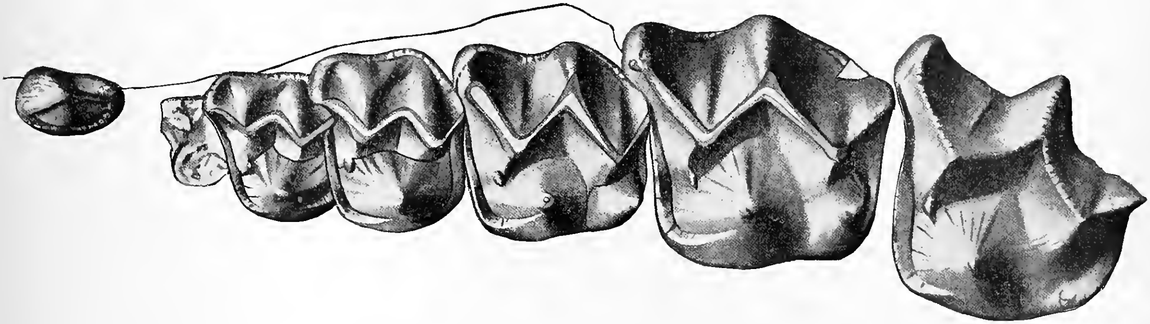

FIGURE 93.—Marsh's type of *Telmatherium validus*

Natural size.

Measurements [Marsh]

	Millimeters
Extent of upper molar series	224
Extent of upper true molars	130
Anteroposterior diameter of last upper molar	54
Anteroposterior diameter of last upper premolar	28
Transverse diameter	33
Anteroposterior diameter of upper canine at base	27
Transverse diameter	22

Etymology.—*validus*, strong, stout; perhaps in allusion to the large size of the upper canines.

Present determination.—This is a valid genus and species. The name *Telmatherium* was amended to *Telmatotherium* by Marsh in 1880 (1880.1) in his "List of genera established by Prof. O. C. Marsh, 1862–1879," and the amended form was accepted by Earle, Osborn, Hatcher, and later writers, but according to the rules of nomenclature now generally accepted the amended form has no standing and the original form *Telmatherium* should be used.

Limnohyus Marsh, 1872

Cf. *Palaeosyops*, this monograph, page 331

Original reference.—Am. Jour. Sci., 3d ser., vol. 4, p. 124, August, 1872 (Marsh, 1872.1).

Type species.—*Limnohyus robustus* Marsh.

Generic characters (Marsh).—The term *Palaeosyops* is restricted to those specimens which, like *P. paludosus*, possess two inner cones on m^3.

The other specimens have but a single internal cone on the last upper molar, and for the genus thus represented the name *Limnohyus* is proposed. These genera may be distinguished from *Telmatherium* by the premaxillaries, which are short, stout, and depressed, with a small median suture.

Etymology.—λίμνη, a marshy lake; ὗς, boar.

Present determination.—Since the type species *Limnohyus robustus* is now believed to be congeneric with Leidy's *Palaeosyops paludosus*, Marsh's genus *Limnohyus* becomes a synonym of *Palaeosyops*.

FIGURE 94.—Marsh's type of *Limnohyus robustus*

Natural size.

Limnohyus robustus Marsh, 1872

Cf. *Palaeosyops robustus* (Marsh), this monograph, page 331

Original reference.—Preliminary description of new Tertiary mammals: Am. Jour. Sci., 3d ser., vol. 4, p. 124, August, 1872; dated "July 18, 1872" (Marsh, 1872.1).

Type locality and geologic horizon.—Near Henrys Fork, Wyo.; *Uintatherium-Manteoceras-Mesatirhinus* zone (Bridger C or D). F. Mead, jr., collector.

Holotype.—A fragmentary skull including nasals and palate with teeth (Yale Mus. 11122).

Characters.—Marsh writes:

> The present species may be distinguished from those above described [*Palaeosyops laticeps* Marsh, *Telmatherium validum* Marsh], especially by the strong basal ridge of the molars. On the last lower molar it extends entirely around the posterior lobe. The first of the upper true molars has the two inner cones nearly of the same size. The small intermediate median tubercles are well developed on the upper molars, and all the teeth are strongly rugose, even in fully adult animals. The nasal bones contract anteriorly and are rounded in front. The outer margin is decurved and thickened. The premaxillaries unite by a very short median suture, similar to that in *Palaeosyops laticeps.* The zygomatic process of the squamosal is stout but much compressed, thus differing widely from both the species already described.

Measurements [Marsh]

	Millimeters
Anteroposterior extent of last three upper molars	110
Anteroposterior diameter of last upper molar	41
Transverse diameter	43. 5
Anteroposterior diameter of last lower molar	51

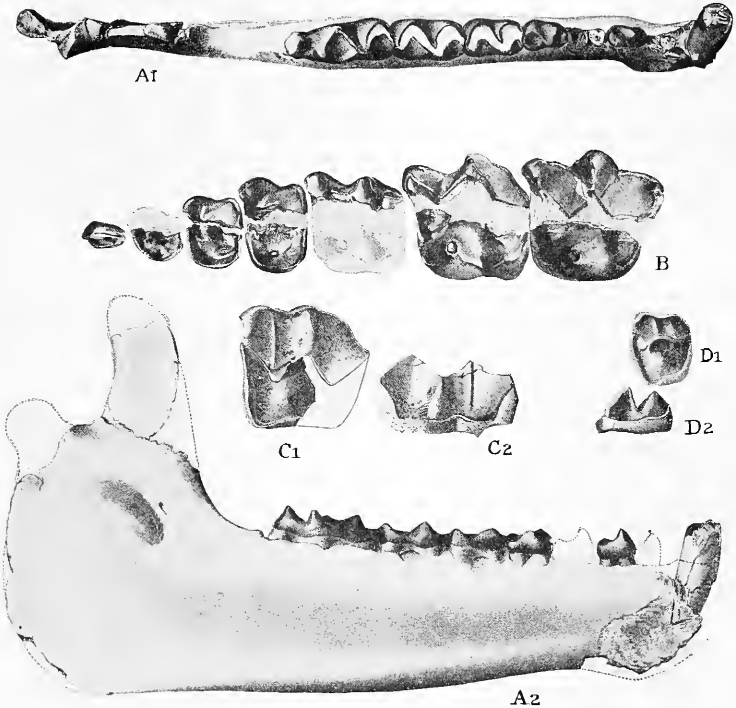

FIGURE 95.—Cope's cotypes of *Palaeosyops vallidens*

After Cope, 1884. A_1, Left mandibular ramus, superior view (lectotype, Am. Mus. 5098); A_2, internal view of same; B, left upper premolars and molars (Am. Mus. 5097); C_1, third left superior molar, crown view; C_2, the same, buccal view (Am. Mus. 5099); D_1, fourth superior premolar, crown view; D_2, the same, buccal view (Am. Mus.).

Etymology.—*robustus,* robust; in allusion to the stout skull and dentition.

Present determination.—The species is probably a valid one, referable to the genus *Palaeosyops.*

Limnohyus Leidy (not Marsh), 1872

Cf. *Palaeosyops,* this monograph, page 155

Original reference.—Acad. Nat. Sci. Philadelphia Proc., 1872, pp. 240–242; published December 17, 1872 (Leidy, 1872.1).

As we have seen above, Marsh's genus *Limnohyus* is simply a synonym of *Palaeosyops,* which had been defined by Leidy as having "but a single lobe to the inner part of the crown" of the "last upper molar." In 1872 Leidy, after pointing out this fact, says that the name *Limnohyus* "might with propriety be applied to the animal with molars like those of *Palaeosyops* except that the last upper one has two inner cones to the crown." This doubtless suggested Marsh's subsequent term *Limnohyops. Limnohyus* Leidy is thus preoccupied by *Limnohyus* Marsh, which is a synonym of *Palaeosyops.*

Etymology.—λίμνη, a marshy lake; ὗς, boar.

Palaeosyops vallidens Cope, 1872

Cf. *Dolichorhinus vallidens* (Cope), this monograph, page 401

Original reference.—Pal. Bull. No. 7, dated "Aug. 22, 1872"; Am. Philos. Soc. Proc., vol. 12, p. 487, 1873 (Cope, 1872.1).

Subsequent reference.—Tertiary Vertebrata, p. 699, pls. 51, fig. 1; 52, fig. 3; 53, fig. 1; 36, figs. 10, 10*a*, 11, 11*a*, 1884 [1885] (Cope, 1885.1).

Type locality and geologic horizon.—"Mammoth Buttes, southwestern Wyoming, near the headwaters of Bitter Creek," Washakie Basin; *Eobasileus-Dolichorhinus* zone (Washakie B 2).

Characters.—Cope writes:

> Represented by the dentition of one maxillary bone with other bones of one individual [Cope, Am. Mus. 5097]; a portion of the same dentition of a second [No. 5099]; with both rami of the mandible with complete dentition of a third [No. 5098]. The species is distinguished by the details of the dental structure and by the superior size. It exceeds, in this respect, the *Palaeosyops major* Leidy; while the three posterior lower molars measure 4.5 inches in length, the same teeth of the present animal measure 5.25 inches. The last superior molar of another specimen measures 2 inches in length; in the third the

> first true molar is 1.5 inches in length, while the last inferior molar is 2.25 inches long. The peculiarity in the structure of the superior molars consists in the existence of two strong transverse ridges, which connect the inner tubercle with the outer crescents, inclosing a pit between them. These are most marked on the premolars, where also is found the peculiarity of the almost entire fusion of the outer crescents into a single ridge. These united crescents are narrower than in *P. major*, and the summits of all the crescents are relatively more elevated. The number of inner tubercles is the same as in that species; all the teeth have very strong basal cingula, which rise up on the inner tubercle. The last inferior molar is relatively narrower than in *P. major*, and the posterior tubercle is larger and longer and is an elevated cone.

From the foregoing description it will be seen that Cope based his specific description upon three specimens (cotypes) without designating any one of the three as being more typical than the others. (See fig. 95.) The name *vallidens*, however, from *vallum*, a wall, seems to refer to the peculiarity in the structure of the superior molars, which

> consists in the existence of two strong transverse ridges, which connect the inner tubercle with the outer crescents. * * * These ridges are most marked on the premolars, where also is found the peculiarity of the almost entire fusion of the outer crescents into a single ridge.

If we had nothing further to guide us we would thus be led to infer that the upper dentition (Am. Mus. 5097), which best shows these peculiarities alluded to in the name *vallidens*, should be regarded as the most typical of the three specimens and should be chosen as the lectotype. But in his "Tertiary Vertebrata" Cope (1885.1, p. 700) says:

> The bones containing the maxillary and mandibular teeth were not found together in any instance, so that it is possible that the different series may represent different species. No other species of the genus was, however, found in the localities to which the respective parts could be referred. Should these prove not to pertain together, the lower jaws may be regarded as typical of the species.

As Cope was the "first reviser" of the species there seems to be no escape from the conclusion, if modern rules of nomenclature are to be followed, that the lower jaw (Am. Mus. 5098) must be treated as Cope's lectotype.

Etymology.—*vallum*, wall or redoubt; *dens*, tooth; allusion as explained above.

Present determination.—This little-known species is allied to but probably specifically distinct from *Dolichorhinus hyognathus* of Washakie B and Uinta B. It is also more primitive than that species (see below).

Limnohyus laevidens Cope, 1873

Cf. *Limnohyops laevidens* (Cope), this monograph, page 305

Original reference.—Pal. Bull. No. 11 ("issued Jan. 31, 1873"); Am. Philos. Soc. Proc., vol. 13, pp. 35, 36, 1873 (Cope, 1873.5).

Subsequent references.—Cope, On the extinct Vertebrata of the Eocene of Wyoming, observed by the expedition of 1872: U. S. Geol. and Geog. Survey Terr. (Hayden) Sixth Ann. Rept., p. 591, 1873 (Cope, 1873.6); Tertiary Vertebrata, p. 701, cotype skull, pl. 50, figs. 1, 2 (holotype), fig. 3 (paratype), 1884 [1885] (Cope, 1885.1).

Type locality and geologic horizon.—Type ("No. 1"), Cottonwood Creek, Bridger Basin, Wyo.; *Palaeosyops paludosus-Orohippus* zone (Bridger B). Cotype ("No. 2"), Bitter Creek, Washakie Basin, Wyo.; horizon uncertain.

Cope's cotypes: "A cranium lacking the posterior part of one side and the lower jaw," from Cottonwood Creek ("No. 1," now Cope collection, Am. Mus. 5104). Also "a nearly complete cranium with dentition from Bitter Creek" ("No. 2," now Cope collection, Am. Mus. 5105). (See fig. 96.)

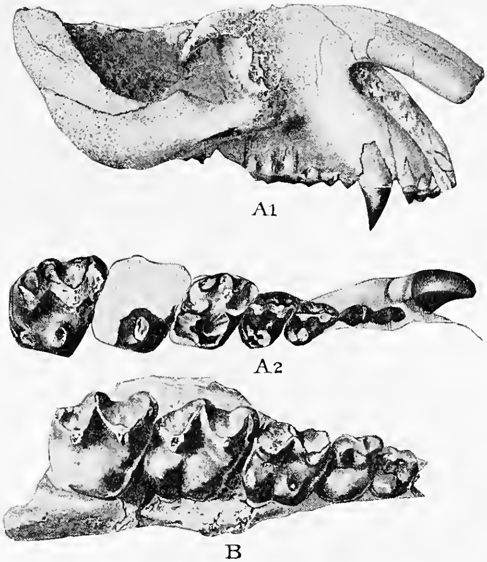

FIGURE 96.—Cope's cotypes of *Limnohyops laevidens*

After Cope, 1885. One-fourth natural size. A, Am. Mus. 5104, lectotype: A_1, "Cranium lacking posterior part of one side and lower jaw, from Cottonwood Creek" (Cope), "No. 1"; A_2, upper teeth of the same. B, Am. Mus. 5105, now refered to *Palaeosyops? copei*, right maxilla, p^3–m^3.

Cope's lectotype: Cope's first-mentioned specimen is the one from Bitter Creek (Washakie B?) (Am. Mus. 5105), now referred to *Palaeosyops? copei.* But the "No. 1" of Cope's description and measurements and the specimen to which the name "*laevidens*" refers is unquestionably the skull Am. Mus. No. 5104, from Cottonwood Creek (level Bridger B), Bridger Basin, now referable to *Limnohyops.* Furthermore, in the "Tertiary Vertebrata" (Cope, 1885.1, pp. 701–703, pl. 50, figs. 1, 2) Cope definitely selects, describes, and figures this specimen as the type, again referring to the Washakie specimen as "No. 2" and admitting that its specific association with the other specimen was doubtful. We therefore follow Cope in regarding

"No. 1," the Bridger specimen (Am. Mus. 5104), as the lectotype.

Characters.—Cope writes:

> This species is one of the larger forms of the group originally represented by *Palaeosyops*, and which has turned out to be so numerous in species. [This statement refers apparently to "No. 2."]
>
> The anterior median small tubercle of the first true molar is wanting. The last true molar has but one interior cone. [All these statements apply evidently to "No. 1," the Bridger or Cottonwood Creek specimen.]
>
> The canine tooth is powerful and bearlike; the outer incisor is the largest. The premaxillary bones are short, and the side of the face elevated and plane to the convex nasal bones. Zygomatic arch massive.

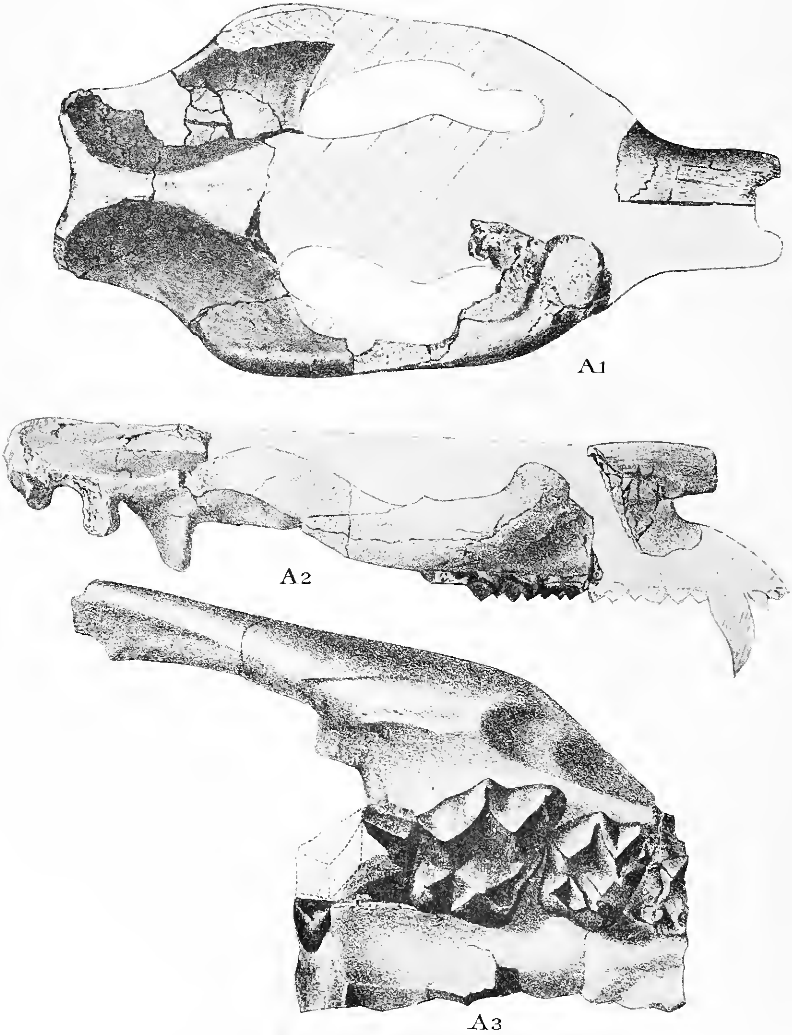

FIGURE 97.—Cope's type (holotype) of *Limnohyus fontinalis*

Am. Mus. 5107. After Cope, 1885. A$_1$, Young skull seen from above, one-half natural size; A$_2$, the same, right side, one-half natural size; A$_3$, right maxilla with dp^4, m^1, m^2, natural size.

> The molars have the general form of those of *L. robustus*, but the second superior premolar has but one outer tubercle. The cingula are much less developed than in that species, those between the inner cones of the molars being entirely absent. These cones are low and, with the rest of the crowns of all the teeth, covered with smooth and shining enamel.

Measurements [Cope, condensed and corrected]

	Millimeters
Length of molar series (No. 1)	141
Length of true molars	84
Length of crown canine (anteroposterior)	20
Length of crown last molar (anteroposterior)	30
Width of crown last molar (transverse)	34

Etymology.—laevis, levis, smooth, shining; *dens,* tooth; apparently in allusion to the "smooth and shining enamel."

Present determination.—This is a valid species referable to the genus *Limnohyops.*

Limnohyus fontinalis Cope, 1873

Cf. *?Palaeosyops fontinalis* Cope, this monograph, page 317.

Original reference.—Pal. Bull. No. 11, "issued January 31, 1873"; Am. Philos. Soc. Proc., vol. 13, pp. 35, 36, 1873 (Cope, 1873.5).

Subsequent references.—Cope, On the extinct Vertebrata of the Eocene of Wyoming, observed by the expedition of 1872: U. S. Geol. and Geog. Survey Terr. (Hayden) Sixth Ann. Rept., p. 594, 1873 (Cope, 1873.6); Tertiary Vertebrata, p. 707, pl. 49, fig. 9; pl. 50, fig. 4; pl. 58a, figs. 4, 5, 1884 [1885], (Cope, 1885.1).

Type locality and geologic horizon.—"Found by the writer on a bluff on Green River, near the mouth of the Big Sandy, Wyoming." ("Isolated patch lying northeast of the badlands." Probably *Eometarhinus-Trogosus-Palaeosyops fontinalis* zone (Bridger A).)

Holotype.—A young, fragmentary skull (Cope collection, Am. Mus. 5107, retaining dp^4, m^1, m^2 of the right side. (See fig. 97.)

Characters.—Cope writes:

> A small species agreeing with the *P. paludosus* in the two interior cones of the last superior molar. It is represented especially by a considerable part of the cranium of an individual in which the last superior molar is not quite protruded, but with the other molars and last premolar of the permanent dentition in place. The enamel of these teeth is in accordance with the age, delicately rugose, and while the cingulum is present fore and aft, it is wanting internally and externally. The anterior median tubercle is present on all the true molars, and the bases of the acute inner cones are in contact. The sagittal crest is truncate, and the squamosal portion of the zygoma very stout. The nasal bones are together very convex in transverse section.

Measurements [Cope]

	Millimeters
Length of true molar series (2.75 inches)	67
Length of last molar	25
Width of last molar	26

Etymology.—fontinalis, of or from a spring, hence original; in allusion to the primitive characters.

Present determination.—Cope was in error in interpreting the teeth of this skull, which belong to a very juvenile animal, the teeth exposed being the last upper milk tooth, dp^4, the first and second molars, m^1, m^2. The cranial characters, too, are very juvenile. So far as they serve to guide us, the animal probably belongs to the genus *Palaeosyops,* and also probably to a distinct species, from a low geologic level, possibly Bridger A.

Palaeosyops diaconus Cope, 1873

Cf. *Palaeosyops robustus* (Marsh), this monograph, page 331.

Original reference.—Pal. Bull. No. 12, p. 4, "published March 8, 1873" (Cope, 1873.1).

Subsequent references.—Cope, On the extinct Vertebrata of the Eocene of Wyoming observed by the expedition of 1872: U. S. Geol. and Geog. Survey Terr. (Hayden) Sixth Ann. Rept., p. 593, 1873 (Cope, 1873.6); Tertiary Vertebrata, p. 706, pl. 51, fig. 3, 1884 [1885] (Cope, 1885.1).

Type locality and geologic horizon.—Henrys Fork of Green River, Wyo.; *Uintatherium-Manteoceras-Mesatirhinus* zone (Bridger C or D).

Holotype.—"Represented by parts of the two maxillary bones, which present the crowns of the third and fourth premolars, and of the second and third true molars, with the bases of the other molars and premolars." (Cope collection, Am. Mus. 5106.) (See fig. 98.)

Characters.—Cope writes:

> Belonging to the genus *Palaeosyops* as understood by Marsh—that is, with two cones on the inner side of the last superior molar. The species is as large as the *Limnohyus major* of Leidy but differs in the relative proportions of the teeth. Thus the last three molars have the same anteroposterior length, while the space occupied by four premolars is shorter. The anterior and posterior cingula of the true molars are very strong, but it is not well marked on the inner side between the cones. The latter are acutely conic, and the median anterior tubercle is strongly developed. Although the wearing of the teeth indicates maturity, the enamel is coarsely and obtusely rugose. The fourth premolar differs from that of *L. major* in its smaller size relatively and absolutely and in the presence of a prominent vertical tubercle on the outer face, rising to the angle of the deep notch between the lobes. The third premolar is as wide as the fourth and about as large as the corresponding tooth in *L. major,* but different from it in the absence of tubercle and ridge that mark its external face. The first premolar has two roots, and the canine is large and short.

FIGURE 98.—Cope's type (holotype) of *Palaeosyops diaconus*

Left upper teeth. Am. Mus. 5106. After Cope, 1885. One-half natural size.

Measurements [Cope]

	Millimeters
Length of entire molar series	171
Length of true molars	106
Length of last molar (crown)	42
Width of last molar (crown)	43. 7

> In comparison with Marsh's description of his *P. laticeps,* the measurements are all larger, and the enamel is as rugose as in *L. major,* instead of smooth. The shortening of the premolar series is greater in *P. diaconus;* thus in *P. laticeps* the two sets of molars are related as 94 to 61 millimeters; in the present one, as 106:65; were the proportions similar, the length of the premolar series should be 69 millimeters.

Etymology.—δὶs, double; κῶνος, cone; because the third upper molar had two inner cones.

Present determination.—The name *P. diaconus* Cope is probably a synonym of *Palaeosyops robustus* (Marsh), as explained in Chapter V of this monograph.

Diplacodon Marsh, 1875

Cf. *Diplacodon* Marsh, this monograph, pages 155, 439

Original reference.—Am. Jour. Sci., 3d ser., vol. 9, p. 246, March, 1875, "dated February 20, 1875" (Marsh, 1875.1).

Type species.—*Diplacodon elatus* Marsh. (See p. 439.)

Generic characters.—Marsh writes:

> The genus here established presents characters in some respects intermediate between *Limnohyus* and *Brontotherium.* It agrees with the former in its complete dentition (44 teeth) and in the general form of the incisors, canines, and true molars. It resembles the latter still more closely in the premolar and molar teeth, and parts of the skeleton, especially in the vertebrae, and bones of the extremities. From the Eocene Limnohyidae, already described, this genus is sharply distinguished by the last upper premolar, which has two distinct inner cones, thus agreeing essentially with the first true molar. This character, which has suggested the name of the genus, is one step toward the modern type of perissodactyl dentition. The dental formula of the genus is the same as *Limnohyus*, viz, incisors $\frac{3}{3}$, canines $\frac{1}{1}$, premolars $\frac{4}{4}$, molars $\frac{3}{3}$. In other respects the teeth most resemble those of the Brontotheridae. From this family *Diplacodon* differs widely in its dentition and the absence of horns.

FIGURE 99.—Marsh's type of *Diplacodon elatus*

One-third natural size.

Etymology.—διπλόος, double; ἀκή, a point; ὀδούs, tooth; because the upper premolars had two inner cones.

Present determination.—This genus is certainly valid so far as it applies to the type species. (See p. 439.)

Diplacodon elatus Marsh, 1875

Cf. *Diplacodon elatus* Marsh, this monograph, page 439

Original reference.—Notice of new Tertiary mammals: Am. Jour. Sci., 3d ser., vol. 9, p. 246, March, 1875; dated "February 20, 1875" (Marsh, 1875.1).

Type locality and geologic horizon.—"Upper Eocene beds of Utah"; horizon probably *Diplacodon-Protitanotherium-Epihippus* zone (Uinta C, true Uinta formation).

Holotype.—A palate with dentition nearly complete, parts of the skull and skeleton (Yale Mus. No. 11180).

Characters.—The specific characters were not formally separated from the generic characters above given under *Diplacodon.*

Measurements [Marsh]

	Millimeters
Extent of upper molar series	242
Extent of upper true molars	152
Anteroposterior diameter of last upper molar	60
Transverse diameter	59
Anteroposterior diameter of [upper] canine, at base	32
Height of crown	27

Etymology.—*elatus*, lofty; apparently in allusion either to the large size or to the advanced stage of evolution.

Present determination.—This important genus and species was based upon an excellent type. The genus and species are valid. (See p. 439.)

Brachydiastematherium Böckh and Maty, 1876

Cf. *Brachydiastematherium* Böckh and Maty, this monograph, page 382

Original reference —Mittheilungen aus Jahrb. K. k. geol. Anstalt, Band 4, pp. 125–150, 1876 (1876.1).

Type species.—*Brachydiastematherium transilvanicum* Böckh and Maty. (See p. 382.)

Generic characters.—The generic characters mingled with the specific characters are given below. (See also p. 382.)

Etymology.—βραχύs, short; διάστημα, an interval; θηρίον, beast; in allusion to the short diastema between the lower canines and first premolars.

Present determination.—The type of this genus is an animal closely similar in size and in stage of evolution to the *Protitanotherium superbum* of the upper Eocene of Utah but differs in certain characters, which are probably of generic value. (See p. 382.)

Brachydiastematherium transilvanicum Böckh and Maty, 1876

Cf. *Brachydiastematherium transilvanicum* Böckh and Maty, this monograph, pages 382, 941

Original reference.—Mittheilungen aus Jahrb. K. k. geol. Anstalt, Band 4, pp. 125–150, pls. 17, 18, 1876 (1876.1). Cf. Toula, Akad. Wiss. Wien Sitzungsber., Band 101, pp. 612 et seq., 1892 (1892.1).

Type locality.—Andrásháza (Siebenbürgen), Hungary (Transylvania, eastern Hungary, about 150 miles northeast of Belgrade). Collected in 1871 by Dr. Alex. Pávay.

Geologic level.—The specimen, according to Professor Koch (Böckh, 1876.1, p. 149), was found in "buntes Thongebilde" of "lower" Eocene age, but the assignment of a form of this advanced stage to a level so low appears unwarrantable, and later evidence indicates that the age of this specimen is more probably upper Eocene. (See p. 382.)

Holotype.—Anterior part of lower jaw, containing incisors, canines, four premolars, and one molar. Originally described and defined by Böckh (1876.1) as a palaeotherioid. (See fig. 100.)

Generic and specific characters.—Böckh and Maty (p. 148) write:

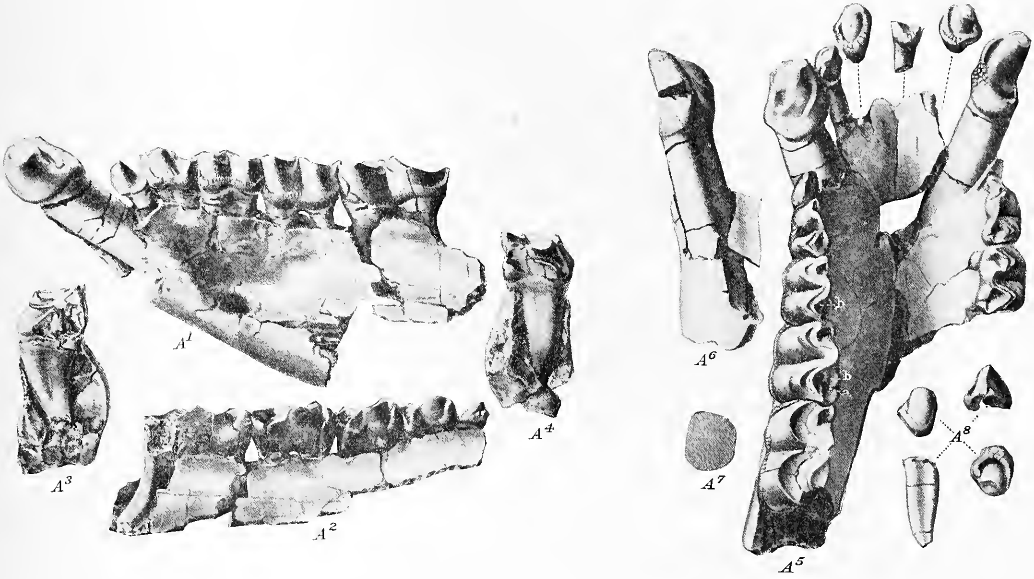

FIGURE 100.—Type (holotype) lower jaw of *Brachydiastematherium transilvanicum*

After Böckh and Maty, 1876. A^1, Side view; A^2, inner side; A^3, rear view of m_1; A^4, front view of m_1; A^5, top view of jaw; A^6, outer view of right lower canine; A^7, section of root of right lower canine; A^8, fragment of right lower incisor. Two-fifths natural size.

> I_3, mit flachkegelförmiger Krone, welche mit warziger Emailwulst versehen ist; C_1, mit kegelförmiger Krone, welche gleichfalls eine warzige, starke Emailwulst besitzt; seine Wurzel ist überaus stark, lang und gerade. Die Zahnlücke ist sehr kurz; p_4, deren erster am kleinsten, und seine nur eine Wurzel besitzende Krone stellt nur einen einfachen Kegel dar; die übrigen drei wachsen gradatim und die warzige Wulst der Basis fehlt an der inneren Seite dieser letzteren. Die drei letzten Praemolare ahmen wohl die Form der entsprechenden Zähne der echten Palaeotherien nach, wirkliche Halbmonde an der Oberfläche seiner abgewetzten Krone zeigt indessen nur der vierte Praemolar; an den demselben vorangehenden zwei Zähnen kann die Verzierung noch nicht als Halbmond bezeichnet werden. Die hintere Bucht des vierten Praemolares ist durch eine Scheide in zwei Theile abgetheilt, und heizu ist der Keim auch schon beim dritten Praemolar zu bemerken; m $(?)_3$, die innere Seite des ersten echten Molares zeigt gleichfalls keine Emailwulst, an der Mitte der hinteren Seite des hinteren Halbmondes vereinigt sich indessen die Wulst mit einer dreieckigen Emailzunge. An der Krone sämmtlicher Zähne sind die Reste einer dünnen cementartigen Kruste zu sehen.

The following measurements are taken from the original figures:

	Millimeters
I_3, anteroposterior	22
I_3, transverse	20
C, maximum anteroposterior diameter (horizontal measurement near base)	38
C, maximum transverse	31
C, height of crown (estimated)	40
Postcanine diastema (at top)	12
P_1–p_4, anteroposterior	107
P_1, anteroposterior	18
P_2, anteroposterior	26
P_2, transverse (through anterior lobe) (estimated)	17
P_3, anteroposterior	31
P_3, transverse (estimated)	22
P_4, anteroposterior	38
P_4, transverse (estimated)	28
M_1, anteroposterior	50
M_1, transverse (estimated)	30

Etymology.—*transilvanicum*, Transylvanian.

Present determination.—The species is probably valid.

Leurocephalus Osborn, Scott, and Speir, 1878

Cf. *Telmatherium* Marsh, this monograph, page 341

Original reference.—E. M. Mus. Geol. and Arch. Princeton Coll. Contr. No. 1, p. 42, pl. 4, 1878 (Osborn, Scott, and Speir, 1878.3).

Type species.—*Leurocephalus cultridens* Osborn, Scott, and Speir. (See p. 341.)

Generic characters.—Scott and Osborn write:

> Upper incisors acute, with strong posterior ridges, lower incisors compressed and laniariform, canines compressed, with serrated cutting edges; first upper premolar with rudimentary anterior lobe, last upper molar with rudimentary postero-internal cusp. Molars constructed as in *Palaeosyops* but higher, with sharper cones and more erect external lobes. Internal median valley very much deeper. Little or no depression at the forehead; zygomatic arch round, comparatively straight and does not project outward, and with obscure postorbital process. Premaxillaries short and straight. Mandible with nearly straight lower margin and shallow masseteric fossa; mental foramen single.

Etymology.—λευρός, smooth; κεφαλή, head; in allusion to the smooth texture of the bone.

Present determination.—*Leurocephalus* is a synonym of *Telmatherium* Marsh.

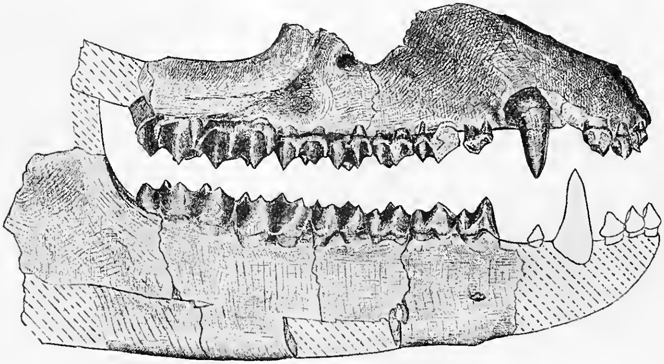

FIGURE 101.—Type (holotype) of *Leurocephalus cultridens*

Right premaxilla, maxilla, and mandibular ramus. Princeton Mus. 10027. After Osborn, 1878. One-third natural size.

Leurocephalus cultridens Osborn, Scott, and Speir, 1878

Cf. *Telmatherium cultridens* (Osborn, Scott, and Speir), this monograph, page 341

Original reference.—E. M. Mus. Geol. and Arch. Princeton Coll. Contr. No. 1, p. 42, pl. 4, 1878 (Osborn, Scott, and Speir, 1878.3).

Subsequent reference.—Earle, A memoir on the genus *Palaeosyops* Leidy and its allies: Acad. Nat. Sci. Philadelphia Jour., 2d ser., vol. 9, pp. 343–348, pl. 10, fig. 3, 1892; type (Earle, 1892.1).

Type locality and geologic horizon.—Henrys Fork divide, near Fort Bridger, Wyo.; *Uintatherium-Manteoceras-Mesatirhinus* zone (Bridger C or D).

Holotype.—"Established on specimen having a nearly complete dentition and portions of the cranium" (Princeton Mus. 10027). (See fig. 101.)

Specific characters.—The specific and generic characters were not distinguished in the original description.

Etymology.—*culter*, a knife; *dens*, tooth; in allusion to the sharp-edged recurved canines.

Present determination.—This genus is a synonym of *Telmatherium* Marsh. The species is valid. (See p. 341.)

Palaeosyops borealis Cope, 1880

Cf. *Eotitanops borealis* (Cope), this monograph, pages 156, 292

Original reference.—Am. Naturalist, vol. 14, p. 746, 1880 (Cope, 1880.1).

Subsequent reference.—Cope, Tertiary Vertebrata, p. 703, pl. 58a, fig. 3, 1884 [1885], (Cope, 1885.1).

Type locality and geologic horizon.—"Badlands in the upper drainage basin of the Big Horn River in western-central Wyoming"; Wind River formation, horizon not determined, probably *Lambdotherium-Eotitanops-Coryphodon* zone (Wind River B). J. L. Wortman, collector.

Holotype.—"Founded on a portion of the right maxillary bone, which supports the three true molars and one premolar" (Cope collection, Am. Mus. 4892). (See fig. 102.)

Characters.—Cope writes:

> Size of *Limnohyus fontinalis*, or much smaller than *P. laevidens*. Anterior median tubercle well developed; anterior and posterior cingula strong, not rising to inner cones. A low ridge extending outward and forward from posterior cone. Enamel smooth. Differs from *P. junior* Leidy in the presence of the intermediate tubercle and crest and in the weak external cingulum. Length of true molar series 63 [millimeters]; diameters of first true molar, anteroposterior, 19; transverse, 20.

Etymology.—*borealis*, relating to Boreas; in allusion to the Wind River formation.

Present determination.—The species is valid but generically distinct from *Palaeosyops*. It is the type of the genus *Eotitanops* Osborn. (See p. 289.)

Lambdotherium Cope, 1880

Cf. *Lambdotherium* Cope, this monograph, page 279

Original reference.—Am. Naturalist, vol. 14, p. 746, 1880 (Cope, 1880.1).

Subsequent reference.—Cope, Tertiary Vertebrata, p. 710, 1884 [1885] (Cope, 1885.1).

FIGURE 102.—Type (holotype) of *Palaeosyops borealis*

Right upper part of right maxilla with p^1–m^3. Am. Mus. 4892. After Cope, 1885. Natural size.

Type species.—*Lambdotherium popoagicum* Cope. (See p. 281.)

Generic characters.—Cope writes:

> Dentition much as in *Limnohyus*, excepting that there is a diastema in front of the second inferior premolar. Presence of first inferior premolar not ascertained. Fourth inferior premolar without posterior cusps. Superior molars with an

> angular ridge extending inward from each inner cusp. Last inferior molar with heel. * * * The V-shaped crests of the inferior molars separate it from *Hyracotherium.*

Etymology.—λάμβδα, lambda; θηρίον, beast; in allusion to the Λ-shaped crests of the lower molars.

Present determination.—The genus is valid and is now referred to the Eocene titanotheres.

Lambdotherium popoagicum Cope, 1880

Cf. *Lambdotherium popoagicum* Cope, this monograph, page 281

Original reference.—Am. Naturalist, vol. 14, pp. 746, 747, 1880 (Cope, 1880.1).

Subsequent reference.—Tertiary Vertebrata, p. 710, pl. 58b, figs. 7 and 7a, 1884 [1885] (Cope, 1885.1).

Type locality and geologic horizon.—Badlands of Wind River, western-central Wyoming; *Lambdotherium-Eotitanops-Coryphodon* zone (Wind River B).

Type.—A lower jaw with dentition (Am. Mus. 4863). (See fig. 103.)

Specific characters.—Cope writes:

> The heels of the second and third premolars have a median keel; the third only has an anterior tubercle. The crest of the heel of the fourth forms an imperfect V. Heel of the last true molar small. No cingula; enamel smooth. Length of molar series 80 [millimeters]; of true molars 44; of last molar 19; depth of ramus at first premolar 21; at last molar 31. * * * About the size of *Hyrachyus agrestis.*

Etymology.—*popoagicum,* in allusion to Popo Agie River, a tributary of Wind River.

Present determination.—The species is valid. (See p. 283.)

Lambdotherium brownianum Cope, 1881

Cf. *Eotitanops brownianus* (Cope), this monograph, page 292

Original reference.—U. S. Geol. and Geog. Survey Terr. Bull., vol. 6, p. 196, 1881 (Cope, 1881.2).

Subsequent reference.—Cope, Tertiary Vertebrata, p. 709, pl. 56a, fig. 10 (not the type), 1884 [1885] (Cope, 1885.1).

Type locality and geologic horizon.—Badlands of Wind River, western-central Wyoming; *Lambdotherium-Eotitanops-Coryphodon* zone (Wind River B).

Holotype.—"The greater part of a lower jaw," with p^2, m^1–m^3 (Cope collection, Am. Mus. 4885). (See fig. 104.)

Characters.—Cope writes:

> Considerably larger than the *L. popoagicum* and about equal to the *Tapirus terrestris.* The greater part of a lower jaw represents the species, and on this, unfortunately, only one of the premolar teeth remains. The three premolars are all two-rooted, and the posterior lobe of the last true molar is well developed. The inferior part of the external side of the ramus contracts or retreats rather abruptly posteriorly, below the last molar. It presents a slight external convexity below the second and third premolars. The alveolar line rises rapidly posteriorly, so that the last true molar is quite oblique. The second (first) premolar has a considerable heel, which is narrow and elevated on the middle line. The principal cusp is large and compressed but obtuse and has no anterior basal tubercle.

Measurements [Cope]

	Millimeters
Length of six molars	90
Length of true molars	55
Diameters of second (first) premolar:	
Vertical	9
Anteroposterior	12
Transverse	6
Length of base of first true molar	15
Width of base of first true molar	9
Length of base of third true molar	23
Width of base of third true molar	11
Depth of ramus at second premolar	30
Depth of ramus at m_3:	
At front of tooth	39
At end of tooth	47

Etymology.—"Dedicated to my friend Arthur E. Brown, superintendent of the Philadelphia Zoological Garden" (Cope).

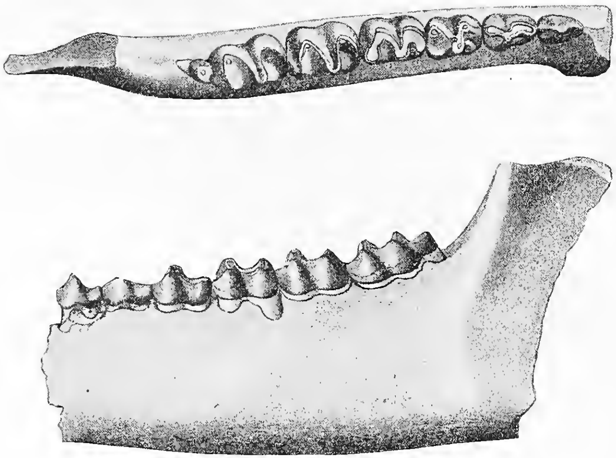

FIGURE 103.—Type (holotype) of *Lambdotherium popoagicum*

Left mandibular ramus, with p_3–m_3. Am. Mus. 4863. After Cope, 1885. Natural size.

Present determination.—The species is valid. The generic reference is to *Eotitanops.* (See p. 292.)

Palaeosyops hyognathus Osborn, 1889

Cf. *Dolichorhinus hyognathus* (Osborn), this monograph, page 409

Original reference.—Am. Philos. Soc. Trans., new ser., vol. 16, p. 513, 1890 [author's reprint issued Aug. 20, 1889; O. P. Hay] (Scott and Osborn, 1890.51).

Subsequent reference.—Earle, A memoir upon the genus *Palaeosyops* Leidy and its allies: Acad. Nat. Sci. Philadelphia Jour., 2d ser., vol. 9, pl. 11, figs. 10, 11 [type], 1892 (Earle, 1892.1).

Type locality and geologic horizon.—Washakie, White River, northeastern Utah; Washakie B.

Holotype and specific characters.—Scott and Osborn write:

> In the Washakie beds is found a large species, about the same size as *P. vallidens* Cope, which is provisionally referred to *Palaeosyops* (*P. hyognathus*, sp. nov., Princeton collection, No. 10273). This is represented by a lower jaw seven-eighths as large as the type mandible of *Diplacodon*. [See fig. 105.] As in the latter, the incisors form a close procumbent series; the tips forming a gently arched line when seen from above. The symphysis is extremely long (11 centimeters) and shallow; the canines are rather small and semiprocumbent. The molar-premolar series measures 24.5 centimeters, the last molar measures 6.5 centimeters, the transverse measurement outside of the canines is 9.6 centimeters; in *Diplacodon elatus* the same measurement is 10 centimeters. Unfortunately, the premolar crowns are broken; it is probable that one or two of the premolars will be found to be like the molars. The characters of the chin and symphysis are significant of close relationship to *Diplacodon elatus*.

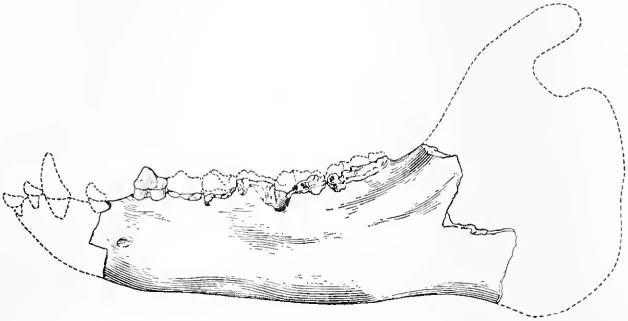

FIGURE 104.—Cope's type of *Lambdotherium brownianum*

One-half natural size.

Etymology.—ὗς, boar; γνάθος, jaw; in allusion to the forward-pointing lower incisors and shallow mandibular symphysis.

Present determination.—The species is valid. The generic reference is to *Dolichorhinus*. (See p. 409.)

Limnohyops Marsh, 1890

Cf. *Limnohyops* Marsh, this monograph, page 303

Original reference.—Am. Jour. Sci., 3d ser., vol. 39, p. 525, 1890 (Marsh, 1890.1).

Type species.—*Palaeosyops laticeps* Marsh (Am. Jour. Sci., 3d ser., vol. 4, p. 122, 1872). (See p. 311.)

Generic characters.—Marsh says:

> In 1872 the writer described a large mammal from the Eocene of Wyoming under the name of *Palaeosyops laticeps*. As the name *Palaeosyops* has since been restricted, this species must be regarded as representing a distinct genus, which may be called *Limnohyops*. In this form the last upper molar has two inner cones, and in *Palaeosyops*, as now defined, there is only one.

Etymology.—λίμνη, shore; ὗς, boar; ὤψ, face.

Present determination.—This is a valid genus and species. For fuller descriptions, see page 303.

Palaeosyops megarhinus Earle, 1891

Cf. *Mesatirhinus megarhinus* (Earle), this monograph, page 388

Original reference.—Am. Naturalist, vol. 25, No. 289, pp. 45–47, 1 fig., January, 1891 (Earle, 1891.1).

Subsequent reference.—Earle, A memoir on the genus *Palaeosyops* Leidy and its allies: Acad. Nat. Sci. Philadelphia Jour., 2d ser., vol. 9, pp. 320–329, pl. 10, fig. 2; pl. 11, figs. 4, 5, 1892 (1892.1).

Type locality and geologic horizon.—Washakie Basin of Wyoming; level undetermined, probably *Uintatherium-Manteoceras-Mesatirhinus* zone (Washakie A).

Type.—"A fine skull (No. 10008) in the Princeton collection" (Earle). (See fig. 106.)

Paratype.—Earle writes:

> There is also another portion of a skull (No. 10041), probably belonging to this species, with the occiput well preserved, from the Bridger proper [Earle, 1891.1, p. 45]. This paratype probably belongs to a more advanced species of this genus. (See p. 388.)

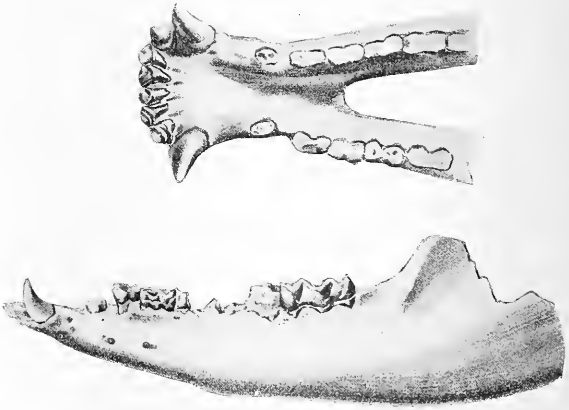

FIGURE 105.—Type (holotype) of *Palaeosyops hyognathus*

Incomplete lower jaw. Princeton Mus. 10273. After Earle, 1892. One-fifth natural size.

Specific characters.—Earle writes:

> Cranium: The characters of this skull are quite unique and depart widely from any of the species of the family that I have examined. The general form of the skull is broad and depressed. Its dorsal contour is very like that of *Palaeotherium crassum*—namely, there is no frontal depression, which is so characteristic of *Palaeosyops paludosus*, and the occipital

> region is only slightly higher than the frontal. The temporal fossae are not deeply excavated, and the occipital crests are weakly developed when compared to this region of the skull in *Limnohyops*. The occiput itself is high and rather narrow. The foramen magnum is wide, bordered by very large condyles. The auditory processes are widely separated. The posttympanics are broad and heavy. The postglenoid is peculiar in form; it is very short and thick; its form is very different from other species in the collection. An internal glenoid process is present in this species. The mastoid was probably exposed. The form of the zygomatic arch is striking; it is very light, nearly straight, with the temporal portion strongly compressed. The malar portion is also peculiar; the malar insertion is very abrupt and strongly depressed, with the external part very broad, thin, and shelf-like. The infraorbital foramen is not exposed. The form of the malar in this species is totally different from all other allied forms that I have examined. The orbit is very small, terminates anteriorly above the anterior border of the second superior molar; the postorbital processes are well marked. The facial region of the skull is very short, compared to the total length of the cranium. The nasals are very long and heavy; their distal portion is expanded and broader than the middle part. The nasal notches are very deep and high. The premaxillaries are triangular in outline; their symphysis is short and narrow, with a prominent anterior keel. The canine alveolus is very prominent. The palate is long and narrow, the roof of the same being strongly arched. The posterior termination of the palate is at the second superior molar. The incisive foramina are not divided.
>
> Teeth: The crowns of the teeth in this skull are badly damaged, but enough remains to give the total measurements and the characters of the last molar. The superior molars in this species form a continuous series, being not interrupted by a diastema. The sections of the incisors are very small. The canines are also very small and diverge widely. Only the second and third molar of each side are partially preserved. They have a square form with low crowns; externally they are totally without a cingulum. The external V's are rather wide and angular, in this respect approaching that of *Telmatotherium*. The last molar is without any intermediate conules.

Measurements

	Millimeters
Length of skull, from premaxillary symphysis to end postglenoid	285
Length from orbit to premaxillary symphysis	125
Length from orbit to postglenoid	160
Depth of nasal notch	84
Length of nasals	100
Entire molar series	148
Last superior molar:	
Anteroposterior	37
Transverse	39

Etymology.—μέγας, great, ῥίς, nose; in allusion to the length of the nasal bones.

Present determination.—This is a valid species which has been made the type of the genus *Mesatirhinus* by Osborn. (See p. 388.)

Palaeosyops minor Earle, 1891

Cf. *Palaeosyops paludosus*, this monograph, page 319

Original reference.—Acad. Nat. Sci. Philadelphia Proc. for 1891, p. 112, issued March 31, 1891 (Earle, 1891.2).

Subsequent reference.—Earle, A memoir upon the genus *Palaeosyops* Leidy and its allies: Acad. Nat. Sci. Philadelphia Jour., 2d ser., vol. 9, pp. 269, 331, 332, 1892 (1892.1).

Earle's cotypes.—In his original description Earle says (1891.2, p. 112), "*P. minor* embraces specimens which Leidy erroneously described as *P. paludosus*, pl. 4, figs. 3–6, of Leidy's report for 1873." In his memoir (1892.1, pp. 269, 330) Earle refers again to Leidy's Plate 4, Figures 3–6, as the types of *P. minor*, but on page 332 he says, "We may consider as the type specimen" the "beautifully preserved mandible figured by Leidy" (Leidy, 1873.1, pl. 5, figs. 10, 11); and again on page 387 he states that the specimen figured in his (Earle's) Plate 12, Figure 14, is "the type of this species and is in the collection of the Academy of Natural Sciences of Philadelphia." But this specimen is apparently the same one figured in Leidy's Plate 4, Figure 5. (See fig. 107.)

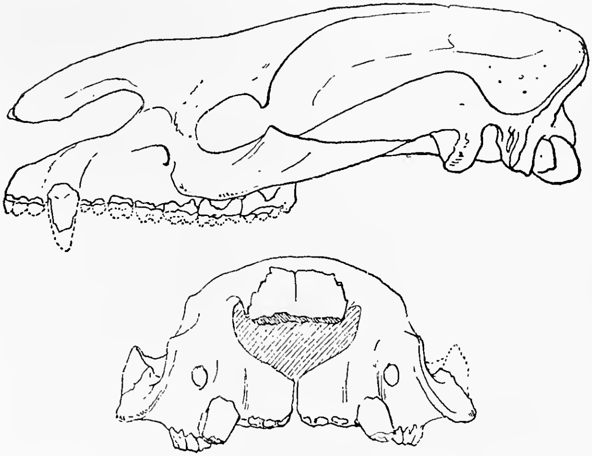

FIGURE 106.—Type (holotype) of skull of *Palaeosyops megarhinus*
Princeton Mus. 10008. After Earle, 1892. No scale given.

Specific characters.—Earle writes:

> Second superior premolar with two external lobes, external lobes of last superior premolar equal. Intermediate conules of true molars reduced, a strong external cingulum present.

Etymology.—*minor*, in allusion to the relatively small size.

Present determination.—Of the first-mentioned specimens (Leidy, 1873.1, pl. 4, figs. 3–6) Figures 3 and 4 represent an upper dentition, which is probably conspecific with *P. paludosus* as determined in this monograph; hence if this is taken as Earle's type *P. minor* becomes a synonym of *P. paludosus*.

On the other hand, Leidy's Plate 4, Figures 5 and 6, represent an upper dentition of uncertain specific reference. The "beautifully preserved mandible" (Leidy's pl. 5, figs. 10, 11) is probably referable to *P. paludosus.* Hence we may regard *P. minor* as a synonym of *P. paludosus.*

Type locality and geologic horizon.—Cottonwood Creek, Bridger Basin, Wyo.; *Palaeosyops paludosus-Orohippus* zone (Bridger B).

Holotype.—"A jaw, No. 10275 [Princeton Mus.], associated with a well-preserved radius, ulna, and two metacarpals."

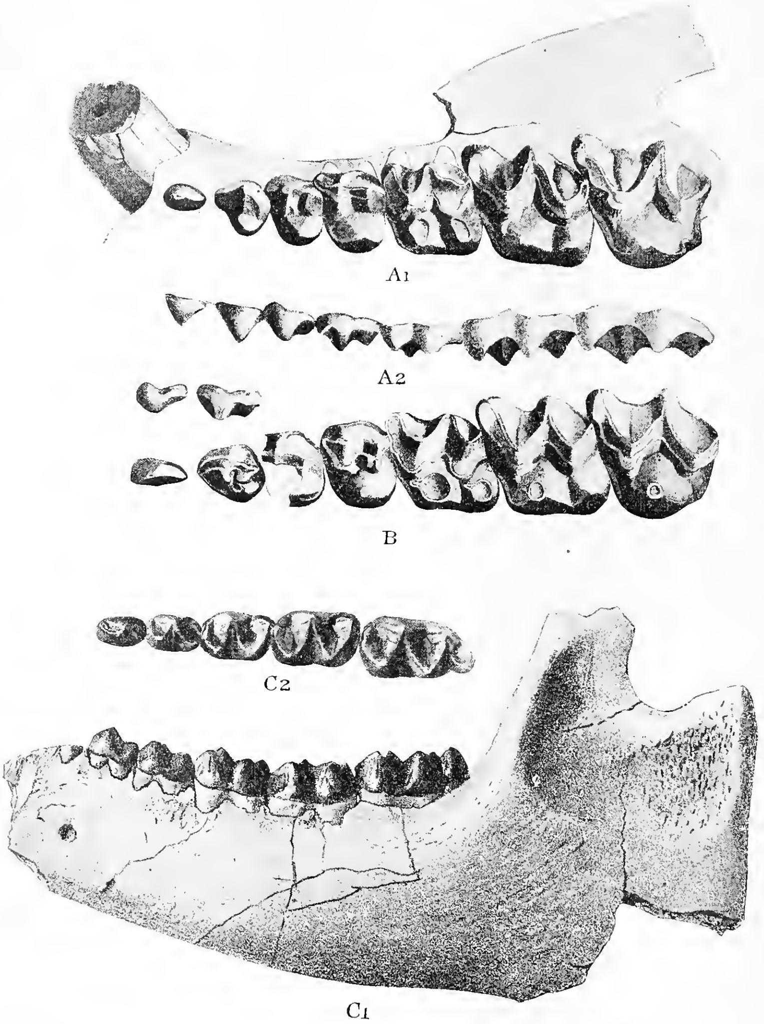

FIGURE 107.—Earle's cotypes of *Palaeosyops minor* in the collection of the Academy of Natural Sciences of Philadelphia

A_1, Left maxilla with root of canine and premolar-molar series. After Leidy, 1873. Two-thirds natural size. A_2, The same; outer view of premolar-molar series. B, Another specimen; left upper premolar-molar series. After Leidy, 1873. Two-thirds natural size. (A reversed view of this specimen, which is of uncertain specific reference, was figured by Earle as the type (Earle's pl. 12, fig. 14).) C_1, Left mandibular ramus with p_3–m_3. After Leidy, 1873 (pl. 5, fig. 11). One-half natural size. C_2, The same, p_3–m_3; crown view. After Leidy, 1873 (pl. 5, fig. 10). One-half natural size. The last two specimens are referable to *Palaeosyops paludosus.*

Palaeosyops longirostris Earle, 1892

Cf. *Palaeosyops longirostris* Earle, this monograph, page 319

Original reference.—Acad. Nat. Sci. Philadelphia Jour., 2d ser., vol. 9, p. 338, 1892 (Earle, 1892.1).

Characters.—Earle writes:

The type jaw of this species, with the parts of the skeleton associated with it, was referred by Scott and Osborn [Osborn, 1878.3, pp. 37, 38] to our *P. minor* (equal, in part, to *P. paludosus* Leidy). After comparing Leidy's type specimen [probably the specimen figured in Leidy's memoir of 1873, pl. 5, fig. 11] with this jaw, I find that there is such a marked difference in some of its characters that I have to give it a specific rank. The following characters distinguish it from Leidy's type: (1) The great posterior extension of the jaw behind the last molar (this is a unique character of this jaw—I have not observed it in any other species of this subfamily); (2) the symphysis is much more elongated than in *P. minor;* (3) the lower border is straighter and less inflected than in *P. minor;* (4) the posterior tubercle of the last inferior molar is much larger than in the last named species; (5) the V's of premolar 4 are not so well developed as in *P. minor*, and there is also a well marked difference in the size of the first molars of the two species.

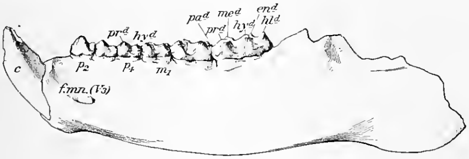

FIGURE 108.—Earle's type of *Palaeosyops longirostris*

Princeton Mus. 10275. One-fourth natural size.

In this jaw the first true molar is considerably smaller than in *P. minor.* The canine is very large and semiprocumbent, its position in the jaw resembling that of *T. hyognathus.*

Etymology.—longus, long; *rostrum,* bill, snout (hence, in this instance, jaw); in allusion to the great posterior extension of the jaw behind the last molar. (Earle.)

Present determination.—This probably valid species is certainly referable to the Palaeosyopinae and probably to *Palaeosyops.* (See p. 319.)

Telmatotherium diploconum Osborn, 1895

Cf. *Rhadinorhinus diploconus* (Osborn), this monograph, page 431

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 7, p. 85, fig. 6, 1895 (Osborn, 1895.98).

Type locality and geologic horizon.—Northeastern Utah; "*Telmatotherium cornutum*" beds, *Eobasileus-Dolichorhinus* zone (Uinta B).

Holotype.—"The type is a skull (No. 1863) [Am. Mus.] in which the nasals are wanting and the midregion of the cranium was crushed." (See fig. 109.)

Characters.—Osborn writes:

Superior premolar-molar series, 174 millimeters. A large hypocone upon last upper molar. Nasofrontals without horn. Long sagittal crest. Canines small, rounded.

This species differs from *T. megarhinum* in the absence of the infraorbital shelf and in the presence of a large hypocone upon the last upper molar. The premolar-molar dentition is similar in size and form to that of *T. cultridens*, but there are the following important general differences: (1) Canines small and circular in section; (2) a very short diastema, if any, behind the canine; (3) a large hypocone upon m^3; (4) the infraorbital foramen close beneath the anterior border of the molar [malar]. [Comparisons with *T. cultridens* follow.]

Etymology.—διπλόος, double; κῶνος, cone; in allusion to the presence of two internal cones on the third upper molar.

Present determination.—The species is valid; it is now referred to the genus *Rhadinorhinus.* (See p. 431.)

Telmatotherium cornutum Osborn, 1895

Cf. *Dolichorhinus hyognathus* (Osborn), this monograph, page 409

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 7, p. 90, figs. 10, 11, 1895 (Osborn, 1895.98).

Type locality and geologic horizon.—Northeastern Utah; "*Telmatotherium cornutum* beds," *Eobasileus-Dolichorhinus* zone (Uinta B 2).

Holotype and paratypes.—Osborn writes:

The type of this species is a fine skull (No. 1851) [Am. Mus.], while several other well-preserved skulls from the same levels give us all the cranial characters and the superior dentition (Nos. 1850, 1847, 1848, 1852, 1837). [See fig. 110.]

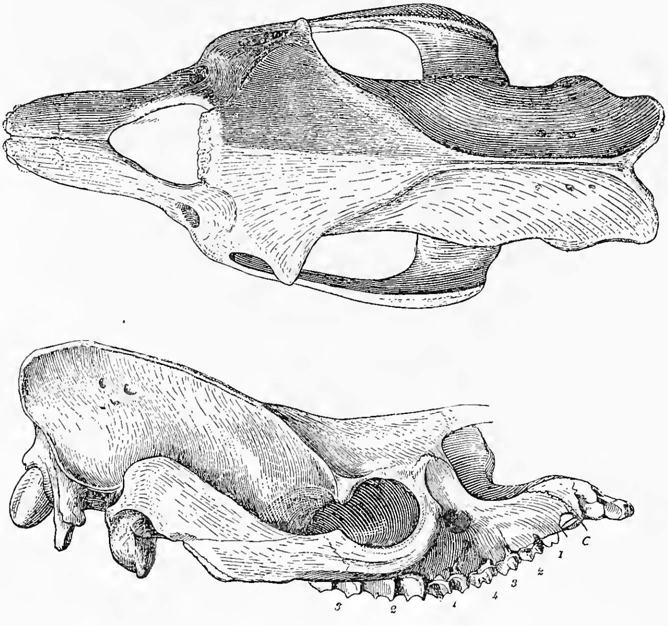

FIGURE 109.—Type (holotype) of *Telmatotherium diploconum*

Superior and lateral views of skull. The nasals are broken off. Am. Mus. 1863. After Osborn, 1895. One-fourth natural size.

Characters.—Osborn writes:

Incisors $\frac{3}{2}$. Premolar-molar series, 208 millimeters. A narrow diastema. Upper canines lanceolate. Long premaxillary symphysis. A well-developed nasofrontal protuberance. Top of cranium completely flattened. No sagittal crest. An infraorbital process upon malar.

This species is remarkable for its very long flat-topped cranium and its incipient knoblike osseous horns borne chiefly upon the nasals but partly upon the frontals. These horns project laterally and rise slightly above the general surface, and are best seen in the anterior view, Figure 110. These characters and the absence of the frontoparietal and interparietal sutures all point well toward *Titanotherium*, but the premolars are still absolutely simple, showing no trace of the postero-internal cusps which characterize *Diplacodon elatus*.

Other striking peculiarities are the upward-arching midcranial region, the extremely long, narrow, and laterally decurved nasals; the strong infraorbital shelf upon the molars [malars] (seen also in *T. megarhinum*), the slender zygomatic arch, the low occiput, the backward extension of the posterior nares by the palatines, and the partial inclosing of the roof of the pharynx by the pterygoids.

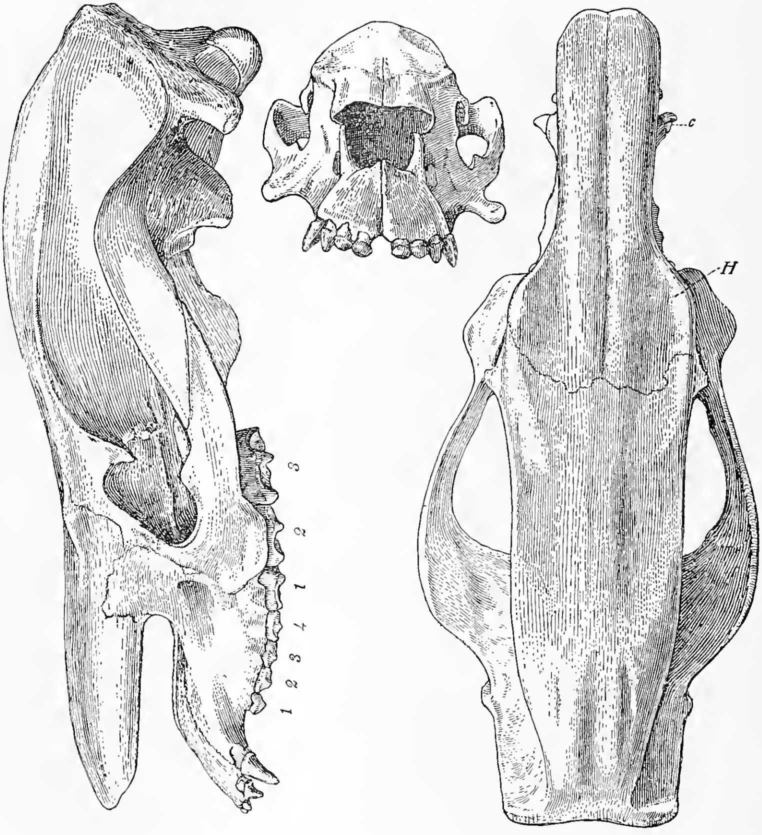

FIGURE 110.—Type (holotype) of *Telmatotherium cornutum*

Side, front, and top views of skull. Am. Mus. 1851. After Osborn, 1895. One-fourth natural size.

This general description of character was followed by a more detailed description.

Etymology.—cornutus, horned; in allusion to the osseous "horns."

Present determination.—Comparison of the lower jaw with the type of *Palaeosyops hyognathus* Osborn indicates that the species *T. cornutum* is a synonym of *P. hyognathus*, a species which is now referred to the genus *Dolichorhinus*.

Sphenocoelus Osborn, 1895

Cf. *Sphenocoelus* Osborn, this monograph, page 417

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 7, pp. 98–102, 1895 (Osborn, 1895.98).

Generic characters.—Osborn writes:

> The distinctive features of the skull may therefore be summed up as follows: Deep paired pits in the alisphenoids, and orbitosphenoids upon either side of the thin presphenoid [basisphenoid]; a long alisphenoid canal; foramen ovale widely separated from for. lac. medium; condyles very broad; foramen magnum large; occipital crest extending anteriorly into a short sagittal crest with convex sagittal ridges; skull apparently long and narrow.

Etymology.—σφήν, a wedge; κοῖλος, hollow; in allusion to the paired cavities in the basisphenoid bone.

Present determination.—This is a valid genus of Eocene titanotheres related to the long-skulled *Dolichorhinus*. (See p. 417.)

Sphenocoelus uintensis Osborn, 1895

Cf. *Sphenocoelus uintensis* Osborn, this monograph, page 419

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 7, pp. 98–102, figs. 12–15, 1895 (Osborn, 1895.98).

Type locality and geologic horizon.—Northeastern Utah; *Metarhinus* zone (Uinta B 1).

Holotype.—"Represented by the posterior portion of a skull" (Am. Mus. 1501). (See fig. 111.)

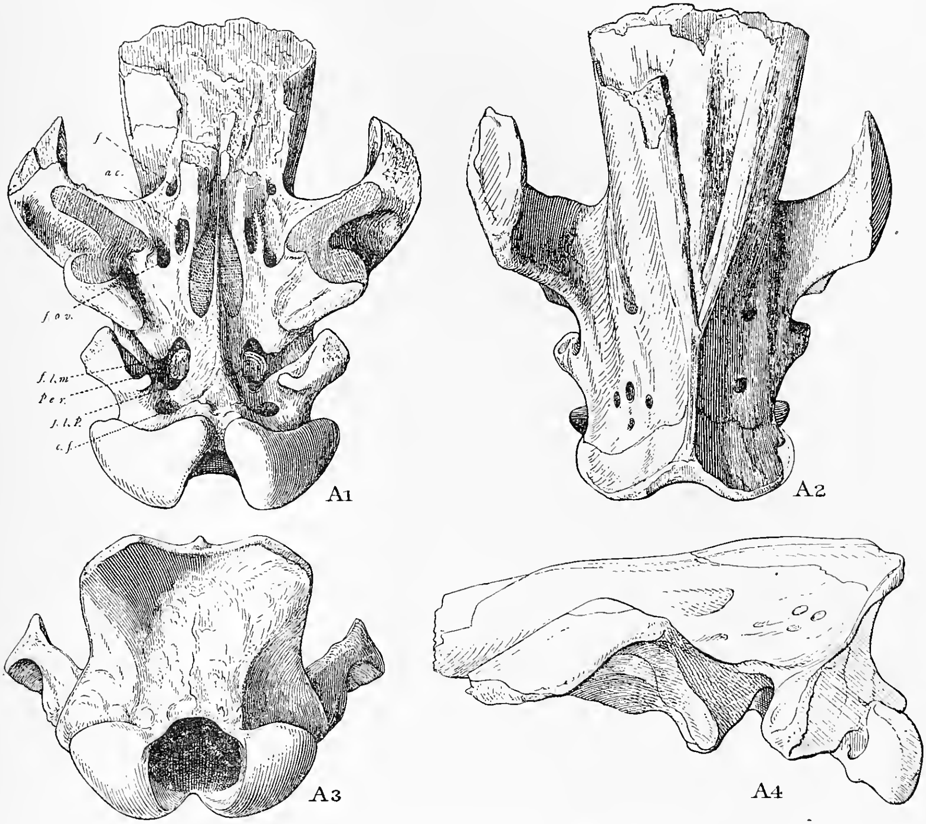

FIGURE 111.—Type (holotype) of *Sphenocoelus uintensis*

Posterior half of cranium. Am. Mus. 1501. After Osborn, 1895. A_1, Basal view; A_2, top view; A_3, occipital view; A_4, view of left side. One-third natural size.

Specific characters.—Osborn writes:

> This new genus is represented by the posterior portion of a skull, which is distinct from any cranium known to the writer. Its most distinctive feature is the presence of a pair of pits in the floor of the skull upon either side of the narrow presphenoid [basisphenoid]. These pits were at first mistaken for the for. lac. media, but more careful investigation shows that they are roofed over by bone and apparently do not communicate at all with the cranial cavity. The pit on the right side is perfectly preserved and clearly exhibits these characters. The pits are 42 millimeters long, 14 millimeters wide, and 2 millimeters deep.
>
> The skull has a long, narrow cranium surmounted posteriorly by a sagittal crest, which diverges anteriorly into two decidedly convex sagittal ridges. The occiput is rather broad, and below it are two widely set occipital condyles which are directed obliquely downward and backward. On either side of these the exoccipitals extend down into obtuse paroccipital processes, which are closely joined to the post-tympanics. The external auditory meatus is open inferiorly. In front of this the postglenoid process faces somewhat inward; the glenoid facet is L-shaped, two narrow arms extending out upon the squamosal, and a broad arm descending upon the postglenoid. The distinctive feature of the zygoma is the presence of a deep depression just behind the lateral arm of the glenoid facet.

Skull measurements

	Millimeters
Width across zygomatic arches	230
Height of occiput	142
Breadth	117
Breadth of occipital condyles	130
Basioccipital to top of sagittal crest	114

> The foramina of the skull are related to those of the Perissodactyla, for there is a long alisphenoid canal, upon the outer side of the anterior opening of which is the foramen. Just behind the posterior opening of the canal is the foramen ovale, and between these foramina are the two pits above mentioned. This foramen is separated by a very wide plate of bone from the for. lac. medium, which is partly filled by the periotic mass.

Etymology.—uintensis, from Uinta, in allusion to the Uinta Basin.

Present determination.—This is a valid genus and species. (See p. 419.)

Protitanotherium Hatcher, 1895

Cf. *Protitanotherium* Hatcher, this monograph, page 374

Original reference.—Am. Naturalist, vol. 29, p. 1084, December, 1895 (Hatcher, 1895.1).

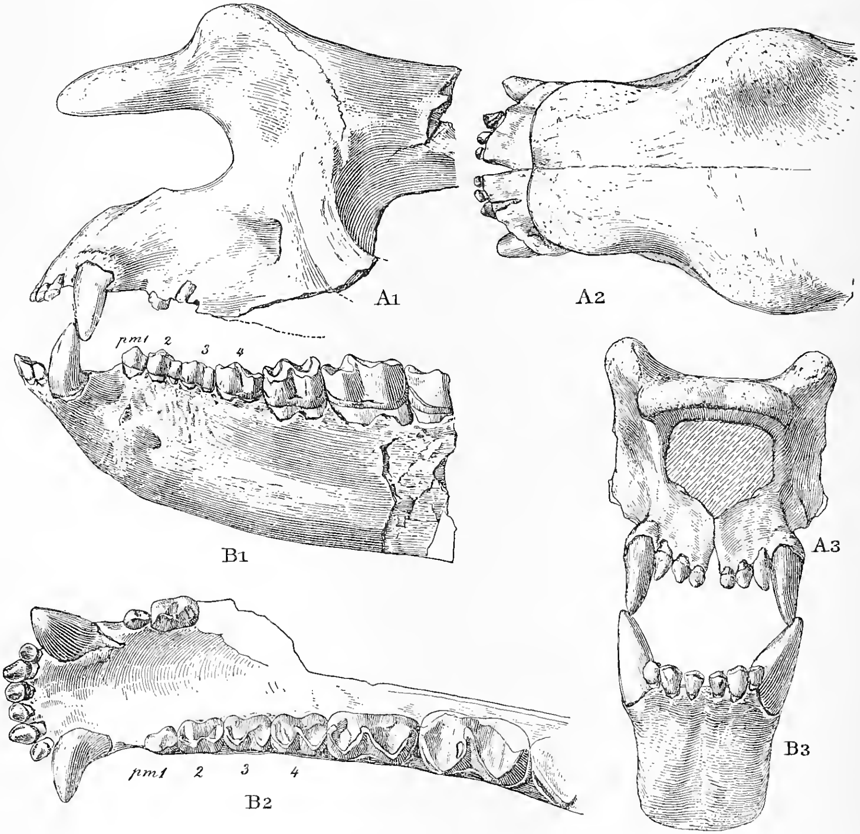

FIGURE 112.—Type (holotype) of *Diplacodon emarginatus*

Facial part of skull and anterior part of mandible. Princeton Mus. 11242. After Hatcher, 1895. A_1, A_2, A_3, Side, top, and front views of skull; B_1, P_2, B_3, side, top, and front views of mandible. One-fourth natural size.

Type species.—Diplacodon emarginatus Hatcher.

Generic characters.—Hatcher writes:

> In referring this skull to *Diplacodon,* I have been compelled to ignore certain characters ascribed to that genus by Professor Marsh. That author, in speaking of the relations of this genus to the Titanotheriidae (Brontotheridae), in his original description of the type specimen, says (Marsh, 1875.1, p. 24): "From this family, *Diplacodon* differs widely in its dentition and the absence of horns." In describing *Diplacodon* as hornless, it would seem that Professor Marsh's conclusion is entirely conjectural, since his material does not show whether there were horns or not. The present skull has a well-developed pair of frontonasal horns, and, since it agrees in all the characters known to that genus, I have preferred to refer it to that genus rather than to propose for it a new one on the strength of this purely conjectural character ascribed to *Diplacodon* by Professor Marsh. Should future discoveries show that there are hornless forms with the same dental characters as *Diplacodon,* it will then be necessary to establish for the present specimen a new genus, which may be called *Protitanotherium.*

Etymology.—pro, before; *Titanotherium*—that is, forerunner of *Titanotherium.*

Present determination.—It is not yet settled whether *Diplacodon elatus* Marsh had horns or not, but it is now believed that even if this character is set aside *D. elatus* is generically distinct from *D. emarginatus,* and we may therefore regard Hatcher's *Protitanotherium* as a valid genus.

Diplacodon emarginatus Hatcher, 1895

Cf. *Protitanotherium emarginatum* Hatcher, this monograph, page 377

Original reference.—Am. Naturalist, vol. 29, pp. 1084–1087, pl. 38, figs. 1–4, December, 1895 (Hatcher, 1895.1).

Type locality and geologic horizon.—Found by J. B. Hatcher "near the base of the *Diplacodon elatus* beds [Uinta C of Osborn], in the upper Eocene or Uinta of Marsh. The locality is about 8 miles north of White River and 25 miles east of Ouray Agency, Utah, and is locally known as Kennedy's Hole."

Holotype.—A skull with lower jaw (Princeton Mus. 11242). The anterior part only of the skull is well preserved. (See fig. 112.)

Characters.—Hatcher writes:

> The present species is at once distinguished from *D. elatus* by its greater size, as is shown by a comparison of the length of the premolar and molar series, which is 310 millimeters in the former and 242 in the latter.
>
> In general appearance the cranium of *D. emarginatus* is remarkably like some of the smaller forms of *Titanotherium.*

Etymology.—*emarginatus*, referring to the emarginate form of the distal end of the nasals.

Present determination.—The species is valid but generically distinct from *Diplacodon* Marsh and is now referred to *Protitanotherium* Hatcher. (See p. 377.)

Manteoceras Hatcher, 1895

Cf. *Manteoceras* Hatcher, this monograph, page 362

Original reference.—Am. Naturalist, vol. 29, p. 1090, 1895 (Hatcher, 1895.1).

Type species.—By designation *Telmatotherium vallidens* (of Osborn, not *Palaeosyops vallidens* Cope) = *Manteoceras manteoceras* Hay ex Osborn, MS., 1902.

Hatcher's description —Hatcher writes:

> The genus *Telmatotherium* as it now stands should be divided, since it embraces at least three distinct forms. The type of *T. vallidens* should be removed from that genus and made the type of a new genus. This new genus may be called *Manteoceras*, as suggested by Wortman from the field; it would be distinguished from *Telmatotherium* by the absence of the infraorbital shelf, the stronger and more expanded zygomata, and the concave superior aspect of the skull and incipient frontonasal horns.

In the above passage the reference to "the type of *T. vallidens*" if taken by itself would lead one to regard "*Palaeosyops*" *vallidens* Cope as the type of the genus *Manteoceras* Hatcher. But a careful study of Hatcher's full text and a knowledge of the history of the subject proves that Hatcher had in mind the "*Telmatotherium vallidens*" of Osborn, not of Cope: because (*a*) Hatcher refers to his Plate 29, Figure 2, as "*Telmatotherium vallidens,*" and this figure is copied from Osborn's "*Telmatotherium vallidens,*" Figure 7; (*b*) these figures represent Wortman's original "prophet horn" skull, to which he had applied the name *Manteoceras* "in a letter from the field" (Osborn); (*c*) the generic characters assigned by Hatcher refer most clearly to this skull and are utterly inapplicable to *Telmatotherium* ("*Palaeosyops*") *vallidens* Cope, in which only the dentition and not the skull is known.

Thus the type of the genus *Manteoceras* Hatcher is *Telmatotherium vallidens* of Osborn not Cope, which is equivalent to *Manteoceras manteoceras* Hay ex Osborn MS. The generic name can not be credited to Wortman, because he never published it, although Osborn (1895.98), mentions it as a manuscript name.

Etymology.—μάντις, prophet; κέρας, horn; in allusion to the incipient "horns" above the orbits.

Present determination.—This valid genus is fully described on page 362.

Dolichorhinus Hatcher, 1895

Cf. *Dolichorhinus* Hatcher, this monograph, page 396

Original reference.—Am. Naturalist, vol. 29, p. 1090, 1895 (Hatcher, 1895.1).

Type species.—*Telmatotherium cornutum* Osborn.

Characters.—Hatcher writes:

> The genus *Telmatotherium* as it now stands should be divided, since it embraces at least three quite distinct forms * * * The type of *T. cornutum* should also be made the type of a new genus which may be called *Dolichorhinus;* it would be distinguished from *Manteoceras* and *Telmatotherium* by the reduced number of inferior incisors, presence of incipient horns, presence of infraorbital shelf, and position of posterior nares.

Etymology.—δολιχός, long; ῥίς, nose.

Present determination.—This is a valid genus. (See p. 396.)

Palaeosyops ultimus Matthew, 1897 (ex Osborn MS.)

Cf. *Telmatherium ultimum* Osborn, 1908, this monograph, page 345

Original reference.—Am. Naturalist, vol. 31, pp. 57–58, 1897 (Matthew, 1897.1).

Subsequent reference.—Bibliography and catalogue of the fossil Vertebrata of North America: U. S. Geol. Survey Bull. 179, p. 631, 1902 (Hay, 1902.1).

Doctor Matthew had no intention of describing a new species. He merely stated incidentally that *P. ultimus*, as established in manuscript by Osborn, and *P. paludosus* both have a short-necked astragalus. No type was mentioned, and the single character given does not separate the species from *P. paludosus.* Hence "*Palaeosyops ultimus* Matthew" (cited by Hay, 1902, p. 631) remained a nomen nudum until the type was fixed by Osborn in 1908. (See p. 345.)

Etymology.—*ultimus*, last, latest; in allusion to the relatively late geologic horizon and to the apparent extinction of the race.

Palaeosyops manteoceras Matthew, 1899 (ex Osborn MS.)

Cf. *Manteoceras manteoceras* Hay, this monograph, page 395

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 12, p. 47, 1899 (Matthew, 1899.1).

In this faunal list the present specific name is merely mentioned. No type is specified, and no characters are given, so that *Palaeosyops manteoceras* Matthew was a nomen nudum until the type was designated by Hay in 1902. (See p. 365.)

Etymology.—μάντις, prophet; κέρας, horn; in allusion to the incipient "horns" above the orbits.

Telmatotherium diploconum var. minus Matthew, 1899

(Nomen nudum)

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 12, p. 50, 1899 (Matthew, 1899.1).

In Matthew's faunal list "*Telmatotherium diploconum* var. *minus*" is recorded but not defined, and no type is specified. Hence *Telmatotherium diploconum minus* is a nomen nudum.

Etymology.—*minus*, less; because smaller than the typical *T. diploconum.*

Canis? marshii Hay, 1899

Cf. *Palaeosyops major?* Leidy, this monograph, page 321

Original reference.—Science, new ser., vol. 10, p. 253, 1899 (Hay, 1899.1). Founded on "*Canis montanus*" Marsh (see p. 158), which was preoccupied by *Canis montanus* Pearson.

Etymology.—Named in honor of Prof. O. C. Marsh.

Present determination.—As explained above, the type of *Canis montanus* Marsh (not Pearson) and *Canis? marshii* Hay is a second lower premolar of an Eocene titanothere, probably *Palaeosyops paludosus* or *P. major.* *Canis? marshii* Hay is therefore either indeterminate or a synonym of *P. paludosus* or *P. major.*

Manteoceras manteoceras Hay, 1902 (ex Osborn MS.)

Cf. *Manteoceras manteoceras* Hay, this monograph, pages 365–370

Original reference.—U. S. Geol. Survey Bull. 179, p. 632, 1902 (Hay, 1902.1).

Lectotype.—A skull (Am. Mus. 1569) lacking the dentition, described and figured by Osborn as "*Telmatotherium vallidens*" (Osborn, 1895.98, pp. 87–90, figs. 7–8). (See fig. 113.)

Paratype.—An incomplete skull (Am. Mus. 1570) with dentition (op. cit., fig. 9) from the same locality and level.

Type locality and geologic horizon.—Washakie Basin, Wyo.; discovered by J. L. Wortman, of the American Museum Bridger expedition of 1893, "in a brown layer of sandstone 3 miles north of the base of Haystack Mountain, upon Bitter Creek" (op. cit., p. 87). *Uintatherium-Manteoceras-Mesatirhinus* zone (Washakie A).

Hay's type.—We have seen above that the name *Palaeosyops manteoceras* Matthew (ex Osborn MS.) was a nomen nudum, because no type had been designated. The type was for the first time clearly indicated by Hay (1902.1, p. 632), who refers to this species Hatcher's (1895.1) Plate 39, Figure 2 (p. 368, this monograph) and Osborn's (1895.98) Figures 7–9 (pp. 366, 368). These are clearly the same two "prophet horn" skulls (Wortman's first "*Manteoceras*" specimens) that had been at first erroneously referred by Osborn to "*Telmatotherium vallidens* Cope." Of these two skulls, Am. Mus. 1569—that is, Osborn's Figures 7, 8 and Hatcher's Figure 2 (copied from Osborn's fig. 7)—may be taken as the lectotype.

The generic name *Manteoceras* and the specific name *manteoceras* were first brought together by Hay in the reference now under consideration.

Specific characters.—In Osborn's original description (Osborn, 1895.98, p. 87) these skulls were erroneously identified as conspecific with the type of *Palaeosyops vallidens* Cope, under the name "*Telmatotherium vallidens* Cope." The specific characters given by Osborn were as follows:

> Superior premolar-molar series, 184–220 millimeters. A narrow diastema. Molar cusps less elevated. A rudimentary nasofrontal tuberosity. Premaxillary symphysis short. Top of cranium flattened; very short bifid sagittal crest.

Etymology.—μάντις, prophet; κέρας, horn; in allusion to the incipient "horns" above the orbits.

Present determination.—The species is a valid one and is fully described on pages 365–370.

Lambdotherium primaevum Loomis, 1907

Cf. *Lambdotherium primaevum* Loomis, this monograph, page 283

Original reference.—Am. Jour. Sci., 4th ser., vol. 23, p. 363, fig. 2, May, 1907 (Loomis, 1907.1).

Type locality and geologic horizon.—Buffalo Basin, near Meeteetse, Wyo. "Wasatch beds of the Big Basin." Horizon regarded by Loomis as equivalent to the base of the Wind River formation—that is, the *Heptodon-Coryphodon-Eohippus* zone (Wind River A).

Holotype.—Amherst Mus. 254, "consisting of upper molars 1 and 2 of the right side and lower molars 1, 2, and 3 from the same side, the specimen being from the Buffalo Basin, near Meeteetse, Wyo. This species is fairly abundant at this horizon and is intermediate in size between *L. brownianum* and *L. popoagicum.*" (See fig. 114.)

Characters.—Loomis writes:

> On the upper molars the parastyle, though strong, is not so well developed as in the foregoing forms; the paraconule is well developed, but the metaconule is so annexed to the metacone as to appear like a buttress of this cusp. The second molar measures 12 millimeters transversely [anteroposteriorly] by 17 millimeters lengthwise [transversely]. The robust lower molars have the protoconid markedly bifid, while the paraconid and hypoconid are each high crescents. The heel of the last molar is a high shallow basin completely surrounded by an outer rim. The three molars occupy 41 millimeters.

The brackets above indicate that in the foregoing description the measurements of the molar teeth have been inadvertently transposed. The description should read: "Second superior molar, anteroposterior, 12 millimeters; transverse, 17 millimeters."

Etymology.—*primaevus*, earliest in age; in allusion to the supposedly low geologic horizon.

Present determination.—Provisionally recognized as a valid species.

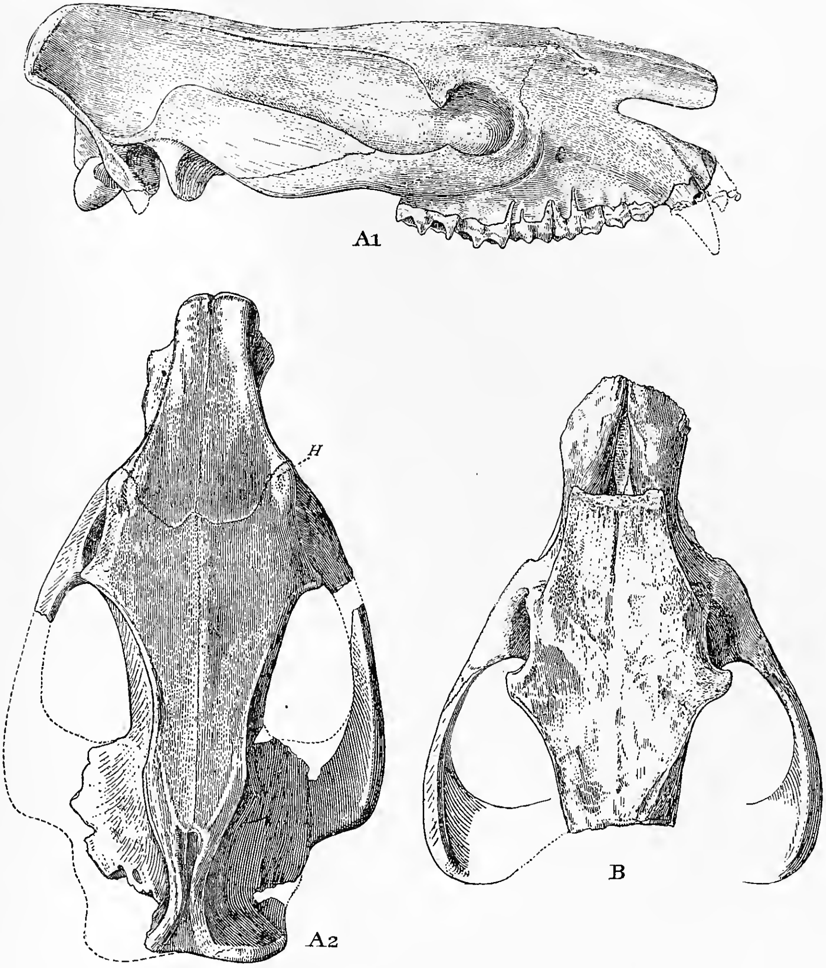

FIGURE 113.—Cotypes of *Manteoceras manteoceras* (*Telmatotherium vallidens*)

After Osborn. A_1, Composite Am. Mus. 1569, 1570; side view of skull; A_2, Am. Mus. 1569 (lectotype), superior view of skull; B, Am. Mus. 1570, superior view of skull. All one-fourth natural size.

Eotitanops Osborn, 1907

Cf. *Eotitanops* Osborn, this monograph, page 289

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 23, p. 242, 1907; type species designated (Osborn 1907.294).

Subsequent reference.—Osborn, New or little-known titanotheres from the Eocene and Oligocene: Am. Mus. Nat. Hist. Bull., vol. 24, pp. 600, 601, 1908 (Osborn, 1908.318).

Type species.—*Palaeosyops borealis* Cope.

Generic characters (Osborn, 1908.318, p. 601).—Superior molars subquadrate and rounded in form; conules reduced, sublophoid; m^1–m^3, 63 millimeters (estimated). Inferior molars without metastylids. Hypoconulid of m^3 subconic. First inferior premolar present. Manus tetradactyl, functionally tridactyl with a tendency to mesaxonic structure. From Wind River formation.

Etymology.—ἠώς, dawn; Τιτάν, a titan; ὤψ, face—that is, first of the titanotheres.

Present determination.—This genus is valid. (See p. 289.)

Limnohyops priscus Osborn, 1908

Cf. *Limnohyops priscus* Osborn, this monograph, page 306

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 24, pp. 601–602, fig. 5, 1908 (Osborn, 1908.318).

Type locality and geologic horizon.—Grizzly Buttes, Bridger Basin, Wyo.; *Palaeosyops paludosus-Orohippus* zone (Bridger B 2).

FIGURE 114.—Type (holotype) of *Lambdotherium primaevum*

Amberst Mus. 254. After Loomis, 1907. A, Right upper molars 1 and 2; B, right lower molars (m_1-m_3). Natural size.

Holotype.—A crushed skull with excellent dentition (Am. Mus. 11687), discovered by the American Museum expedition of 1903. (See fig. 115.)

FIGURE 115.—Type (holotype) of *Limnohyops priscus*

Am. Mus 11687. P^1–m^3 left. After Osborn, 1908. One-half natural size.

Characters.—Osborn writes:

> P^1–m^3, 148 (type) to 161 millimeters. Distinguished from the contemporary *Limnohyops laevidens* Cope by its larger size and by the more progressive character of pm^2–pm^3. Second superior premolar obliquely elongate with a very rudimentary tritocone. Large hypocone on m^3.

Etymology.—*priscus*, ancient, in allusion "to the low geological level and primitive characters of this species." (Osborn.)

Present determination.—The species and generic reference are probably valid. (See p. 306.)

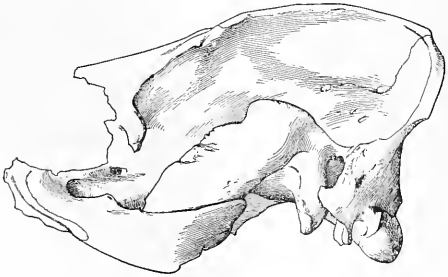

FIGURE 116.—Type (holotype) skull of *Limnohyops matthewi*

Am. Mus. 11684. After Osborn, 1908. One-fourth natural size.

Limnohyops matthewi Osborn, 1908

Cf. *Limnohyops matthewi* Osborn, this monograph, page 308

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 24, p. 602, fig. 6, 1908 (Osborn, 1908.318).

Type locality and geologic horizon.—Grizzly Buttes, Bridger Basin, Wyo.; *Palaeosyops paludosus-Orohippus* zone (Bridger B 2).

Holotype.—A skull (Am. Mus. 11684) lacking the anterior portion and dentition. Discovered by the American Museum expedition of 1903. (See fig. 116.)

Specific characters.—Osborn writes:

> Intermediate in size between *L. laevidens* and *L. monoconus*. M^3 of small size with large hypocone and quadrate inner half Occiput very high and narrow. Cranial portion of skull greatly abbreviated, bringing post-tympanic and postglenoid processes into broad union. Temporal openings subcircular as defined by zygomatic arches.

Etymology.—Named "in honor of Dr. W. D. Matthew, of the American Museum staff." (Osborn.)

Present determination.—The species is probably valid. (See p. 308.)

FIGURE 117.—Type (holotype) skull of *Limnohyops monoconus*

Am. Mus. 11679. After Osborn, 1908. One-fourth natural size.

Limnohyops monoconus Osborn, 1908

Cf. *Limnohyops monoconus* Osborn, this monograph, page 309

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 24, p. 603, fig. 7, 1908 (Osborn, 1908.318).

Type locality and geologic horizon.—Grizzly Buttes, Bridger Basin, Wyo.; *Palaeosyops paludosus-Orohippus* zone (Bridger B 2).

Holotype.—A crushed skull with dentition (Am. Mus. 11679). Discovered by Mr. Quackenbush, of the American Museum expedition of 1903. (See fig. 117.)

Specific characters.—Osborn writes:

> M^3 without hypocone, roundly triangular in form, with broadly extended ectoloph and parastyle. P^2–m^3 150, p^1–m^3 163 millimeters. Condyle to incisive border 510. Occiput very high, cranium relatively elongated, with space (4 millimeters) between post-tympanic and postglenoid processes. Temporal openings as defined by zygomatic arches elongate.

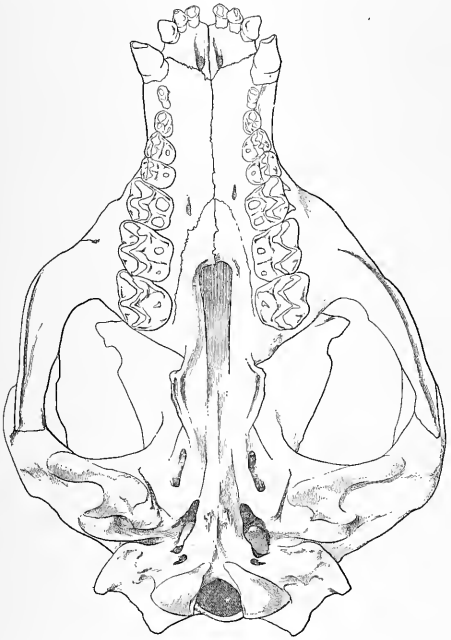

FIGURE 118.—Type (holotype) skull of *Palaeosyops leidyi*

Inferior view. Am. Mus. 1544. After Osborn, 1908. One-fourth natural size.

Etymology.—μόνος, single; κῶνος, cone; named "in reference to the presence of but a single cone on the inner side of the third superior molar, an exceptional condition in the genus *Limnohyops*." (Osborn.)

Present determination.—The specific and generic references are probably valid. (See p. 309.)

Palaeosyops leidyi Osborn, 1908

Cf. *Palaeosyops leidyi* Osborn, this monograph, page 323

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 24, p. 604, fig. 8, 1908 (Osborn, 1908.318).

Type locality and geologic horizon.—Henrys Fork, Bridger Basin, Wyo.; *Uintatherium-Manteoceras-Mesatirhinus* zone (Bridger C 2 to C 4). Discovered by the American Museum expedition of 1893, under Dr. J. L. Wortman.

Holotype.—A well-preserved skull (Am. Mus. 1544) associated with considerable portions of the skeleton. This specimen, which is associated with a considerable portion of the postcranial skeleton, is now mounted in the American Museum, the missing parts having been supplied from other individuals. (See p. 323; Pls. XXVII, L, LXI; and fig. 118.)

Specific characters.—Osborn writes:

> Of larger size; total length of skull 415 millimeters; p^2–m^3, 158; p_2–m_3, 168; diastema behind canines; p^3, p^4 superior, with mesostyles. Barely defined swellings representing the rudiments of osseous frontonasal horns.

Etymology.—Named "in honor of Joseph Leidy, the discoverer of the family and [founder] of the genera *Palaeosyops*, *Titanotherium*, and *Megacerops*." (Osborn.)

Present determination.—The species is probably valid.

Palaeosyops grangeri Osborn, 1908

Cf. *Palaeosyops grangeri* Osborn, this monograph, page 335

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 24, p. 604, fig. 9, 1908 (Osborn, 1908.318).

Type locality and geologic horizon.—Twin Buttes, Bridger Basin, Wyo.; *Uintatherium-Manteoceras-Mesatirhinus* zone (Bridger C 1).

Holotype.—A palate and grinding teeth with portions of the lower jaw and skull (Am. Mus. 12189), American Museum expedition of 1904. (See fig. 119.)

Specific characters.—Osborn writes:

> Exceeding *P. robustus* in certain dental proportions; p^2–m^3, 165 millimeters. Fourth superior premolar enlarged (transverse, 31 mm.). Molars with extremely prominent parastyles and oblique ectolophs.

Etymology.—Named "in honor of Mr. Walter Granger, of the American Museum staff, whose explorations have transformed our knowledge of the Bridger animals." (Osborn.)

Present determination.—The species is probably valid. (See p. 335.)

FIGURE 119.—Type (holotype) of *Palaeosyops grangeri*

Right maxillary with p^1–m^1. Am. Mus. 12189. After Osborn, 1908. One-half natural size.

Palaeosyops copei Osborn, 1908

Cf. *Palaeosyops copei* Osborn, this monograph, page 336

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 24, p. 606, fig. 10, 1908 (Osborn, 1908.318).

Type locality and geologic horizon.—Lone Tree Henrys Fork, Bridger Basin, Wyo.; *Uintatherium-Manteoceras-Mesatirhinus* zone (Bridger D 3).

Holotype.—A series of superior grinding teeth (Am. Mus. 11708). (See fig. 120.)

Specific characters.—Osborn writes:

Of more diminutive size (p^2–m^3, 153 mm.), but the most progressive species of *Palaeosyops* known in the evolution of its superior premolars and molars. Heavy cingula embracing the inner sides of the crowns. A rudimentary tetartocone on p^2.

Etymology.—Named "in honor of the late Prof. E. D. Cope, the describer of *Lambdotherium*, '*Palaeosyops' borealis*, and other species of Eocene titanotheres." (Osborn.)

FIGURE 120.—Type (holotype) of *Palaeosyops copei*

P^1–m^3, right. Am. Mus. 11708. After Osborn, 1908. One-half natural size.

Present determination.—The species is probably valid.

Manteoceras washakiensis Osborn, 1908

Cf. *Manteoceras washakiensis* Osborn, this monograph, page 371

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 24, p. 607, fig. 11, 1908 (Osborn, 1908.318).

Type locality and geologic horizon.—Base of Haystack Mountain, Washakie Basin, Wyo.; summit of *Uintatherium-Manteoceras-Mesatirhinus* zone (Washakie A).

Holotype.—A well-preserved skull with dentition (Am. Mus. 13165). Discovered by Mr. Paul Miller, of the American Museum expedition of 1906. (See fig. 121.)

Specific characters.—Osborn writes:

Distinguished from *M. manteoceras* of a somewhat lower geological level by its more progressive characters, as follows: Canines short, obtuse, recurved; internal lobes of pm^2, pm^3 broadening, with shelf for development of deuterocone; p^2 (ap. 19 mm., tr. 17) with marked external convexities and a reduced external cingulum; p^3 (ap. 19, tr. 25) exhibits the tetartocone fold somewhat more conspicuously than in the most progressive Bridger level D specimens. P^4 (ap. 24, tr. 30) is progressive in transverse measurement and in the development of the tetartocone shelf. The molars are progressive in their large size (m^2 ap. 42, tr. 48), in the strong development of the internal cingulum, and in the elongate ectolophs.

Etymology.—*washakiensis;* "so named because it is a more recent phase, probably characteristic of the Washakie rather than of the Bridger." (Osborn.)

Present determination.—The species and the generic reference are valid. (See p. 371.)

Mesatirhinus Osborn, 1908

Cf. *Mesatirhinus* Osborn, this monograph, page 387

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 24, p. 608, 1908 (Osborn, 1908.318).

Type species and geologic horizon.—*Palaeosyops megarhinus* Earle. Bridger Basin, Wyo., levels Bridger C and D; Washakie Basin, Wyo., levels Washakie A and base of Washakie B.

Specific characters.—Osborn writes:

Titanotheres of small size (skull length 354–425 mm.) typically mesaticephalic, persistent or progressing to dolichocephalic. The horns when present incipient or rudimentary, chiefly borne on the nasals. An infraorbital shelf. Cranium with a sagittal crest. Humerus relatively abbreviated—that is, with reference to *Palaeosyops*—carpus and tarsus narrow, astragalus with elongate neck, the sustentacular distal and cuboidal facets continuous and forming a reversed L (⌋); metapodials slender.

Etymology.—μέσατος, middle; ῥίς, nose; because the length of the snout is moderate compared with that in the allied genus *Dolichorhinus*.

Present determination.—The genus is valid. (See p. 387.)

Mesatirhinus petersoni Osborn, 1908

Cf. *Mesatirhinus petersoni* Osborn, this monograph, page 389

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 24, p. 608, fig. 12, 1908 (Osborn, 1908.318).

Holotype.—A skull with dentition (Am. Mus. 12184) from Cattail Spring, Bridger Basin, Wyo., levels Bridger D 3 and C 3. (See fig. 122.) The species is also recorded from Washakie Basin, Wyo., level Washakie A.

Specific characters.—Osborn writes:

Pm^1–m^3, 156 millimeters; m^1–m^3, 90. Skull length, premaxillaries to condyles 412 (estimated); preorbital facial region more elongate (217). Other characters as in *Mesatirhinus megarhinus*—that is, broad occipital condyles, broad infraorbital shelf on malar, etc.

Comparison of this animal with the type of *M. megarhinus* can leave no doubt that we have to do here with a much more advanced stage of evolution. The skull is longer, the preorbital region especially. The grinding teeth occupy more space, and there is an average advance in all the rectigradations which proves that these differences in form and size are not merely due to fluctuations of size or differences of sex.

FIGURE 121.—Type (holotype) skull of *Manteoceras washakiensis*

Left side. Am. Mus. 13165. After Osborn, 1908. One-fifth natural size.

Etymology.—"The species is named in honor of Mr. O. A. Peterson, now of the Carnegie Museum, whose titanothere collections in the Uinta formation greatly extended our knowledge." (Osborn.)

Present determination.—The species and generic reference are valid. (See p. 389.)

Metarhinus Osborn, 1908

Cf. *Metarhinus* Osborn, this monograph, page 420

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 24, p. 609, 1908 (Osborn, 1908.318).

Type species and geologic horizon.—*Metarhinus fluviatilis* Osborn. Washakie Basin, Wyo., level Washakie B; Uinta Basin, Utah, levels Uinta B 1 and B 2.

FIGURE 122.—Type (holotype) skull of *Mesatirhinus petersoni*

Top view. Am. Mus. 12184. After Osborn, 1908. One-fourth natural size.

Specific characters.—Osborn writes:

> Small titanotheres (skull length 355 to 440 mm.), persistently mesaticephalic. Narrow, abbreviated preorbital region, premaxillary symphysis greatly elongated, and anterior narial openings deeply recessed in side view. Infraorbital shelf present, or wanting (*M. diploconus*); occipital condyles narrow. Grinding teeth subhypsodont; premolars progressive; hypoconulid of m_3 small, conic.

Etymology.—μετά, after; *rhinus* (that is, *Mesatirhinus*). "The name alludes to the somewhat later geological appearance of this genus as compared with *Mesatirhinus*." (Osborn.)

Present determination.—The genus is valid. (See p. 420.)

Metarhinus fluviatilis Osborn, 1908

Cf. *Metarhinus fluviatilis* Osborn, this monograph, page 421

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 24, p. 609, fig. 13, 1908 (Osborn, 1908.318).

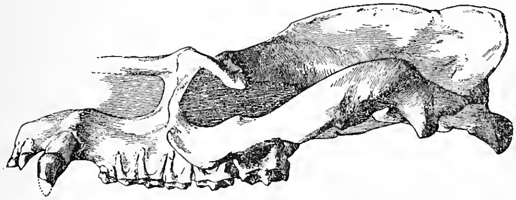

FIGURE 123.—Type (holotype) skull of *Metarhinus fluviatilis*

Left side. Nasals broken off. Am. Mus. 1500. After Osborn, 1908. One-fourth natural size.

Type locality and geologic horizon.—Uinta Basin, Utah; *Metarhinus* zone (Uinta B 1).

Holotype.—A skull (Am. Mus. 1500) discovered by the American Museum expedition of 1894 in horizon B 1 of the Uinta Basin. (See fig. 123.)

Specific characters.—Osborn writes:

> Pm^1–m^3=144 millimeters. A relatively short (355 mm., estimated), broad (200 mm., estimated) skull. Eye sockets small and very prominent. Premaxillary symphysis elongate, grinding teeth subhypsodont, m^3 with a cingulum-hypocone in the type.

Etymology.—*fluviatilis*, fluviatile. "The name is given in allusion to the possibly river-living or amphibious habits of the animal." (Osborn.)

Present determination.—The species and the generic reference are valid. For fuller specific distinctions see page 421.

Metarhinus earlei Osborn, 1908

Cf. *Metarhinus earlei* Osborn, this monograph, page 426

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 24, p. 610, fig. 14, 1908 (Osborn, 1908.318.)

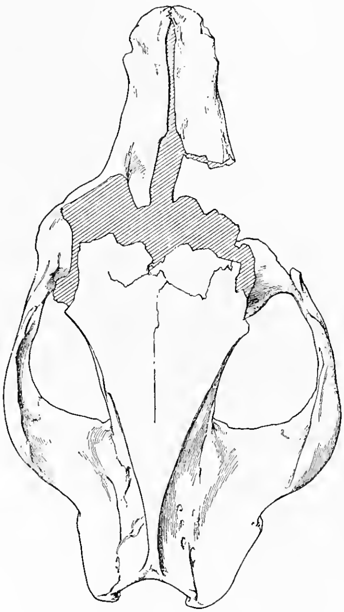

FIGURE 124.—Type (holotype) skull of *Metarhinus earlei*

Top view. Am. Mus. 13166. After Osborn, 1908. One-fourth natural size.

Type locality and geologic horizon.—North side of Haystack Mountain, Washakie Basin, Wyo.; *Metarhinus* zone (Washakie B 1).

Type.—A skull (Am. Mus. 13166) lacking the nasals, American Museum expedition of 1906. (See fig. 124.)

Specific characters.—Osborn writes:

> Pm^1–m^3=167 millimeters. Skull proportions, length 380, breadth 230. Narrow occipital condyles. Extremely elongate premaxillary symphysis. A short sagittal crest. No hypocone on m^3.
>
> This animal is readily distinguished from *M. diploconus* by (1) the infraorbital shelf of the malars; (2) the elongate premaxil-

lary; (3) the absence of a double cone on m^3. In many other respects it resembles *M. diploconus*, especially in its proportions. It is distinguished from *M. megarhinus* by (1) the elongate premaxillary symphysis, correlated with the long, narrow facial region; (2) the narrowness of its occipital condyles. It is distinguished from *M. fluviatilis* by (1) its greatly superior size and (2) the lesser prominence of the orbits.

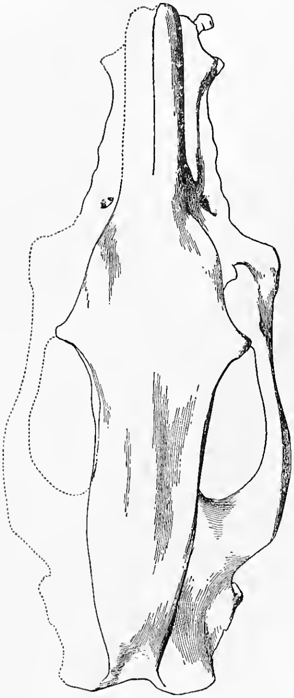

FIGURE 125.—Type (holotype) skull of *Dolichorhinus intermedius*

Top view. Am. Mus. 1837. After Osborn, 1908. One-fourth natural size.

Etymology.—Named "in honor of Charles Earle, the first monographer of the genus *Palaeosyops* and its allies." (Osborn.)

Present determination.—The species is probably valid. (See p. 426.)

Dolichorhinus intermedius Osborn, 1908

Cf. *Dolichorhinus intermedius* Osborn, this monograph, page 405

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 24, p. 611, fig. 15, 1908 (Osborn, 1908.318).

Type locality and geologic horizon.—Uinta Basin, northeastern Utah; *Eobasileus-Dolichorhinus* zone (Uinta B 2).

Holotype.—A skull with dentition (Am. Mus. 1837), discovered by the American Museum expedition of 1894. (See fig. 125.)

Specific characters.—Osborn writes:

> Distinguished from *D. hyognathus* Scott and Osborn by (1) its inferior size (pm^1–m^3 179, m^1–m^3 109 mm.); (2) premolars less progressive, with subconic deuterocones; (3) all cingula less robust; (4) nasals more pointed and less expanded distally; (5) infraorbital shelf of malar relatively narrow.

Etymology.—"The name '*intermedius*' is given because in some characters this species is intermediate between *Mesatirhinus petersoni* and *Dolichorhinus hyognathus*, although on the whole it is much more nearly allied to the latter." (Osborn.)

Present determination.—The generic reference appears certain; the species is probably valid. (See p. 405.)

Telmatherium ultimum Osborn, 1908

Cf. *Telmatherium ultimum* Osborn, this monograph, page 345

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 24, p. 613, fig. 17, 1908 (Osborn, 1908.318).

Type locality and geologic horizon.—Uinta Basin, northeastern Utah; *Diplacodon-Protitanotherium-Epihippus* zone (Uinta C, lower levels).

Holotype.—A well-preserved skull with dentition (Am. Mus. 2060). Discovered by Mr. Peterson, of the American Museum expedition of 1895. (See fig. 126.)

Synonymy.—This species was mentioned by Matthew as *Palaeosyops ultimus* Osborn MS. (see p. 177), but as no type was indicated or specific diagnosis given the name remained a nomen nudum until a type was designated and a diagnosis given by Osborn in 1908.

Specific characters.—Osborn writes:

> P^1–m^3, 226 mm. Lateral superior incisors greatly enlarged, caniniform. $Pm^{2,3,4}$ with internal subcrescentic deuterocone ridges, with faint rudiments of tetartocones posteriorly. Ectolophs of premolars elevated and biconvex.

Etymology.—*ultimus*, latest. "The specific name is given because this appears to be the last representative of the *Palaeosyops-Limnohyops-Telmatherium* group." (Osborn.)

Present determination.—This species is certainly a valid one. The grounds for regarding it as allied to the genus *Telmatherium* are given on page 345.

Telmatherium? altidens Osborn, 1908

Cf. *Telmatherium altidens* Osborn, this monograph, page 351

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 24, p. 614, fig. 18, 1908 (Osborn, 1908.318).

Type locality and geologic horizon.—Uinta Basin, northeastern Utah; *Diplacodon-Protitanotherium-Epihippus* zone (Uinta C).

Holotype.—A lower jaw with dentition (Am. Mus. 2025) discovered by the American Museum expedition of 1895. (See fig. 127.)

Specific characters.—Osborn writes:

> Pm_1–m_3, 330 millimeters; a wide diastema (70 mm.) behind the canines. Canines in male exceptionally elevated (76) and pointed. P_1, p_2 laterally compressed, nonmolariform; p_3, p_4 submolariform; dolichocephalic, anterior portion of face elongate.

FIGURE 126.—Type (holotype) skull of *Telmatherium ultimum*

Side view. Am. Mus. 2060. After Osborn, 1908. One-fifth natural size. The skull has been somewhat deformed by pressure.

The specific characters are more fully given on page 351 of this monograph.

Etymology.—"The specific name refers to the high-crowned piercing canine."

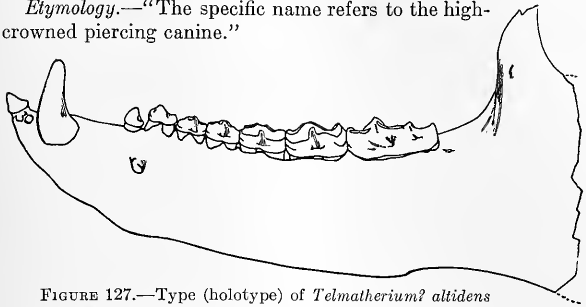

FIGURE 127.—Type (holotype) of *Telmatherium? altidens*
Lower jaw. Am. Mus. 2025. After Osborn, 1908. One-sixth natural size.

Present determination.—The species is probably valid. The generic reference is somewhat less certain. (See p. 351.)

Protitanotherium superbum Osborn, 1908

Cf. *Protitanotherium superbum* Osborn, this monograph, page 379

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 24, p. 615, fig. 19, 1908 (Osborn, 1908.318).

Type locality and geologic horizon.—Uinta Basin, northeastern Utah; *Diplacodon-Protitanotherium-Epihippus* zone (Uinta C); probably higher levels.

Holotype.—A well-preserved lower jaw with dentition (Am. Mus. 2501). (See fig. 128.)

Specific characters.—Osborn writes:

> P_1–m_3, 318 millimeters. Canines in males very robust; p_1 double fanged; postcanine diastema abbreviated; premolar series relatively abbreviated; p_2 with very large talonid and crescentic protoconid; p_3, p_4 with talonid heavy and prominent—that is, submolariform—but no entoconid. M_3 with hypoconulid sharply constricted off at base.

Etymology.—*superbum*, haughty, arrogant. "The name is given in reference to the great size and presumed power of this Uinta titanothere, which considerably exceeds that of the smaller [lower] Oligocene titanotheres." (Osborn.)

Present determination.—The species is probably valid. The generic reference is somewhat less certain. (See p. 379.)

Telmatherium? incisivum Douglass, 1909

Cf. *Sthenodectes incisivus* (Douglass), this monograph, page 354

Original reference.—Carnegie Mus. Annals, vol. 6, No. 2, pp. 305–307, text figs. 1, 2, 3, pl. 13, fig. 1, 1909; "issued November 6, 1909" (Douglass, 1909.1).

Type locality and geologic horizon.—Uinta Basin, Utah, about 3 miles northeast of well 2, from "a thick deposit of sandstone and small gravel evidently of stream origin, near the middle of horizon B." Near the summit of *Eobasileus-Dolichorhinus* zone (Uinta B 2). Discovered by Mr. J. F. Goetschius.

Type.—A skull, lacking the ends of the nasals (Carnegie Mus. 2398). (See figs. 129, 130.)

Specific characters.—Douglass writes:

> I think that this skull represents a different genus from *Telmatherium*, but I prefer to place it provisionally here rather than establish another genus. The skull is broad and short, but not high. The forehead is broad and flat. The premaxillaries are oblique, not transverse. The face is short and concave. Apparently there are vacuities anterior to the orbits. Beneath these there is a rounded angle on the malar, but there is no flattened shelf beneath the orbit. The zygomatic arch is spreading and moderately heavy. The sagittal crest is quite high and thin. The superior wings of the occiput are also thin. The brain case is small; the outward-projecting zygomatic processes of the squamosals shelf-like and broad anteroposteriorly. The paroccipital processes extend laterally and are continuous with the paramastoid processes posterior to the external auditory meatus and the postglenoid process. The anterior portion of the opening of the posterior nares is between the anterior portions of the last molars. The teeth increase quite regularly in size from p^2 to m^2. The premolars have heavy cingula. The deuterocones on p^2 and p^3 are oblong anteroposteriorly, while that on p^4 is high and conical.

Measurements [Douglass]

	Millimeters
Length of skull, basal	490
Width of skull	330
Length of dental series	295
Length of molar-premolar series	212
Transverse diameter of i^1	21
Anteroposterior diameter of i^1	22
Transverse diameter of i^2	27
Anteroposterior diameter of i^2	25
Transverse diameter of i^3	22
Anteroposterior diameter of i^3	25
Transverse diameter of canine	24
Anteroposterior diameter of canine	27
Transverse diameter of p^2	22
Anteroposterior diameter of p^2	20
Transverse diameter of p^3	30
Anteroposterior diameter of p^3	24
Transverse diameter of p^4	37
Anteroposterior diameter of p^4	27
Transverse diameter of m^1	48
Anteroposterior diameter of m^1	44
Transverse diameter of m^2	53
Anteroposterior diameter of m^2	46
Transverse diameter of m^3	53
Anteroposterior diameter of m^3	46

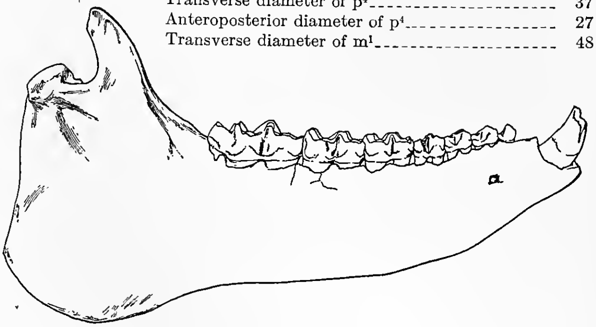

FIGURE 128.—Type (holotype) of *Protitanotherium superbum*
Lower jaw. Am. Mus. 2501. After Osborn, 1908. One-sixth natural size.

Etymology.—*incisivum,* provided with incisors; in allusion to the great size of the superior incisors.

Present determination.—The species probably represents a genus distinct from *Telmatherium* (see p. 353) named *Sthenodectes* by Gregory.

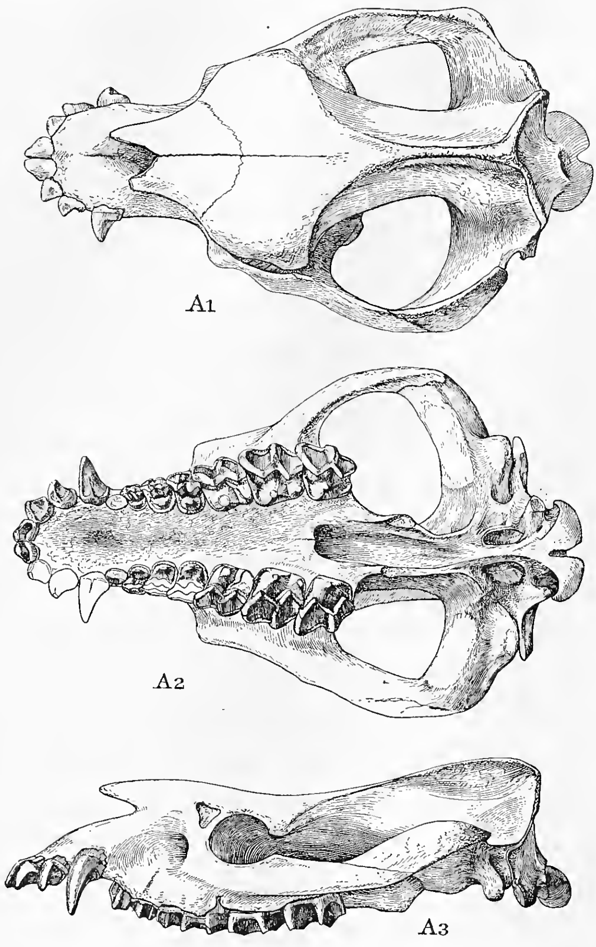

FIGURE 129.—Type (holotype) skull of *Telmatherium? incisivum*

Carnegie Mus. 2398. After Douglass, 1906. A_1, Superior view; A_2, palatal view; A_3, lateral view. One-fifth natural size.

Manteoceras uintensis Douglass, 1909

Cf. *Manteoceras uintensis* Douglass, this monograph, page 372

Type reference.—Carnegie Mus. Annals, vol. 6, No. 2, pp. 307–310, text figs. 4, 5, pl. 13, fig. 4, 1909; "issued November 6, 1909" (Douglass, 1909.1).

Type locality and geologic horizon.—Uinta Basin, Utah, about 5 miles northeast of well 2, from "gray sandstone in red Uinta beds. Lower portion of horizon C." *Diplacodon-Protitanotherium-Epihippus* zone (Uinta C).

Type.—A skull lacking the posterior portion (Carnegie Mus. 2388). (See figs. 131 and 132.)

Specific characters.—Douglass writes:

> The skull is high, the forehead broad, and the zygomatic arches spreading. The premaxillary region as seen from the front is broad, though the incisors are only moderately large. The canines are directed outward. The free nasals are short and moderately broad. Apparently the infraorbital foramen is not excessively large. The malar is rounded beneath the orbit and has no protuberance or shelf. The zygomatic arch is not very heavy and is only moderately deep anterior to the glenoid articular surface. It is not nearly so heavy as in *Telmatherium ultimum.* The opening of the posterior nares extends forward to the middle of the second molars. Their border is rounded and thickened.
>
> The incisors are moderately large but not cupped. They are arranged in an oblique line about halfway between a transverse and anteroposterior direction. The crowns of i^1 and i^2 are low. The anterior faces are very convex. There are two posterior flattened surfaces separated by a rounded ridge. There are no cups, but the posterior portion forms a kind of ledge or keel. I^3 is higher and is directed more downward. The posterior portion is flattened, and there is a low flat ledge behind the conical cusp. The canine has a moderately high curved crown, on which there are antero-internal and postero-external ridges, passing downward from the base to the apex. There is also a narrow postero-internal ledge.
>
> Unless the skull is more crushed laterally than it appears to be, there is a sudden contraction posterior to the canine, so that the first two premolars are much nearer to the median line of the palate than are the canines. The diastema between the canine and p^1 is about 3 centimeters in length.
>
> P^1 is a simple oblong conical tooth, which has a small antero-internal depression, and a small ridge passes backward from the apex to the posterior portion of the rudimentary keel. P 2, 3, and 4 have low cusps. The teeth increase nearly uniformly in width and size from p^2 to the last molar. The two outer elements in each are well defined and are subequal in size, although the anterior cusp is slightly the larger. The internal cusp on p^2 is small, oblong anteroposteriorly, and is placed far back. The internal cusp on p^3 is much larger and is crescent-shaped. On p^4 it is more nearly conical. There are rudimentary cingula on the inner faces of the last three premolars. The postero-internal cusp on m^3 is represented by a low crescent-shaped ridge.

Measurements [Douglass]

	Millimeters
Length of skull, anterior portion to glenoid	430
Length of dental series	356
Length of molar-premolar series	247
Length of premolar series	106
Length of molar series	141
Transverse diameter of i^1	16
Anteroposterior diameter of i^1	18
Transverse diameter of i^2	16
Anteroposterior diameter of i^2	18
Transverse diameter of i^3	20
Anteroposterior diameter of i^3	22
Transverse diameter of canine	22
Anteroposterior diameter of canine	26

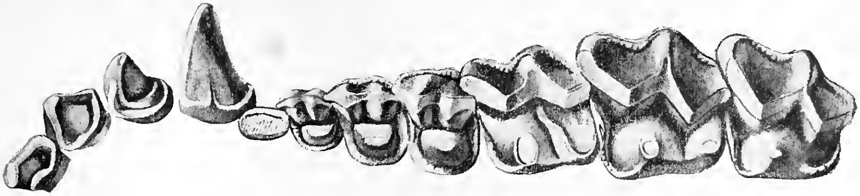

FIGURE 130.—Type (holotype) of *Telmatherium? incisivum*

Left upper teeth, crown view. After Douglass, 1909. One-half natural size.

	Millimeters
Transverse diameter of p^1	12
Anteroposterior diameter of p^1	22
Transverse diameter of p^2	21
Anteroposterior diameter of p^2	28
Transverse diameter of p^3	28
Anteroposterior diameter of p^3	27
Transverse diameter of p^4	33
Anteroposterior diameter of p^4	30
Transverse diameter of m^1	44
Anteroposterior diameter of m^1	40
Transverse diameter of m^2	53
Anteroposterior diameter of m^2	55
Transverse diameter of m^3	56
Anteroposterior diameter of m^3	51
Width of palate between canines?	68
Width of palate between first premolars	54
Width of palate between last molars	83

Etymology.—uintensis, in reference to the Uinta Basin.

Present determination.—The generic reference to *Manteoceras* appears to be correct. The species is a valid one.

Dolichorhinus heterodon Douglass, 1909

Cf. *Dolichorhinus heterodon* Douglass, this monograph, page 416

Original reference.—Carnegie Mus. Annals, vol. 6, No. 2, pp. 310–311, text figs. 6, 7, pl. 13, fig. 3, 1909; "issued November 6, 1909" (Douglass, 1909.1).

Type locality and geologic horizon.—Uinta Basin, Utah, 6 or 7 miles northeast of well 2; from "upper part of horizon B or lower part of horizon C"; *Eobasileus-Dolichorhinus* zone (Uinta B 2).

Type.—A skull lacking the front teeth and both zygomatic arches (Carnegie Mus. 2340). (See figs. 133 and 134.) Discovered by Mr. J. F. Goetschius.

FIGURE 132.—Type (holotype) of *Manteoceras uintensis*

Upper teeth. Carnegie Mus. 2388. After Douglass, 1909. One-third natural size.

Specific characters.—Douglas writes:

> The skull is long, narrow, and moderately high. The face is short and the brain case long. The free nasals are long, the posterior opening of the anterior nares extending well backward toward the orbit. The lower borders of the nasals approach each other, but this is probably in part due to lateral crushing.

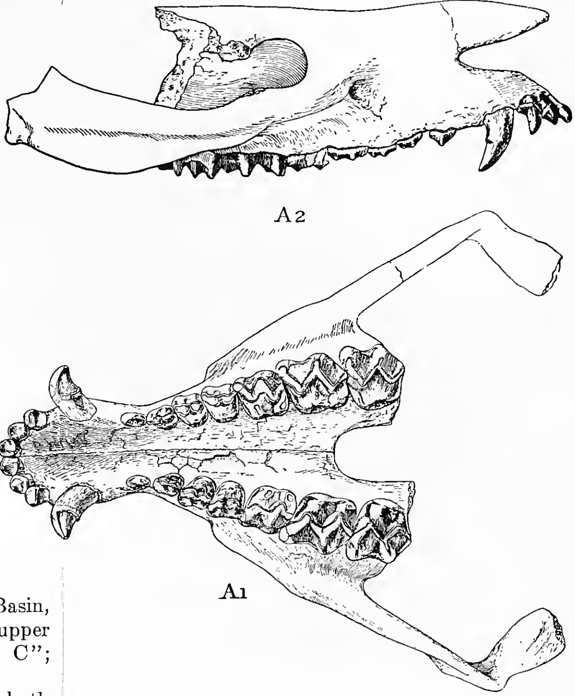

FIGURE 131.—Type (holotype) skull of *Manteoceras uintensis*

Carnegie Mus. 2388. After Douglass, 1909. A1, Palatal view; A2, view of right side. One-fifth natural size.

> The infraorbital foramen is large. The infraorbital shelf is represented by a protuberance, which is thickened on the free outer surface. If there were horn cores above the orbit they were very small. The long brain case was apparently arched from before backward, the posterior descent to the crest of the occiput being very steep, though this may be somewhat exaggerated by crushing. The occipital condyles are very large. The median portion of the occiput above them is convex, while above this there is a large concavity. The postglenoid processes are not excessively large.
>
> The premolars are small, the last being very decidedly smaller than the first molar. The first premolar is not preserved, but it was evidently a simple tooth. In the last three premolars there is a lobe or buttress on the antero-external portion of the tooth, which makes the anterior margin oblique.

The inner cusps (deuterocones) are low with rounded summits. They are more nearly opposite the postero-external than the antero-external cusp. There are inner cingula on p^3 and p^4. The antero-internal cusp in m^2 is quite high and m^1 conical. The postero-internal cusp is due simply to an increase in height of the cingulum.

Measurements

	Millimeters
Total length of top of skull	500
From anterior orbit to front of nasals	160
Width of occiput	128
Height of occiput	140
Length of molar-premolar series	190
Length of premolar series	75
Length of molar series	115
Length of p^2	20
Width of p^2	16
Length of p^3	21
Width of p^3	20
Length of p^4	24
Width of p^4	27
Length of m^1	34
Width of m^1	35
Length of m^2	46
Width of m^2	42
Length of m^3	48
Width of m^3	42

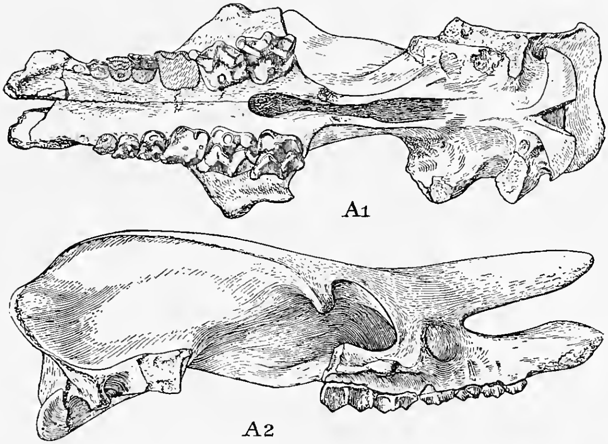

FIGURE 133.—Type (holotype) skull of *Dolichorhinus heterodon*

Carnegie Mus. 2340. After Douglass, 1909. A$_1$, Palatal view; A$_2$, right lateral view. One-fifth natural size.

Etymology.—ἕτερος, different, or various; ὀδούς, tooth. Allusion not clear; name possibly given because no two teeth in the superior premolar-molar series are alike.

Present determination.—The form is closely allied to *D. intermedius,* of which it may be the successor. Its specific separateness is somewhat doubtful.

Dolichorhinus longiceps Douglass, 1909

Cf. *Dolichorhinus longiceps* Douglass, this monograph, page 406

Original reference.—Carnegie Mus. Annals, vol. 6, No. 2, pp. 312–313, text fig. 8; pl. 13, fig. 2; pls. 14, 15, 1909; "issued November 6, 1909" (Douglass, 1909.1).

Type locality and geologic horizon.—Uinta Basin, Utah, "about 1½ miles east of well No. 2," from "the lowest level at which fossils were found in horizon 'B' of the Uinta, about 700 feet below the bottom of the Uinta red beds (horizon 'C')." *Eobasileus-Dolichorhinus* zone (Uinta B 2).

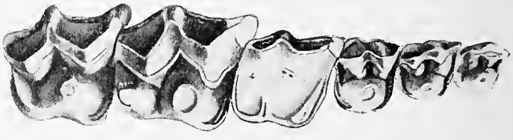

FIGURE 134.—Type (holotype) *of Dolichorhinus heterodon*

Upper premolar series. Carnegie Mus. 2340. After Douglass, 1909. Slightly less than one-half natural size.

Type.—A skull lacking the incisors, part of the dentition, and the basioccipital region (Carnegie Mus. 2347). (See figs. 135 and 136.)

Specific characters.—Douglass writes:

> This skull in general outline is very much like that of *Dolichorhinus hyognathus,* though broader. In describing it I prefer to point out the characters which distinguish it from that species. Apparently it is somewhat broader proportionally than that of *D. hyognathus.* The skull is somewhat crushed, but it evidently was not flattened on top. The present specimen had no heavy protuberances or horn cores, though there may have been the slightest beginning of such. There is a rather narrow shelf, or lateral expansion of the malars, with rounded outer borders, beneath the anterior portion of the orbit, but it is not like the infraorbital process of *D. hyognathus.* The postorbital hook does not appear to have been long or prominent. Evidently the zygomatic arches extend laterally outward more than in the last-named species; the postglenoid processes are not nearly so heavy; the palate is broader; the top of the cranium, though there is no zygomatic arch, becomes narrower anterior to the crest of the occiput.

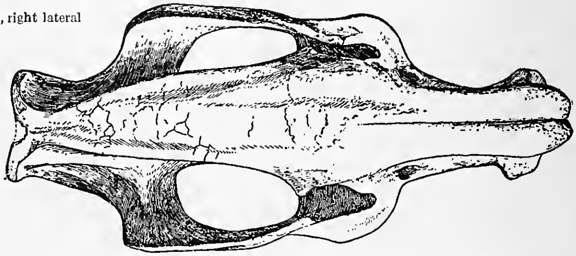

FIGURE 135.—Type (holotype) skull of *Dolichorhinus longiceps*

Top view. Carnegie Mus. 2347. After Douglass, 1909. One-sixth natural size.

The teeth are very similar to those of *Dolichorhinus heterodon*, so much so that, if only the teeth were known, they might be referred to that species. They, as well as the skull, are larger.

Measurements [Douglass]

	Millimeters
Length of top of skull	590
Length of free nasals	150
Length of skull posterior to anterior portion of orbit	393
Width of skull at glenoid articular surface	267
Width at infraorbital shelves	247
Length of molar-premolar series	192
Length of premolar series	88
Length of molar series	112
Length of p^1	15
Width of p^1	11
Length of p^2	20
Width of p^2	20
Length of p^3	24
Width of p^3	25
Length of p^4	27
Width of p^4	31
Length of m^1	30
Width of m^1, about	37
Length of m^2	37
Width of m^2	44
Length of m^3, about	41
Width of m^3, about	43

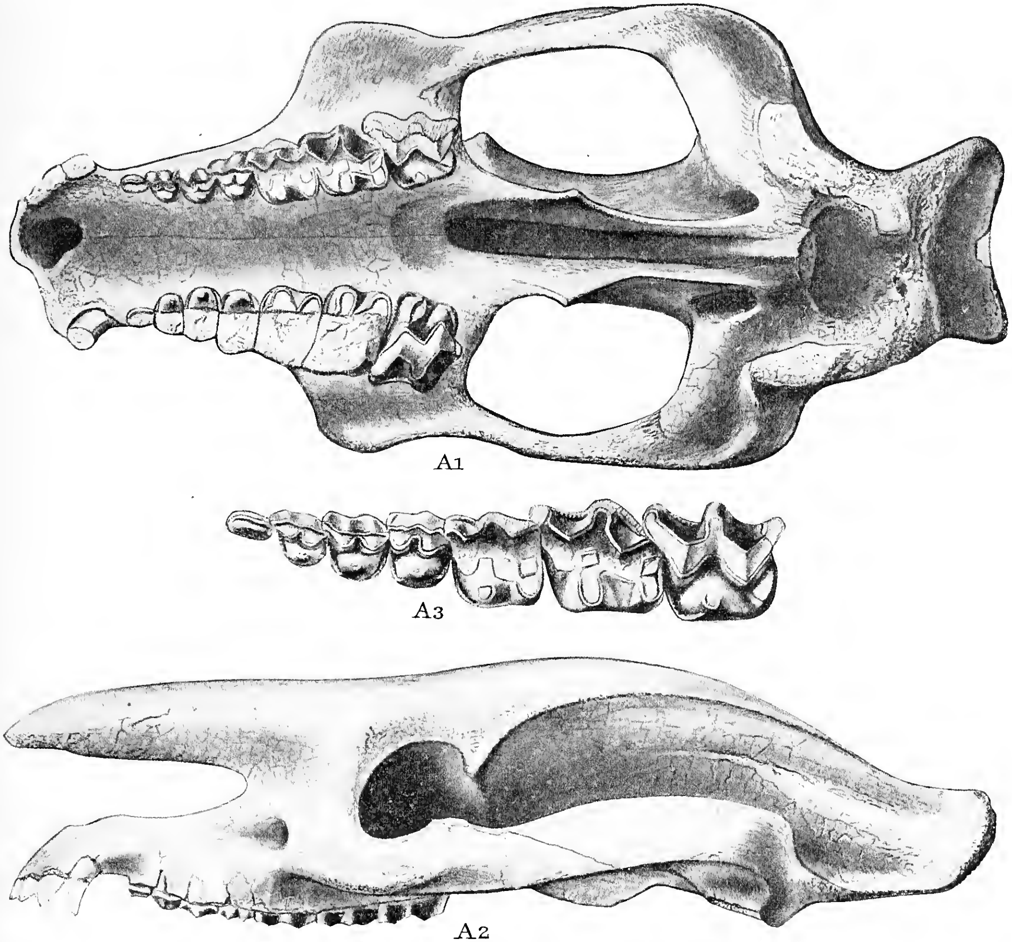

FIGURE 136.—Type (holotype) of *Dolichorhinus longiceps*

Carnegie Mus. 2347. After Douglass, 1909. A_1, Palatal view of skull, somewhat less than one-third natural size; A_2, left lateral view of skull, somewhat less than one-third natural size; A_3, crown view of right upper premolar series, one-half natural size.

Etymology.—longiceps, in allusion to the long skull.

Present determination.—For the reasons stated above it appears that this form is connected with the typical *D. hyognathus* by a skull of intermediate characters. Its status as a distinct species is therefore somewhat doubtful.

Sthenodectes Gregory, 1912

Cf. *Sthenodectes*, this monograph, page 353

Original reference.—Science, new ser., vol. 35, No. 901, p. 545, April, 1912 (Gregory, 1912.1).

Subsequent reference.—Riggs, New or little known titanotheres from the lower Uinta formations: Field Mus. Nat. Hist. Pub. 159, Geol. ser., vol. 4, No. 2, p. 38, June, 1912 (Riggs, 1912.1).

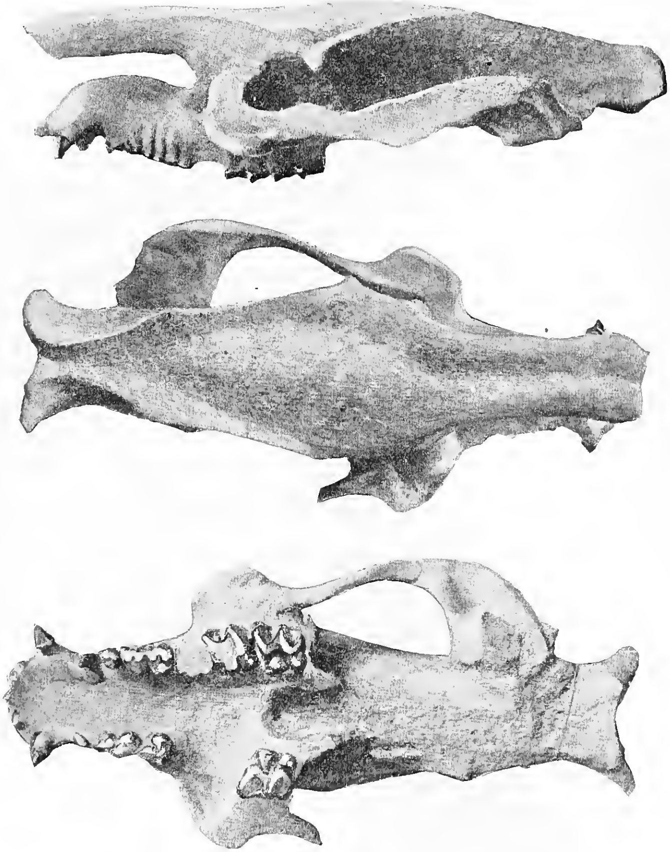

FIGURE 137.—Type (holotype) skull of *Mesatirhinus superior*

Field Mus. 12188. After Riggs, 1912. Side, top, and palatal views. Less than one-fourth natural size.

Type species.—*Telmatherium? incisivum* Douglass.

Generic characters.—Gregory writes:

> This genus is distinguished from *Telmatherium ultimum* Osborn by the following assemblage of characters: (1) The incisors are far larger and more advanced in evolution, i^1 being closely appressed to its fellow in the median line, with anterior face elongate, antero-internal tip blunt, median basin large, posterior wall or cingulum very massive, i^2, i^3 extremely large with low recurved tips and very heavy posterior cingula. (2) The postcanine diastema is reduced or absent. (3) Superior premolars 2, 3, 4 are much more advanced than in *T. ultimum*, having very heavy internal cingula, pronounced external cingula, high slender internal cusps (deuterocones); p^2 especially is in a relatively advanced stage as compared with *T. ultimum*. (4) The least tranverse diameters of p^4 and of the anterior lobe of m^1 are greater, that of m^3 much less, than in *T. ultimum*. (5) The basicranial region differs in many details, such as the apparent junction of the postglenoid and post-tympanic processes below the auditory meatus. (6) The occiput is low, with a sharp, long sagittal crest. (7) The forehead is relatively wide. (8) The nasals taper distally.
>
> From *Manteoceras* (especially *M. uintensis*) the genus under consideration is distinguished by (1) the form and size of the incisors and canines, (2) the much more advanced stage of evolution of the premolars, (3) the shorter anteroposterior diameter of m^2, (4) the reduction of the postcanine diastema, (5) the arched and spreading zygomata, etc.
>
> From *Dolichorhinus* and *Mesatirhinus* it is separated by the shortness and relative breadth of the skull, the great size of the incisors, the relatively heavy zygomata, and many other details.

Etymology.—σθένος, strength, δηκτής, a biter; in allusion to the great power and development of the incisors and canines.

Present determination.—A valid genus, offshoot of the typical *Telmatherium* phylum.

Mesatirhinus superior Riggs, 1912

Cf. *Dolichorhinus superior* (Riggs), this monograph, page 405

Original reference.—Field Mus. Nat. Hist. Pub. 159, Geol. ser., vol. 4, No. 2, p. 26, pl. 6, June, 1912 (Riggs, 1912.1).

Type locality and geologic horizon.—White River divide, northeastern Utah; upper "*Metarhinus* sandstones," summit of *Metarhinus* zone (Uinta B 1). (See fig. 137.)

Holotype.—A skull (Field Mus. 12188).

Specific characters.—Riggs writes:

> Skull 485 by 255 millimeters, molar series 182 millimeters, nasals free to a point over last premolar, infra-orbital process present, arches slender anteriorly, nasals infolded at margins, sagittal area expanded, canines small, p^2 and p^3 oblique to axis of series. Molars relatively small, strong hypocone on m^3, posterior nares opening opposite the anterior margin of last molar.

Etymology.—*superior*, in allusion to its large size and high stage of evolution.

Present determination.—This is a valid stage immediately ancestral to the *Dolichorhinus* stage.

Metarhinus riparius Riggs, 1912

Cf. *Metarhinus riparius*, this monograph, page 429

Original reference.—Field Mus. Nat. Hist. Pub. 159, Geol. ser., vol. 4, No. 2, p. 28, pl. 7, fig. 1, June, 1912 (Riggs, 1912.1).

Type locality and geologic horizon.—White River canyon and divide, northeastern Utah; "entire upper *Metarhinus* beds," base of *Metarhinus* zone (Uinta B 1).

FIGURE 138.—Type (holotype) skull of *Metarhinus riparius*

Field Mus. 12186. After Riggs, 1912. About one-fourth natural size.

Holotype.—Skull (Field Mus. 12186). (See fig. 138.)

Paratype ("cotype").—"Lower jaws" (Riggs, pl. 7, figs. 2, 3).

Specific characters.—Riggs writes:

> Skull long and narrow (405 by 210 mm.). Anterior cranial region expanded, sagittal crest short. Interorbital region relatively narrow and rounded, rudimentary horn cores above orbits, canines large, molar series short (88–93 mm.), hypocone usually present on m^3, mandible straight in the ramus, lower canine long and recurved.

Etymology.—*riparius*, riparian, in allusion to the nature of the habitat.

Present determination.—A valid species in the *Metarhinus* phylum.

Metarhinus cristatus Riggs, 1912

Cf. *Metarhinus cristatus*, this monograph, page 429

Original reference.—Field Mus. Nat. Hist. Pub. 159, Geol. ser., vol. 4, No. 2, p. 28, pl. 9, fig. 3, June, 1912 (Riggs, 1912.1).

Type locality and geologic horizon.—White River canyon, northeastern Utah; "upper *Metarhinus* beds," lower section of *Metarhinus* zone (Uinta B 1).

Holotype.—A skull, lacking the muzzle (Field Mus. 12194). (See fig. 139.)

Specific characters.—Riggs writes:

> Skull length approximately 380 millimeters, molar series 94 millimeters. Frontal region broad, sagittal crest long and high, molars short-crowned, no hypocone on m^3, arches relatively heavy. Represented by a single skull lacking the nasals and the premaxillaries.

Etymology.—*cristatus*, crested; in allusion to the high sagittal crest.

Present determination.—A valid stage in the *Metarhinus fluviatilis* phylum.

Dolichorhinus fluminalis Riggs, 1912

Cf. *Dolichorhinus fluminalis*, this monograph, page 417

Original reference.—Field Mus. Nat. Hist. Pub. 159, Geol. ser., vol. 4, No. 2, p. 33, pl. 10, figs. 1–3, June, 1912 (Riggs, 1912.1).

Type locality and geologic horizon.—Uinta Basin, northeastern Utah; "*Amynodon* sandstone," summit of *Eobasileus-Dolichorhinus* zone (Uinta B 2).

Holotype.—A fine skull, Field Mus. 12205; collector M. G. Mehl. (See fig. 140.)

Specific characters.—Riggs writes:

> Skull small and narrow (520 by 230 mm.), facial region much shorter than cranial, nasals narrow and slightly tapering, posterior nares opening between hamular processes, postorbital process of jugal back of the last molar, molar-premolar series 171 millimeters; canines short and recurved, incipient horn cores in the form of high, narrow ridges. * * *
>
> The skull is slender, light and complex in structure as compared with the massive and rounded *D. cornutus*. The molar teeth are no longer in the crown than those of *Metarhinus earlei*. The jugal process of the maxillaries arises at a point back of the last molar rather than beside it as in *D. longiceps*. There is no offset in the palate between the last molars, though the primary position of the posterior narial opening is marked by a slight rugosity.

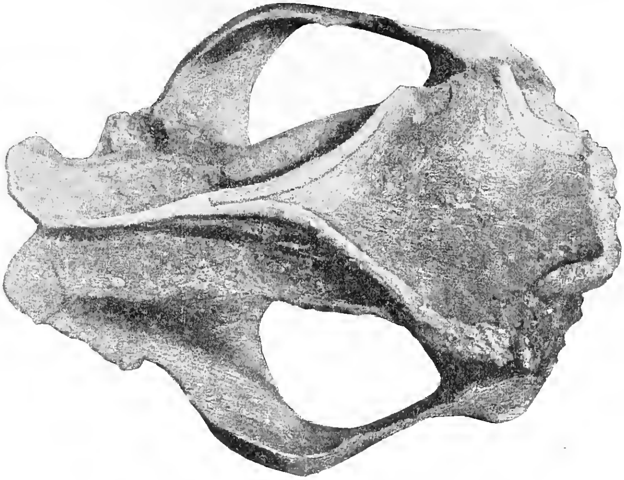

FIGURE 139.—Type (holotype) skull of *Metarhinus cristatus*

Field Mus. 12194. After Riggs, 1912. One-third natural size.

> *D. fluminalis* is most nearly related to *D. intermedius*. The skull exceeds in length the type of that species in the ratio of 520:465 millimeters. The molar teeth are proportionately much smaller; the series measures relatively 99:109 millimeters.

The position of the posterior narial opening is the most distinctive character, appearing much farther back in *D. fluminalis* than in any other described species. The two forms agree more closely in the tapering form of the nasals and in the narrow recess separating them from the maxillaries.

Etymology.—*fluminalis*, pertaining to rivers; in allusion to the habitat.

Present determination.—A stage in the *Dolichorhinus* phylum, not very clearly distinguished specifically from other progressive stages.

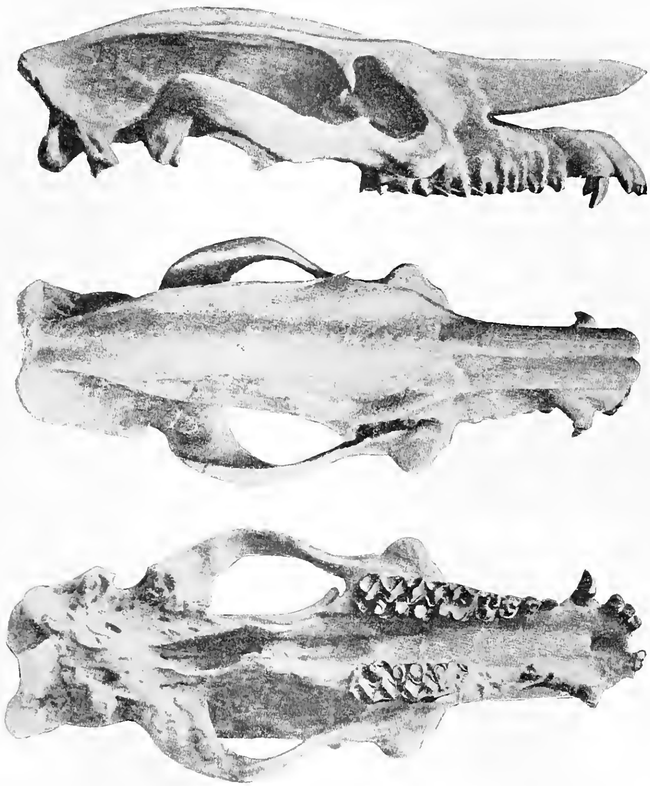

FIGURE 140.—Type (holotype) skull of *Dolichorhinus fluminalis*

Field Mus. 12205. After Riggs, 1912. Side, top, and palatal views. About one-fifth natural size.

Rhadinorhinus Riggs, 1912

Cf. *Rhadinorhinus*, this monograph, page 430

Original reference.—Field Mus. Nat. Hist. Pub. 159, Geol. ser., vol. 4, No. 2, p. 36, June, 1912 (Riggs, 1912.1).

Type species.—*Rhadinorhinus abbotti* Riggs.

Generic characters.—Riggs writes:

> Titanotheres with slender skulls, nasals deeply recessed laterally and tapering, molars long-crowned, $p^{2, 3, 4}$ subrectangular, a wide median area between the incisors, no infra-orbital process. The name *Rhadinorhinus* alludes to the tapering nasals which characterize this genus.

Etymology.—ῥαδινός, slender; ῥίς, nose.

Present determination.—Probably a valid stage, an extreme offshoot of the *Metarhinus* phylum. (See p. 17, fig. 15.)

Rhadinorinus abbotti Riggs, 1912

Cf. *Rhadinorhinus abbotti*, this monograph, page 430

Original reference.—Field Mus. Nat. Hist. Pub. 159, Geol. ser., vol. 4, No. 2, p. 36, pl. 11, figs. 2, 3, June, 1912 (Riggs, 1912.1).

Type locality and geologic horizon.—Northeastern Utah; "upper *Metarhinus* beds," center of *Metarhinus* zone (Uinta B 1).

Holotype.—A fine skull (Field Mus. 12179). (See fig. 141.)

Specific characters.—Riggs says:

> Length of skull 435 millimeters, molar-premolar series 168 millimeters, nasals shorter than premaxillaries, thickened at suture, and tapering toward a terminal rugosity. Arches slender, posterior nares open opposite middle of m^2. Sagittal crest long and narrow. Hypocone of m^3 vestigial, diastema short.

Etymology.—Named in honor of Mr. J. B. Abbott, of the Field Museum of Natural History.

Present determination.—A valid specific stage.

Eotitanops gregoryi Osborn, 1913

Cf. *Eotitanops gregoryi*, this monograph, page 291

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 32, p. 407, fig. 1; p. 411, fig. 4B, September 2, 1913 (Osborn, 1913.400).

Type locality and geologic horizon.—Type from Wind River Basin, Wyo., 100 feet above Alkali Creek "red stratum." *Lambdotherium-Eotitanops-Coryphodon* zone (Wind River B, "Lost Cabin").

Type.—An incomplete lower jaw, containing the right lower premolar-molar series (p_2–m_3), also fragments of left maxilla containing m^2, m^3 (Am. Mus. 14889). (See fig. 142.)

Specific characters.—Osborn writes:

> Of inferior size. P_2–m_3, 78.4 millimeters; m_{1-3}, 49; p_{2-3} with the internal cusps, paraconid and metaconid, consisting of rectigradations of most rudimentary stage; hypoconulid of m_3 very small; m^3 with a single internal cone, no hypocone.

This very sharply defined species may represent a persistent primitive stage, because its recorded (Granger) geologic level, 100 feet above the Alkali Creek "red stratum," is higher than that of the typical and relatively progressive *E. borealis.* Its primitive condition is shown in the comparison of the premolars with the same teeth in *E. borealis* (Cope) and *E. princeps* Osborn.

The third inferior premolar is seen to be much less progressive than in *E. princeps* or even in *Lambdotherium;* the other premolars are also very primitive. P_2 short, compressed, with a very rudimentary hypoconid; p_3 laterally compressed, hypoconid distinct, paraconid, metaconid, and entoconid extremely rudimentary rectigradations. In the molar teeth, m_{1-3}, the metastylid and entostylid are also in an extremely rudimentary or rectigradational stage. In m_3 the hypoconulid is small, subconic, external in position.

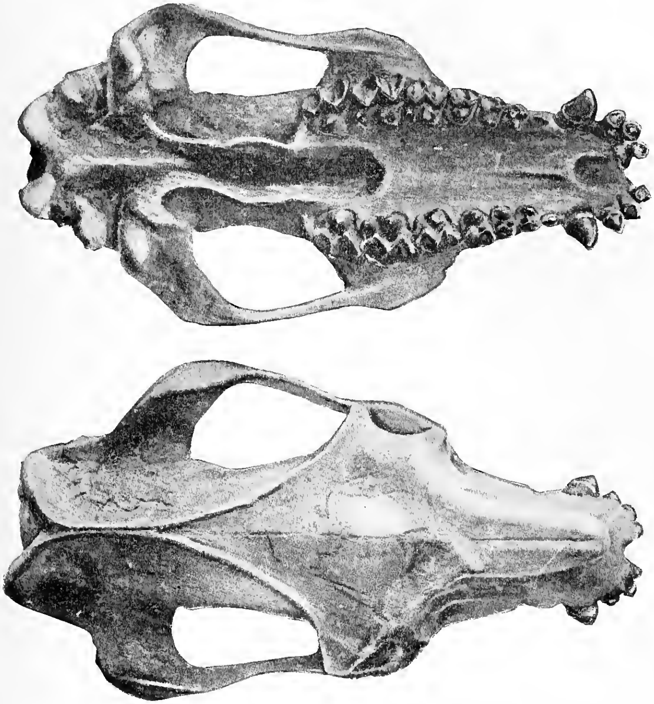

FIGURE 141.—Type (holotype) skull of *Rhadinorhinus abbotti*

Field Mus. 12179. After Riggs, 1912. About one-fourth natural size.

Etymology.—Named in honor of Dr. W. K. Gregory, of the American Museum of Natural History, the colleague of the author in the preparation of this monograph.

Present determination.—A valid specific stage.

Eotitanops princeps Osborn, 1913

Cf. *Eotitanops princeps,* this monograph, page 295

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 32, pp. 410–411, fig. 4E, September 2, 1913 (Osborn, 1913.400).

Type locality and geologic horizon.—Wind River Basin, Wyo.; *Lambdotherium-Eotitanops-Corphyodon* zone (Wind River B, "Lost Cabin," exact level not recorded). J. L. Wortman, collector.

Type.—Am. Mus. 296, including lower jaw, femur, humerus, right manus, one cervical, three dorsal, and one caudal vertebrae. (See figs. 143, 144.)

Specific characters.—Osborn writes:

> Of still larger size, p_2–m_3 105 millimeters (estimated). Inferior premolar teeth somewhat more complicated, as shown in the type specimen. P_2 with elevated, distinct, but very rudimentary paraconid and metaconid; entoconid very rudimentary; talonid narrow. P_3, paraconid quite distinct, elevated; metaconid small, distinct; entoconid rudimentary; talonid broad. P_4, talonid broad; entoconid distinct. Hypoconulid of m_3 rounded, more robust. Ramus, larger and more robust.
>
> The more advanced development of the premolar rectigradations, the increased size of the teeth and of the jaw, the larger size of the hind feet in the referred specimen (Am. Mus. 4902) combine to distinguish this specimen as a mutation or subspecific stage between *E. borealis* and *E. major.*

Etymology.—*princeps,* chief; in allusion to its comparatively large size.

Present determination.—A valid specific stage.

Eotitanops major Osborn, 1913

Cf. *Eotitanops major,* this monograph, page 296

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 32, pp. 412–413, figs. 5D, 6, September 2, 1913 (Osborn, 1913.400).

Type locality and geologic horizon.—From Alkali Creek, Wind River Basin, Wyo.; *Lambdotherium-Eotitanops-Coryphodon* zone (Wind River B, "Lost Cabin"; exact level unrecorded).

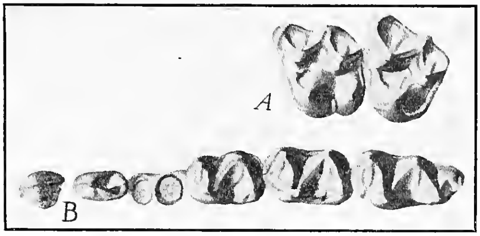

FIGURE 142.—Type (holotype) teeth of *Eotitanops gregoryi*

Am. Mus. 14889. After Osborn, 1913. A, Left m^2–m^3; B, right lower premolar series (p_2–m_3). Natural size.

Type.—Am. Mus. 14894, a left median metatarsal; also the distal end of the tibia. (See fig. 145.)

Specific characters.—Osborn writes:

> Of superior size, Mts III 104 millimeters longitudinal, 16 transverse, index 15.

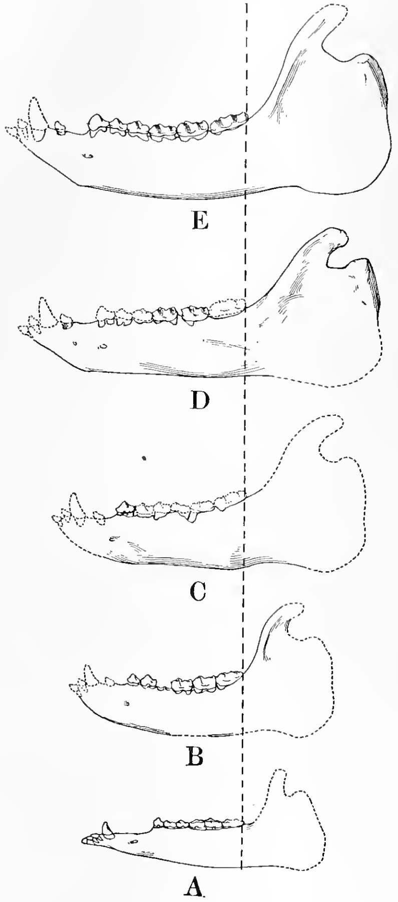

FIGURE 143.—Lower jaws of *Lambdotherium* and *Eotitanops*

A, *Lambdotherium popoagicum;* B, *Eotitanops gregoryi* (holotype); C, *Eotitanops brownianus;* D, *Eotitanops borealis;* E, *Eotitanops princeps* (type). One-fourth natural size. After Osborn, 1913.

> This ill-defined species indicates the existence in Wind River times of a relatively large, short-footed titanothere, which is possibly ancestral to some of the short-footed middle Eocene types. The comparative measurements with the median metatarsal of *E. borealis* are as follows:

	E. borealis	E. major
	Mm.	*Mm.*
Median metarsal, III, length	86	104
Width of shaft	13	16
Index	15	15
Tibio-astragalar facet, transverse	21	25

Etymology.—*major,* larger; in allusion to the superior size of this animal compared with others of the same genus.

Present determination.—A valid specific stage.

Lambdotherium priscum Osborn, 1913

Cf. *Lambdotherium priscum,* this monograph, page 286

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 32, pp. 413–414, figs. 7A, 9A, September 2, 1913 (Osborn, 1913.400).

Type locality and geologic horizon.—Wind River Basin, 3 miles east of Lost Cabin, Wyo.; *Lambdotherium-Eotitanops-Coryphodon* zone (Wind River B). Granger, American Museum expedition, 1905.

Type.—Am. Mus. 12822, anterior portion of jaw with p_2–p_4, m_1 of right side, also p_3, m_1, m_2 of left side. Rami fragmentary. (See fig. 146.)

Specific characters.—Osborn gives the following description:

> P_2–p_4, 25 millimeters. Second and third lower premolars extremely simple, with rudimentary paraconid. Metaconid of p_3 rudimentary, placed very low upon slope of protoconid; talonid narrow, depressed, with cingular rudiment of entoconid.
>
> The extremely simple or primitive structure of the second lower premolar clearly distinguishes this stage.
>
> A referred specimen (Am. Mus. 14908) is slightly more advanced in the structure of the second lower premolar, but is still much more primitive than the type of *L. popoagicum.*
>
> This specimen was found in the Wind River Basin, Dry Muddy Creek, 18 miles up (Granger, Am. Mus. expedition, 1909).
>
> The measurements of these two specimens are:

	Type (No. 12822)	Referred specimen (No. 14908)
	Mm.	*Mm.*
Second to fourth premolar, inclusive	25	--------
Third premolar, anteroposterior	8	8
Third premolar, transverse	5	5
Fourth premolar, anteroposterior	9	8. 5
Fourth premolar, transverse	6. 5	--------
First molar, anteroposterior	11. 5	10
First molar, transverse	7. 5	7
First to third molar, inclusive	--------	37

Etymology.—*priscus,* ancient; in allusion to the primitive character of the species.

Present determination.—A valid specific stage.

Lambdotherium progressum Osborn, 1913

Cf. *Lambdotherium progressum,* this mongraph, page 286

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 32, p. 415, fig. 8, September 2, 1913 (Osborn, 1913.400).

Type locality and geologic horizon.—Wind River Basin, Wyo. (Alkali Creek, Buck Spring); *Lambdotherium-Eotitanops-Coryphodon* zone (Wind River B). Granger, American Museum expedition, 1909.

Type.—Am. Mus. 14917. Right ramus and symphysis of jaw containing p_2–m_2 of right side, also left canine. (See fig. 147.)

Specific characters.—Osborn writes:

> P_2–p_4 16.5 millimeters. Second, third, and fourth lower premolars progressive. Rudiment of metaconid on p_2. P_3 with elevated metaconid subequal with protoconid, broad talonid with rudimentary entoconid. P_4 with bifid metaconid and distinct entoconid.

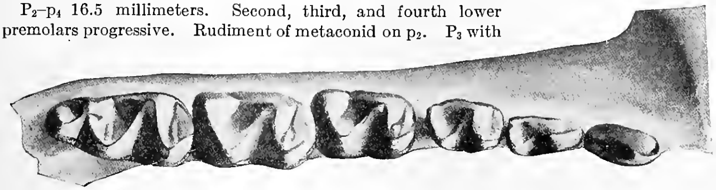

FIGURE 144.—Type (holotype) of *Eotitanops princeps*

Left lower grinding teeth. Am. Mus. 296. After Osborn, 1913. Natural size.

This species is readily distinguished from both *L. priscum* and *L. popoagicum* by the advanced condition of p_3, which may be described as submolariform.

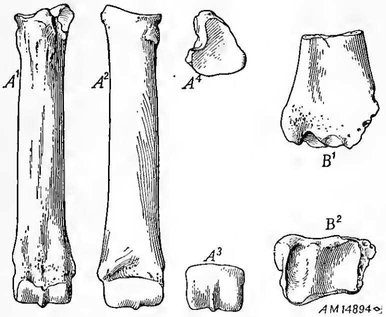

FIGURE 145.—Type (holotype) of *Eotitanops major*

Metatarsal (A) and fragment of tibia (B). Am. Mus. 14894. After Osborn, 1913. A, Median metatarsal: A^1, posterior view; A^2, anterior; A^3, distal; A^4, proximal. B^1, Distal end of left tibia, anterior view; B^2, the same, distal view. All one-half natural size.

Measurements of type

	Millimeters
Second to fourth lower premolar, inclusive	26
Second premolar, anteroposterior	8
Second premolar, transverse (trigonid)	4. 8
Third premolar, anteroposterior	9
Third premolar, transverse	6
Fourth premolar, anteroposterior	9. 3
Fourth premolar, transverse	7. 3
First molar, anteroposterior	11. 5
First molar, transverse	8. 5
Second molar, anteroposterior	12. 5
Second molar, transverse	9. 5

Etymology.—progressum, progressive.

Present determination.—A valid specific stage.

Diploceras Peterson, 1914

Cf. *Eotitanotherium,* this monograph, page 435

Original reference.—Carnegie Mus. Annals, vol. 9, Nos. 1–2, pp. 29–52, text figs. 1–15, pls. 6–10, 1914; "issued August 17, 1914" (Peterson, 1914.1).

Type species.—*Diploceras osborni.*

Generic characters.—Peterson writes:

> Dentition: $I\frac{3}{3}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$; premolar series proportionally long; p^3 with two distinct internal tubercles; horn cores well developed; limbs relatively long and slender; tibial trochlea not extended back on the calcaneum. Astragalus high, with long neck, calcaneal and cuboidal facets laterally located.

Etymology. — διπλός, double; κέρας, horn.

Present determination.—The name *Diploceras* being preoccupied, *Eotitanotherium* was later substituted. (See below.) The genus itself is probably related to the typical *Diplacodon* Marsh.

Diploceras osborni Peterson, 1914

Cf. *Eotitanotherium osborni,* this monograph, page 435

Original reference.—Carnegie Mus. Annals, vol. 9, Nos. 1–2, pp. 29–52, text figs. 1–15, pls. 6, 7, 1914; "issued August 17, 1914" (Peterson, 1914.1).

Type locality and geologic horizon.—On Duchesne River near Myton, Uinta County, Utah; *Eobasileus-Dolichorhinus* zone (upper levels of Uinta B 2).

Type.—Front of skull, lower jaws, portion of pelvis, atlas, portion of axis, fragments of scapula and foot bones, No. 2859 (Peterson, figs. 2, 3, 4, 7, 12; pls. 6, 7, 10). (See figs. 148, 149.)

Paratypes.—Front of skull, No. 2858; vertebral column, fragments of ribs, bones of limb and foot, No. 2860; crowns of two upper molars, No. 2860a; humerus, No. 2861; tibiae, No. 2862 (Peterson, figs. 1, 5, 6, 8, 9, 10, 11, 13, 14, 15; pl. 8).

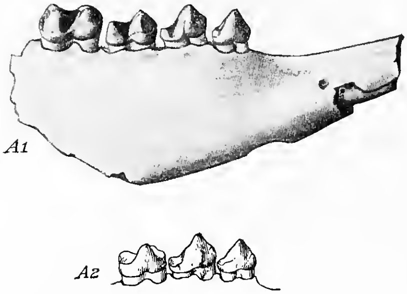

FIGURE 146.—Type (holotype) of *Lambdotherium priscum*

Am. Mus. 12822. A_1, Anterior part of lower jaw; A_2, inner view of right p_2–p (reversed). After Osborn, 1913. Natural size.

Specific characters.—Peterson writes:

> Alveolar borders of the premaxillaries extending well in front of the canines; nasals long and relatively thin, their anterior portion abruptly turned downward and convex on the anterior border; incisors well in front of the canines and relatively subequal in size; canines proportionally small.

Etymology.—Named in honor of Prof. H. F. Osborn.

Present determination.—The genus is doubtfully separable from *Diplacodon* Marsh, but the species differs in the more advanced development of the third upper premolar.

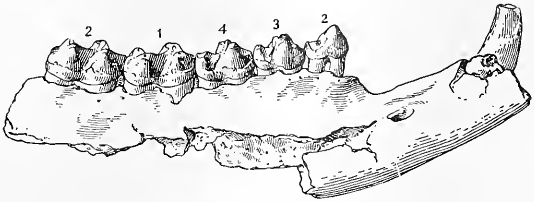

FIGURE 147.—Type (holotype) of *Lambdotherium progressum*
Lower jaw. Am. Mus. 14917. After Osborn, 1913. Natural size.

Heterotitanops Peterson, 1914

Cf. *Metarhinus*, this monograph, page 420

Original reference.—Carnegie Mus. Annals, vol. 9, Nos. 1–2, pp. 53–57, text figs. 1, 2; pl. 11, "issued August 17, 1914" (Peterson, 1914.2).

Type species.—*Heterotitanops parvus* Peterson.

Generic characters.—Peterson writes:

> Dentition: $I\frac{3}{3}?$, $C\frac{1}{1}?$, $P\frac{3}{3}?$, $M\frac{3}{3}$. Deciduous dentition: $I\frac{3}{3}?$, $C\frac{1}{1}$, $M\frac{3}{3}?$. Rapid increase in size of the deciduous upper cheek teeth from first to last tooth. D^4 with perfectly formed internal tubercles (proto- and hypocones) and the antero-external angle very greatly developed. Molars hypsodont. M^1 with large conical proto- and hypocones, the external faces of the ectoloph less emarginated anteroposteriorly than in the titanotheres generally and the median vertical ridge of the ectoloph projecting forward to a greater degree.

Etymology.—ἕτερος, other, different; Τιτάν, Titan; ὤψ, face; in allusion to its supposed possible relationship to such forms as *Eotitanops*.

Present determination.—According to Dr. W. K. Gregory, who has studied the type specimen of *Heterotitanops parvus*, the animal probably represents a very young individual of *Metarhinus* or *Rhadinorhinus*.

Heterotitanops parvus Peterson, 1914

Cf. *Metarhinus* sp. or *Rhadinorhinus* sp., this monograph, page 198

Original reference.—Carnegie Mus. Annals, vol. 9, Nos. 1–2, pp. 53–57, text figs. 1, 2, pl. 11, 1914; "issued August 17, 1914" (Peterson, 1914.2).

Type locality and geologic horizon.—White River, Uinta County, Utah; base of *Metarhinus* zone (Uinta B 1). The type specimen "was found articulated in a hard sandstone concretion, and lower down in horizon A [15] of the Uinta sediment than any mammalian remains hitherto described from that formation." (Peterson.)

Type.—Skull, lower jaws, vertebral column, ribs, limb bones, calcaneum, and astragalus of young individual (Carnegie Mus. 2909). (See figs. 150, 151, 152, 360.)

Specific characters.—Not determined.

Etymology.—*parvus*, poor, small.

Present determination.—According to Dr. W. K. Gregory the type specimen probably represents a very young individual of an undetermined species of one of the previously described genera of Uinta Basin titanotheres, probably of *Metarhinus*.

Eotitanotherium Peterson, 1914

(To replace *Diploceras* Peterson, 1913, preoccupied)
Cf. *Eotitanotherium*, this monograph, page 435

Original reference.—Carnegie Mus. Annals, vol. 9, p. 220, September 12, 1914 (Peterson, 1914.4); *Eotitanotherium*, a new generic name to replace *Diploceras* Peterson. (See Peterson, 1914.1.)

> In my article entitled "A new titanothere from the Uinta Eocene" I employed the generic name *Diploceras*, having overlooked the fact that this name is already preoccupied, having been employed by Conrad as early as 1844 to designate a genus belonging to the Mollusca. For this name I now substitute the name *Eotitanotherium*, which, after a diligent search of the literature, I believe is not preoccupied. (Peterson.)

Etymology.—ἠώς, dawn; Τιτάν, a Titan; θηρίον, a beast.

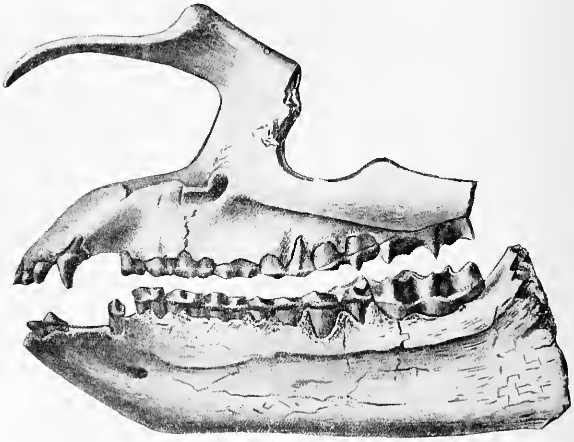

FIGURE 148.—Type of *Diploceras osborni*
Skull and lower jaw. Carnegie Mus. 2859. After Peterson, 1914. One-fourth natural size.

Present determination.—The genus is doubtfully separable from *Diplacodon* Marsh.

Telmatherium? birmanicum Pilgrim and Cotter, 1916

Cf. *Telmatherium? birmanicum*, this monograph, pages 196–199

Original reference.—India Geol. Survey Records, vol. 47, pt. 1, pp. 72–74, pl. 5, figs. 9–11, 1916 (Pilgrim and Cotter, 1916.1).

---

[15] The upper or fossiliferous part of Uinta A of previous reports is Uinta B 1 of this monograph.

Type locality and geologic horizon.—Myaing Township of the Pakokku district, Burma; Pondaung sandstone (upper to middle Eocene).

Cotypes.—Pilgrim and Cotter write:

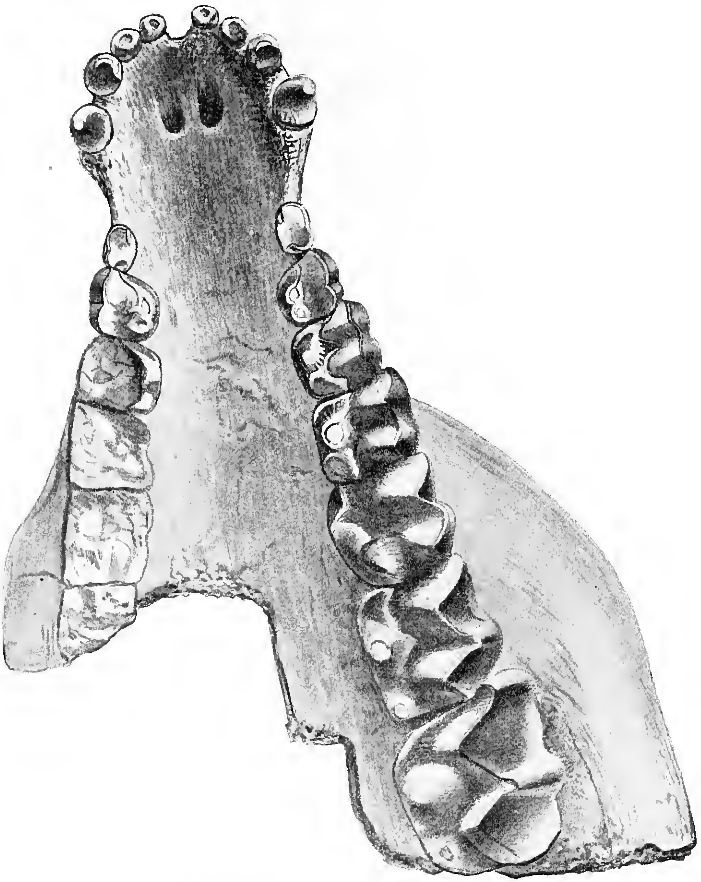

FIGURE 149.—Type of *Diploceras* (*Eotitanotherium*) *osborni*

Palatal view. Carnegie Mus. 2859. After Peterson, 1914. One-half natural size.

> This species is represented by five fragments of upper molars, two of which are almost identical in shape and comprise the antero-internal quarter of two of the upper molars probably occupying successive positions in the maxilla and being either m² and m³ or m¹ and m², two other portions of the wall of the external crescents, and another an isolated protocone. A sixth fragment consists only of the internal half of what we take to be the last upper premolar. Three of these pieces are figured in Plate 5, Figure 11 [9–11]. [See fig. 153.]

Systematic characters.—Pilgrim and Cotter write:

> It is obvious that these are not chalicotheroid; first because there is no trace of a protoconule, which in the Chalicotheriidae is always present between the protocone and the paracone, being invariably united to the latter by a transverse crest; secondly, because the protocone in our specimens lies considerably more behind the level of the paracone than is the case in the Chalicotheriidae; thirdly, because in pm⁴ there is a single large rounded and isolated inner cusp—the protocone, which is totally unconnected with the two main outer cusps—a condition which never occurs in any chalicotheroid. In that family the protocone in the premolars is connected to the outer cusps either by a single or by a double crest. In addition to these specific differences, the general structure of the tooth is unlike that of any chalicotheroid that is known to us.
>
> On the other hand, it approximates so nearly to that of many of the Titanotheriidae that we have no hesitation in assigning these fragments to that family. A careful comparison with the various known species of the Titanotheriidae convinces us that the Burmese fragments belong to a new species, but whether this is to be referred to one of the known genera of that family or whether it belongs to a new genus is a point which the material at our disposal is insufficient to enable us to determine. We shall therefore do no more than indicate its probable affinities, leaving a definite conclusion to the future, when we may hope that more abundant material may come to light.

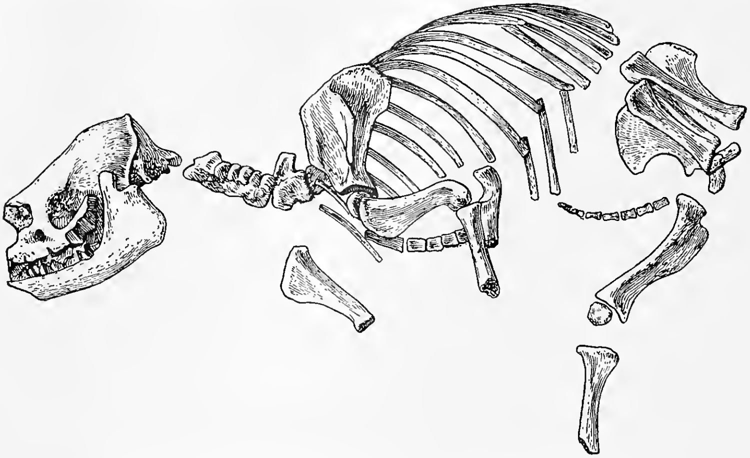

FIGURE 150.—Type (holotype) skeleton of *Heterotitanops parvus*

Carnegie Mus. 2909. After Peterson, 1914. One-fourth natural size.

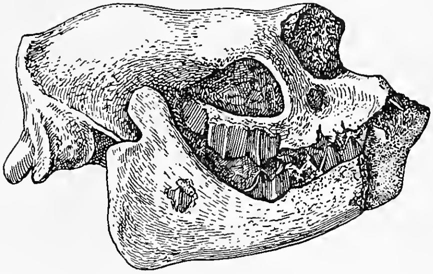

FIGURE 151.—Type (holotype) skull of *Heterotitanops parvus*

Carnegie Mus. 2909. After Peterson, 1914. One-half natural size.

One of the most crucial points which has presented itself to us for decision in connection with the material belonging to this species is the position in the jaw of the tooth (G. S. I. No. C. 315) figured in Plate 5, Figure 11. Although in some respects this specimen reminds us of the last upper molar in some of the upper Eocene members of the Palaeosyopinae, yet its small size as compared with the two other specimens of the upper molars militates against this view. Further, the almost rectangular shape of the inner portion of the tooth, which alone is preserved to us, is inconsistent with the external widening which we must assume to have taken place in m^3 of this species. Again the faint V-ing of the line which connects the two external crescents points to these being more closely connected than is the case in the last upper molar of a titanothere. On the other hand these features are such as the last upper premolar of that family would present, the only peculiarities being the rounded nature of the inner cone and the highly developed cingula on the anterior and posterior margins of the fragment, dying away internally and apparently also on either side of the two main external cusps.

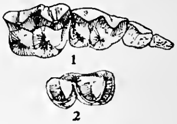

FIGURE 152.—Type (holotype) of *Heterotitanops parvus*

Upper and lower teeth. Carnegie Mus. 2909. After Peterson, 1914. 1, Deciduous upper premolars, first permanent molar; 2, permanent m_1. One-half natural size.

It is evident that this simple structure of pm^4 prohibits the possibility of this species being one of the Titanotheriinae of the Oligocene, while on the other hand the increased development of the cingulum and the absence of an intermediate tubercle point to its representing one of the latest developmental stages of the Eocene subfamily of the Palaeosyopinae. A similar indication is afforded by the fragmentary upper molars, in which the protocone is rather lofty and the only vestige of a protoconule is the presence of a minute row of beads, fringing the protocone between it and the paracone.

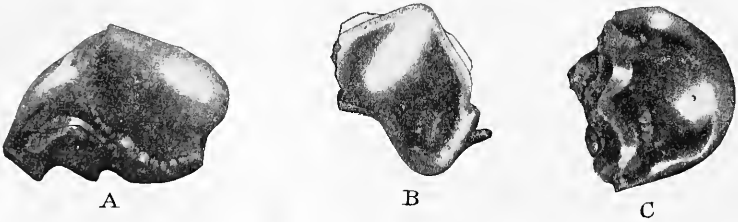

FIGURE 153.—Cotypes of *Telmatherium? birmanicum*

In the collection of the Geological Survey of India. After Pilgrim and Cotter, 1916. Natural size. A, "The antero-internal portion of a right upper molar, surface view"; B, "external portion of an upper molar, showing the gently rounded median fold, external view"; C, "internal portion of last upper premolar, surface view."

These start from the prominent cingular protostyle and culminate in a more elevated portion some 13 millimeters to the rear, diminishing again behind this point.

Attention may also be called to the presence in one of the specimens of a broad, gently rounded median fold in the center of the external paraconal wall of the tooth, although in the other specimen no such fold is visible. According to Earle such a median rib is characteristic of all the early titanotheres, tending to vanish in the upper Eocene and being entirely absent in the Oligocene subfamily of the Titanotheriinae. In any case the external lobes are broad and flat and considerably elevated, like those of the latest members of the *Palaeosyops-Diplacodon* phyla.

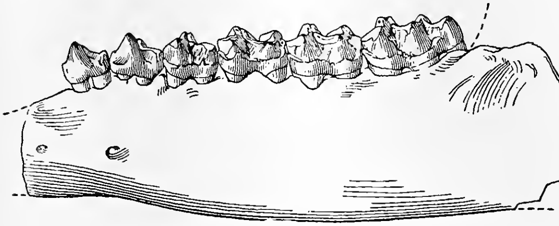

FIGURE 154.—Type (holotype) of *Lambdotherium magnum*

Lower jaw. Am. Mus. 17527. After Osborn, 1919. Natural size.

Perhaps taking everything into consideration the present species shows greater affinities with *Telmatherium* than any other known titanotherid genus.

Etymology.—*birmanicum*, relating to Burma.

Present determination.—Position uncertain. The very close beading and massive cones of the single grinding tooth figured suggest comparison with *Palaeosyops*, a progressive species like *P. copei*. These teeth might belong to a chalicothere, such as *Macrotherium* or *Moropus*, but the resemblance is not close.

Lambdotherium magnum Osborn, 1919

Cf. *Lambdotherium magnum*, this monograph, page 288

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 41, p. 562, fig. 3, 1919 (Osborn, 1919.494).

Type locality and geologic horizon.—Lower horizon of the Huerfano formation (Huerfano A) of Colorado.

Specific characters.—Osborn writes:

> Exceeding in size any other known lambdothere is the type jaw (Am. Mus. 17527) from the Garcia Cañon, lower Huerfano, containing a complete inferior series, p_2–m_3 of both sides, represented in Figure 3. (1) These teeth exceed in length over all (74 mm.) those of the type of *L. popoagicum*, in which the same teeth measure 69 millimeters. (2) P_3 has a rudimentary metaconid and paraconid, in the same stage of evolution as in *L. popoagicum*. (3) Of similar large size is a referred specimen, Am. Mus. 15600, from the Big Horn, west end of Tatman Mountain. These referred grinders, m^1, m^2, coincide closely in size with the type of *L. magnum* and may be regarded as a paratype. [See fig. 154.]

Measurements of inferior teeth p_2–m_3 and superior teeth m^1–m^2

		Millimeters
P_2–m_3:	Huerfano A. *L. priscum* (ref.), Am. Mus. 17526	67
	Wind River B. *L. popoagicum* (type), Am. Mus. 4863	69
	Wind River B. *L. progressum* (type), Am. Mus. 14917 (estimated)	71
	Huerfano A. *L. magnum* (type), Am. Mus. 17527	74
M^1–m^2:	Huerfano A. *L. priscum* (ref.), Am. Mus. 17529	21. 5
	Huerfano A. *L. priscum* (ref.), Am. Mus. 2688	22. 5
	Wind River B. *L. popoagicum* (ref.), Am. Mus. 14902	25
	Huerfano A. *L. progressum* (ref.), Am. Mus. 17530	23. 5
	Wind River B. *L. magnum* (ref.), Am. Mus. 15600	27. 5

These measurements show that there is not a great range in size between the smaller and the larger animals referred to this genus.

Etymology.—*magnum*, large.

Present determination.—A valid specific stage.

Eotitanops minimus Osborn, 1919

Cf. *Eotitanops minimus*, this monograph, page 296

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 41, p. 564, fig. 4, A, A¹, 1919 (Osborn 1919.494).

Type locality and geologic horizon.—Two miles north of Gardner, Huerfano Basin, Colorado; from the lower level of the upper horizon of the Huerfano formation (Huerfano B).

Specific characters.—Osborn writes:

> In reference to the fact that it is the smallest true titanothere known, these type lower molar teeth, p_4–m_3, Am. Mus. 17439 (fig. 4, A, A¹), * * * are assigned a new specific name on the following grounds: (1) The measurement of p_4–m_3 (53 mm.) is much less than that (58) of the corresponding teeth in *E. gregoryi;* (2) the other characters are so similar to those of *E. gregoryi* as to suggest that this is a related form. [See fig. 155.]
>
> The accompanying figures (fig. 4, A, B, C) exhibit the dimensional proportions of the above species of *Eotitanops*. It has been found from the large number of measurements of Eocene titanotheres that no single species exhibits so great a range of size.

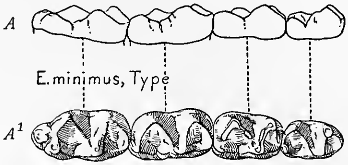

FIGURE 155.—Type (holotype) of *Eotitanops minimus*

Lower teeth. Am. Mus. 17439. After Osborn, 1919. *A*, Lingual or internal view; *A*¹, crown view. Natural size.

Etymology.—*minimus*, small.

Present determination.—A valid specific stage.

Eometarhinus Osborn, 1919

Cf. *Eometarhinus*, this monograph, page 419

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 41, pp. 568, 569, 1919 (Osborn, 1919.494).

Generic characters.—Osborn writes:

> Small; ancestral to *Metarhinus;* with rudimentary frontonasal horn; nasals elongate; overhanging premaxillaries, decurved as in *Metarhinus;* no infraorbital shelf; characters apparently intermediate between those of the *Metarhinus* and *Mesatirhinus* phyla.

Etymology.—ἠώς, dawn; *Metarhinus*, a genus of the middle Bridger beds; indicating an ancestral form of *Metarhinus*.

Present determination.—This genus appears to be ancestral to the *Dolichorhinus* phylum.

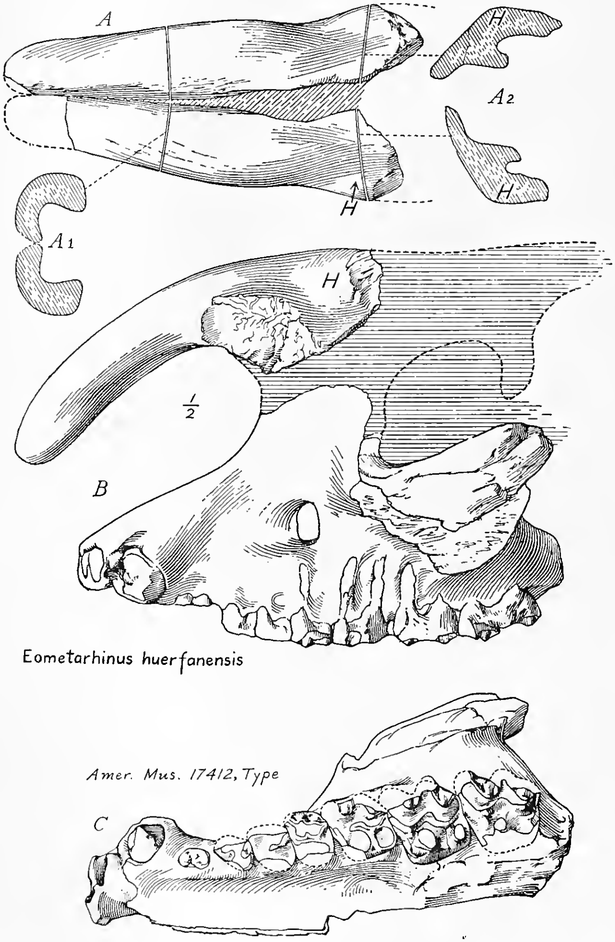

FIGURE 156.—Type (holotype) skull of *Eometarhinus huerfanensis*

Am. Mus. 17412. After Osborn, 1919. A, Nasals, superior view; A_1, A_2, sections; B, skull, view of left side; C, right upper jaw and teeth. One-half natural size.

Eometarhinus huerfanensis Osborn, 1919

Cf. *Eometarhinus huerfanensis*, this monograph, page 420

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 41, pp. 567–569, fig. 6, 1919 (Osborn, 1919.494).

Type locality and geologic horizon.—Huerfano-Muddy divide, 3 miles west of Gardner, Huerfano Basin, Colo.; Huerfano formation, 205 feet below top (Huerfano B).

Type.—Anterior portion of skull (Am. Mus. 17412). (See fig. 156.)

Specific characters.—Inferior in all measurements to *Mesatirhinus megarhinus*. Premolars with small deuterocone. p^1–m^3, 124 millimeters; p^1–p^4, 53; m^1–m^3, 72.

Etymology.—*huerfanensis*, in allusion to type locality.

Present determination.—A valid specific stage.

SECTION 3. ORIGINAL DESCRIPTIONS OF TYPES OF OLIGOCENE TITANOTHERES

LIST OF GENERA AND SPECIES

The following list shows that 49 species of Oligocene titanotheres in North America and Europe have been described and made the types of 17 different genera, of which seven are regarded as valid. The types come from many geologic levels. In finally determining the genera we are reluctantly compelled to adopt *Menodus* Pomel in preference to *Titanotherium* Leidy, to adopt *Megacerops* Leidy although it is based on a poor type, and to reject *Symborodon* Cope, because the genotype species belongs to *Menodus.* The genera that rest on the genotypic specimens are *Brontotherium* Marsh and *Brontops* Marsh. *Diplacodon* Marsh is the least soundly determined. It is close to *Brontops* and may represent a sport. *Teleodus* Marsh represents an inferior stage of the *Brontops* phylum, transitional to *Protitanotherium.*

Chronologic list of the genera and species of Oligocene titanotheres

[Generic names accepted in this work as valid are printed in small capitals; abandoned names are inclosed in brackets.]

	Date	Genus	Species	Author	Present determination
	1846	["Gigantic Palaeotherium."]		Prout	Menodus Pomel.
I	1849	MENODUS		Pomel	Do.
1	1849	Menodus	giganteus	do	Menodus giganteus Pomel.
2	1850	[Palaeotherium(?)]	proutii	Owen, Norwood, and Evans.	Menodus proutii (Owen, Norwood, and Evans).
II	1852	[Titanotherium]		Leidy	Do.
3	1852	[Palaeotherium]	[maximum]	do	(Indeterminate.)
4	1852	[Rhinoceros]	[americanus]	do	Do.
III	1853	[Eotherium.] (Type Rhinoceros americanus Leidy.)		do	Subfamily Menodontinae, genus indeterminate.
5	1854	[Palaeotherium]	[giganteum]	do	(Indeterminate.)
IV	1860	[Leidyotherium]		Prout	Do.
V	1870	MEGACEROPS		Leidy	Megacerops Leidy.
6	1870	Megacerops	coloradensis	do	Megacerops coloradensis Leidy.
VI	1873	BRONTOTHERIUM		Marsh	Brontotherium Marsh.
7	1873	Brontotherium	gigas	do	Brontotherium gigas Marsh.
VII	1873	[Symborodon]		Cope	Menodus Pomel.
8	1873	[Symborodon]	torvus	do	Menodus torvus (Cope).
VIII	1873	[Miobasileus]		do	(Indeterminate.)
9	1873	[Miobasileus]	[ophryas]	do	Do.
10	1873	Megaceratops	acer	do	Megacerops acer Cope.
11	1873	[Megaceratops]	heloceras	do	Menodus heloceras (Cope).
12	1873	[Symborodon]	bucco	do	Megacerops bucco (Cope).
13	1873	[Symborodon]	[altirostris]	do	Megacerops acer Cope.
14	1873	[Symborodon]	trigonoceras	do	Menodus trigonoceras (Cope).
15	1873	[Brontotherium]	[ingens]	Marsh	Menodus giganteus Pomel.
16	1874	[Symborodon]	hypoceras	Cope	Brontotherium hypoceras (Cope).
IX	1875	[Anisacodon]		Marsh	(Indeterminate.)
17	1875	[Anisacodon]	[montanus]	do	Menodus giganteus Pomel.
X	1876	[Diconodon (not Anisacodon).]		do	Menodus giganteus? Pomel.
18	1886	[Menodus]	angustigenis	Cope	?Brontops angustigenis (Cope).
19	1887	[Menodus]	tichoceras	Scott and Osborn	Brontotherium tichoceras (Scott and Osborn).
20	1887	[Menodus]	dolichoceras	do	Brontotherium dolichoceras (Scott and Osborn).
21	1887	[Menodus]	platyceras	do	Brontotherium platyceras (Scott and Osborn).
XI	1887	BRONTOPS		Marsh	Brontops Marsh.
22	1887	Brontops	robustus	do	Brontops robustus Marsh.
23	1887	Brontops	dispar	do	Brontops dispar Marsh.
XII	1887	[Menops]		do	Menodus Pomel.
24	1887	[Menops]	varians	do	Menodus varians (Marsh).
XIII	1887	[Titanops]		do	Brontotherium Marsh.
25	1887	[Titanops]	curtus	do	Brontotherium curtum (Marsh).
26	1887	[Titanops]	[elatus]	do	Brontotherium gigas Marsh.
XIV	1887	ALLOPS		do	Allops Marsh.

Chronologic list of the genera and species of Oligocene titanotheres—Continued

[Generic names accepted in this work as valid are printed in small capitals; abandoned names are inclosed in brackets.]

	Date	Genus	Species	Author	Present determination
27	1887	Allops	serotinus	Marsh	Allops serotinus Marsh.
XV	1889	[Haplacodon] [a]		Cope	Allops sp.
28	1889	[Menodus]	selwynianus	do	Diploclonus selwynianus (Cope).
29	1889	[Menodus]	syceras	do	?Megacerops syceras (Cope).
XVI	1890	DIPLOCLONUS		Marsh	Diploclonus Marsh.
30	1890	Diploclonus	amplus	do	Diploclonus amplus Marsh.
XVII	1890	TELEODUS		do	Teleodus Marsh.
31	1890	Teleodus	avus	do	Teleodus avus Marsh.
32	1891	Allops	crassicornis	do	Allops crassicornis Marsh.
33	1891	Brontops	[validus]	do	Brontops dispar Marsh.
34	1891	[Titanops]	medius	do	Brontotherium medium (Marsh).
35	1891	[Menodus]	[peltoceras]	Cope	?Brontotherium curtum (Marsh).
36	1892	[Menodus(?)]	rumelicus	Toula	?Brontotherium rumelicum (Toula).
37	1896	[Titanotherium]	ramosum	Osborn	Brontotherium ramosum (Osborn).
38	1902	[Megacerops]	brachycephalus	do	Brontops brachycephalus (Osborn).
39	1902	[Megacerops]	bicornutus	do	?Diploclonus bicornutus (Osborn).
40	1902	[Megacerops]	marshi	do	Allops marshi (Osborn).
41	1902	Brontotherium	leidyi	do	Brontotherium leidyi Osborn.
42	1905	[Megacerops]	tyleri	Lull	?Diploclonus tyleri (Lull).
43	1908	Brontotherium	hatcheri	Osborn	Brontotherium hatcheri Osborn.
44	1908	[Symborodon]	copei	do	Megacerops copei (Osborn).
45	1908	[Megacerops]	primitivus	Lambe	Teleodus primitivus (Lambe).
46	1908	Megacerops	assiniboiensis	do	Megacerops assiniboiensis Lambe.
47	1913	[Titanotherium]	[bohemicum]	Kiernik	Menodus giganteus Pomel.
48	1916	Allops	walcotti	Osborn	Allops walcotti Osborn.
49	1916	Megacerops	riggsi	do	Megacerops riggsi Osborn.

[a] Genotype *Menodus angustigenis*, upper teeth only. See No. 18, above.

PROUT'S DESCRIPTIONS OF A FRAGMENTARY LOWER JAW, THE FIRST TITANOTHERE MADE KNOWN TO SCIENCE

"Gigantic Palaeotherium," Prout, 1846

Original reference.—Am. Jour. Sci., 2d ser., vol. 2, pp. 288–289, 1 fig., 1846 (Prout, 1846.1).

Subsequent references.—Leidy, Description of the remains of extinct Mammalia and Chelonia from Nebraska Territory, in Owen, Report of a geological survey of Wisconsin, Iowa, and Minnesota, p. 551, 1852 [Tab. 9, figs. 3, 3a, is not Prout's specimen] (Leidy, 1852.1); The ancient fauna of Nebraska, pp. 72, 114, pl. 16, fig. 1, 1853 (Leidy, 1854.1).

Original description.—Dana and Silliman write:

> *Gigantic Palaeotherium.*—We have recently received information from Mr. H. A. Prout, of his discovery of the remains of a *Palaeotherium* in the Tertiary near St. Louis, and we are also indebted to him for a cast of the jaw, a view of the posterior tooth of which is represented below. Mr. Prout is preparing a memoir on the subject; and in the meantime we state the following facts from his letter.
>
> This fossil was found in the great northwestern Tertiary belt, which is deflected from the north by the Black Hills and which crosses the Missouri River at about latitude 43°. It was accompanied by several *Baculites compressus*, an *Inoceramus concentricus*, a vertebra of a large fish, and some crystallized gypsum. [As noted later by Prout these were from the Cretaceous and from another locality.] The entire jawbone, judging from the decrease in size of the teeth, must have been at least 30 inches long, which far exceeds in size the *Palaeotherium magnum*. The face of the posterior tooth is 4⅔ inches in length; and from the posterior side of the last tooth to the anterior side of the antepenultimate molar of the same side the distance in the specimen is 11 inches. [See fig. 157.] This is the aggregate length, in the line of the jaw, of but three out of seven teeth; and with the most liberal allowance for decrease of size in the other four the whole of the seven could not have measured less than 16 or 18 inches, which is about one-half larger than in the *P. magnum*.

Remarks.—This specimen was "the first of the many mammalian remains which have been brought to the notice of the scientific world from the vast Eocene cemetery of Nebraska" (Leidy, 1852.1, p. 551). It was the subject of Prout's second article cited below and was the type of *Menodus giganteus* Pomel and one of the cotypes of *Palaeotherium? proutii* Owen, Norwood, and Evans (1850.1) and of *Titanotherium proutii*.

"Fossil maxillary bone of a Palaeotherium," Prout, 1847

Original reference.—Am. Jour. Sci., 2d ser., vol. 3, pp. 249, 250, 1 fig., 1847 (Prout, 1847.1).

Subsequent references.—(See p. 204.)

Prout's description.—The following notice, written by Dr. Prout himself, is a full description of the same lower jawbone mentioned in his letter of the preceding year:

> The palaeotherial bone here described was sent to me some time ago by a friend residing at one of the trading posts of the St. Louis Fur Co., on the Missouri River. From information since obtained from him, I learn that it was discovered in the

Mauvais Terre, on the White River, one of the western confluents of the Missouri, about 150 miles south of St. Pierre, and 60 east of the Black Hills, at a point which would very nearly correspond with the intersection of latitude 43° with longitude 26° west of Washington.

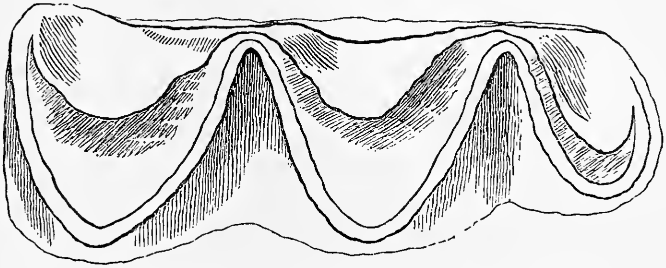

Figure 157.—"Vertical view of the posterior tooth belonging to the lower jaw of Mr. Prout's *Palaeotherium*"

After Prout, 1846. Natural size.

The *Baculites* and the *Inoceramus* which accompanied it and which I at first supposed belonged to the same locality were found in another formation—probably the Cretaceous—distant about 100 miles, and included in the Grande Detour or Great Bend of the Missouri River.

This fossil bone is a fragment of the inferior maxillary of the left side, consisting of the posterior part of the bone, together with the last three molar teeth. The ramus is much fractured and presents an irregular surface; yet the general direction of its outline may be made out. The length of this fragment is 15 inches, its depth from the highest point of the ramus (*a*) to the lowest (*b*) is 9½ inches: it narrows regularly forward so as to measure only 3½ inches from the lower surface of the bone at (*d*) to the alveolar process of the antepenultimate tooth at (*c*). The inner surface of the bone is more uniform, being marked merely by depressions for the attachment of muscles. The alveolar portion is here very prominent and well rounded, the teeth being planted more than an inch from a vertical line which is tangential to the inner surface of the bone. It is covered in places with a concretionary matter which could not be removed without injury to the specimen; on analysis, this was found to consist chiefly of carbonate of lime, with some alumina, and a small proportion of silex.

The last molar tooth has the three lobes of the Palaeotheria, as shown in Figure 2. The inner surface is nearly smooth and flat and shows no trace of lobes. The size of the tooth from posterior to anterior sides is 4½ inches, of which 1⅝ inches belong to the anterior lobe, the same to the middle, and 1¼ inches to the posterior. In an upper view the two larger lobes have a deltoid form, with the sides somewhat convex, and a rounded outer angle. The thickness through from the outer to the opposite side is 1¾ inches. The enamel of the inner side folds over the surface, covering nearly a semicircular space and leaving between it and the edge of the posterior enamel a subcrescent-shaped space (deltoido-lunate) of dentine, somewhat concave, which is nearly seven-eighths of an inch broad at its widest part. These crescent-shaped areas of the two lobes are connected by a continuous tract of dentine, nearly 1½ lines wide at the narrowest part; and the same tract continues from the middle lobe to the posterior; upon the latter it does not widen over the interior, as the reflexed inner enamel covers the whole of the crown, excepting a narrow space adjoining the posterior enamel. The prominent points of the crown between the lobes project about half an inch; and probably much more in the perfect tooth.

The fifth and sixth molars (first and second true molars) resemble the one described, except that they want the third lobe, and the dentine area on the crown of each lobe is much larger. The sixth is 3⅛ inches from front to posterior side. The posterior lobe is 2 inches from the outer to the inner surface and 1⅞ inches long in the line of the jaw. The whole distance on the jaw occupied by the three teeth is 11 inches. In the largest *Palaeotherium* hitherto described, the *P. magnum*, the same teeth occupy a space scarcely one-third that of the Missouri animal.

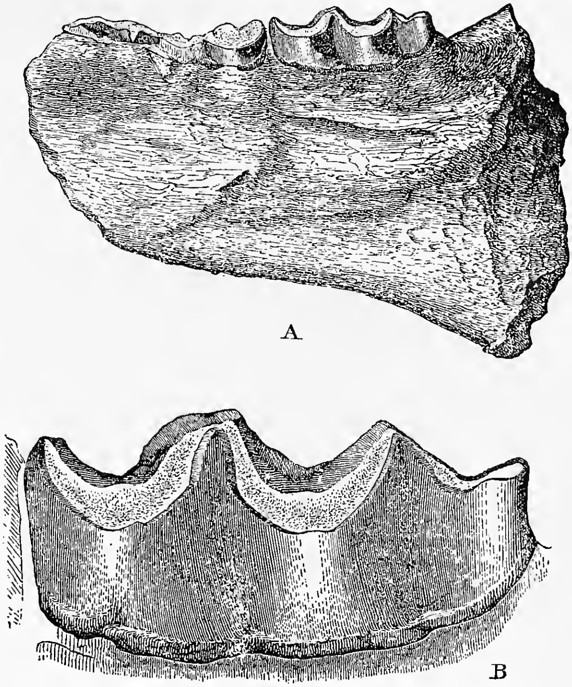

Figure 158.—Original figures of Prout's "gigantic *Palaeotherium*," the first titanothere discovered

After Prout, 1847. A, "Fragment of the inferior maxillary of the left side," one-fourth natural size; B, last lower molar on the left side, four-fifths natural size.

St. Louis, December 10, 1846.

POMEL'S GENUS MENODUS, BASED ON PROUT'S DESCRIPTION AND FIGURE OF THE FRAGMENTARY LOWER JAW

Menodus Pomel, 1849

Cf. *Menodus*, this monograph, page 522

Original reference.—Bibliothèque universelle de Genève (Supp.) Arch. sci. phys. nat., vol. 10, pp. 73–75, January, 1849 (Pomel, 1849.1).

Type species.—*Menodus giganteus* Pomel.

Original description.—Pomel writes:

> Ce fossile a été découvert à Mauvais-Terre sur la Rivière Blanche à 43° latitude nord et 26° longitude ouest de Washington, sur le versant occidental du bassin du Missouri. C'est un fragment de mandibule portant les deux dernières molaires et l'alvéole de l'antépénultième, qui montrent tous les caractères du genre palaeotherium. La dernière molaire, la mieux conservée, indique une espèce plus voisine des vrais palaeotherium (dont les P. magnum, medium, etc., sont les types) ou du sous-genre plagiolophus, que des anchitherium et des paloplotherium, en ce que la troisième colline est bien développée, et forme un troisième croissant à la couronne; les autres croissants sont un peu anguleux (croissants deltoïdes, dit l'auteur). La base de la couronne est entourée d'un petit bourrelet comme dans les palaeotherium d'Europe; mais si le dessin est exact, la manière dont les croissants principaux se reunissent indiquerait quelque rapport avec ce qui existe chez les anchitheriums et les paloplotheriums, cette partie étant plus épaissie. Il serait nécessaire d'en connaître une molaire supérieure pour fixer sa véritable place; nous serions porté à présumer toutefois, que ce palaeotherium est le type d'un sous-genre particulier; car indépendamment de la brièveté du fût de la couronne des molaires, sa taille est trop au-dessus de celle de nos plus grandes espèces européennes, pour qu'on puisse admettre sans hésitation son identité subgénérique avec celles-ci. En effet, l'arrière-molaire du palaeotherium magnum est à peine le tiers de celle de l'espèce américaine: aussi cette dernière est-elle réellement colossale, mesurant 0m,116, dont 0m,032 appartiennent à la troisième colline; son épaisseur est 0m,045. L'os mandibulaire est, comme on devait s'y attendre, très-robuste; il a 0m,112 de diamètre vertical entre les deux arrière-molaires; il s'elargit considérablement à la partie du bord inférieur située sous la branche montante.
>
> Malheureusement on ignore l'âge du terrain où ce fossile remarquable a été découvert, quoiqu'il soit probable que c'est dans la série des formations de l'époque alluviale qu'il faudra le ranger. Cette différence d'âge entre ce palaeothère et ceux de l'Europe occidentale, ne doit pas étonner, puisque l'on trouve dans l'Amérique du sud, dans des formations de même âge, un animal de la même tribu (on pourrait dire du même grand genre), le macrauchenia qui, lui aussi, est d'une taille supérieure aux espèces d'Europe. On sait, du reste, que sa dernière molaire inférieure n'a que deux collines, comme dans le paloplotherium, et que ses membres sont assez grêles, tandis qu'il est probable qu'un animal aussi gigantesque que ce nouveau palaeotherium a été assez trapu. Nous proposons de désigner cette forme animale fossile sous le nom de *Menodus giganteus*, en la considérant comme un sous-genre des palaeotherium.

Etymology.—μήνη, the moon; ὀδούς, tooth; in allusion to the crescents of the lower molars.

Present determination.—Pomel proposed *Menodus* as a subgenus of *Palaeotherium*, using the latter term in a very comprehensive sense, as later authors would speak of a family. In 1873 Marsh (1873.1, p. 486) rejected the name *Menodon* on the ground that it was essentially the same word as *Menodon* Meyer, 1838, a genus of reptiles (Palmer, 1904.1, p. 410); but, as the two names are spelled differently, according to the modern rules of nomenclature *Menodus* Pomel can not be rejected on that ground. As shown below, the type species *Menodus giganteus* rests upon Prout's specimen, of which an excellent figure was given later by Leidy (1854.1, pl. 16, fig. 1).

FIGURE 159.—Type of *Menodus giganteus*

Prout's original specimen. After Leidy, 1854. One-third natural size.

Menodus giganteus Pomel, 1849

Cf. *Menodus giganteus*, this monograph, pages 530, 535

Original reference.—See genus *Menodus*, above.

Type specimen.—As noted above, the species rests upon Prout's original specimen, which was figured by Prout in 1847 (1847.1, p. 249, and 1 fig.) and by Leidy under the name *Titanotherium proutii* in 1854 (1854.1, pl. 16, fig. 1 only). The type may have been destroyed in the "great fire" of St. Louis.

Neotype (Osborn).—A carefully made model, based on Leidy's figures and measurements of the lower jaw, was compared with various specimens of *Menodus* until an upper dentition was found (in a skull, Am. Mus. 505) which appears to fit very well the lower teeth of the type. Hence the skull (Am. Mus. 505) has been selected as a neotype of *Menodus giganteus.*

Specific characters.—Not separated from the generic characters in Pomel's description. (See p. 530.)

Etymology.—giganteus, gigantic; because larger than the *Palaeotherium magnum.*

Present determination.—Although Prout's original specimen, the type of *Menodus giganteus* Pomel, has been lost, Leidy's carefully executed figure of this specimen, together with his measurements and descriptions, reveals generic and specific identity with the dolichocephalic titanothere which Osborn in 1902 designated (1902.208, p. 96) *Titanotherium ingens* Marsh. *Titanotherium ingens* is therefore to be regarded as a synonym of *Menodus giganteus* Pomel.

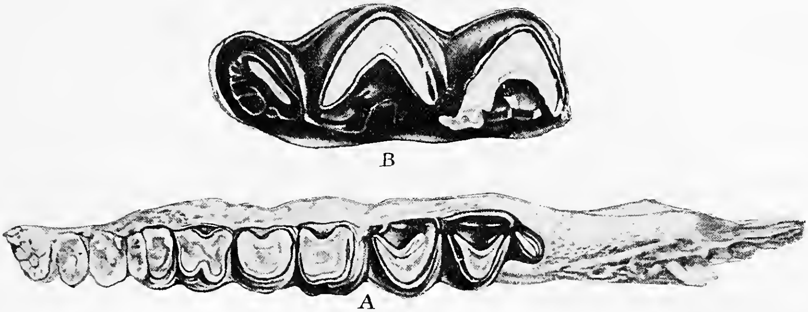

FIGURE 160.—Owen's specimens of *Palaeotherium? proutii*

After Leidy, 1852. A, Type of *Palaeotherium? proutii* (Owen's specimen), Nat. Mus. 113. One-third natural size. This was the principal specimen referred to by Leidy in proposing the name *Titanotherium* (1852.1). B, Third left lower molar, another of Owen's specimens used by Leidy in describing *Titanotherium.* Two-thirds natural size.

EARLY NOTICES BY LEIDY AND OTHERS, 1850–1870

Palaeotherium? proutii Owen, Norwood, and Evans, 1850

Cf. *Titanotherium proutii* Leidy

Original reference.—Acad. Nat. Sci. Philadelphia Proc., vol. 5, p. 66, August, 1850 (Owen, Norwood, and Evans, 1850.1).

Subsequent reference.—"*Palaeotherium? proutii* Owen, Norwood, and Evans," Leidy, Description of the remains of extinct Mammalia and Chelonia from Nebraska Territory, in Owen, Report of a geological survey of Wisconsin, Iowa, and Minnesota, pp. 551–552, tab. 9, figs. 3a, 3, 1852 [Owen's specimens, not Prout's] (Leidy, 1852.1); "*Titanotherium proutii* Leidy," The ancient fauna of Nebraska, pp. 72–73, pl. 16, figs. 1–3, 1853 (Leidy, 1854.1).

Original description.—Owen, Norwood, and Evans state that

> These remarkable remains are thus named in compliment to Dr. Prout of St. Louis who first noticed them in the American Journal of Science and Arts. The generic characters, however, are not yet satisfactorily decided.

Type.—From a study of the foregoing references it is evident that Owen, Norwood, and Evans intended the name *Palaeotherium? proutii* to cover both Prout's original specimen and "Owen's specimen," discovered by Evans, the lower jaw which was figured by Leidy in 1852 (1852.1, pl. 9, figs. 3, 3a) and is still preserved in the United States National Museum (No. 113; our fig. 160). Prout's specimen is the type of *Menodus giganteus* Pomel; hence, by the method of elimination, Owen's specimen becomes the type of *Palaeotherium? proutii* Owen, Norwood, and Evans.

Etymology.—Named in honor of Dr. Hiram Prout.

Present determination.—"Owen's specimen" (Nat. Mus. 113) appears to represent a *Menodus,* of a stage slightly smaller than *M. trigonoceras.* (See p. 528.)

Titanotherium Leidy, 1852

Cf. *Menodus,* this monograph, page 522

Original reference.—"*Palaeotherium? proutii* Owen, Norwood, and Evans," Owen, Report of a geological survey of Wisconsin, Iowa, and Minnesota, p. 552 1852 (*Titanotherium*) (Leidy, 1852.1).

Subsequent reference.—"*Titanotherium proutii* Leidy," Leidy, The ancient fauna of Nebraska, pp. 72, 114, 1853 (Leidy, 1854.1).

Type species.—Palaeotherium? proutii Owen, Norwood, and Evans.[16] (See p. 526.)

Generic characters.—Not separated by Leidy from specific characters.

Etymology.—Τιτάν, a Titan; θηρίον, beast.

Present determination.—Leidy based the genus *Titanotherium* collectively upon a number of specimens, including, first, Prout's original specimen; second, "Owen's specimen" (Nat. Mus. 113); and third, certain other fragmentary specimens. Prout's specimen was already the type of *Menodus giganteus* Pomel, hence by elimination the genus *Titanotherium* rests upon the species *Palaeotherium? proutii* Owen, Nor-

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[16] In his work of 1853 Leidy placed his own name after the specific name *proutii,* evidently following the practice of those who placed the name of the author of the genus after the specific name.

wood, and Evans, the type of which is the second specimen described by Leidy, namely, Evans's specimen (Nat. Mus. 113). This specimen is believed by Osborn to be congeneric with the type of *Menodus giganteus* Pomel.

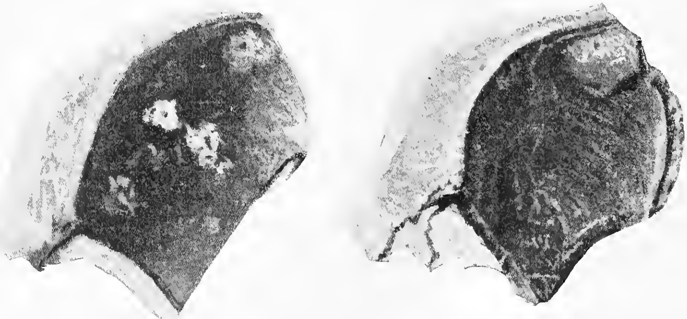

FIGURE 161.—Type (holotype) of *Palaeotherium maximum*

Parts of the outer wall (the ectoloph) of two upper molars. After Leidy, 1852. Natural size.

Proposal of the generic name Titanotherium.—After describing under the name *Palaeotherium? proutii* the specimens made known by Prout and by Owen, Norwood, and Evans, Leidy (1852.1, p. 552) says:

> All the preceding specimens, except probably the latter two, I suspect belong to a different genus from either *Palaeotherium* or *Anchitherium*, and should the suspicion prove correct, *Titanotherium* would be a good name for the animal, as expressive of its very great size.

Palaeotherium maximum Leidy, 1852

Original reference.—Leidy, in Owen, Report of a geological survey of Wisconsin, Iowa, and Minnesota, description of tab. 12 B, figs. 3, 4, 1852 (Leidy, 1852.1).

Type locality and geologic horizon.—White River, "Nebraska" [South Dakota]; Chadron formation (*Titanotherium* zone).

Type.—Parts of the outer wall or ectoloph of two superior molars. Types now lost. (See fig. 161.)

Characters.—Leidy writes: "I am at present very much inclined to consider these as belonging to a true species of *Palaeotherium*, which from its very great size might be appropriately named *Palaeotherium maximum*."

Etymology.—*maximum*, greatest—that is, greater than *P. magnum*.

Present determination.—These fragments belong to a large Oligocene titanothere of wholly uncertain reference.

Rhinoceros americanus Leidy, 1852

Original reference.—Acad. Nat. Sci. Philadelphia Proc., vol. 6, p. 2, 1852 (Leidy, 1852.2).

Subsequent reference. — Leidy, The ancient fauna of Nebraska, p. 76, pl. 17, figs. 1–4, 1853 (Leidy, 1854.1).

Type locality.—White River, "Nebraska" [South Dakota].

Type.—Two superior premolars belonging upon opposite sides of the jaw. Part of a collection procured by Mr. Thaddeus A. Culbertson for the Smithsonian Institution. Types not located. (See fig. 162.)

Characters. — The proceedings of the Philadelphia Academy contain the following note:

> Dr. Leidy called the attention of the members to a fossil tooth and a fragment of a second, from the collection made by Mr. Culbertson in Nebraska Territory, which, he observed, belonged to a new species of *Rhinoceros*, or probably *Acerotherium*. The former specimen is probably a third premolar, the latter a portion of the fourth. A great peculiarity in the teeth is the confluence of the inner lobes with each other and their separation to the base from the outer lobes. They

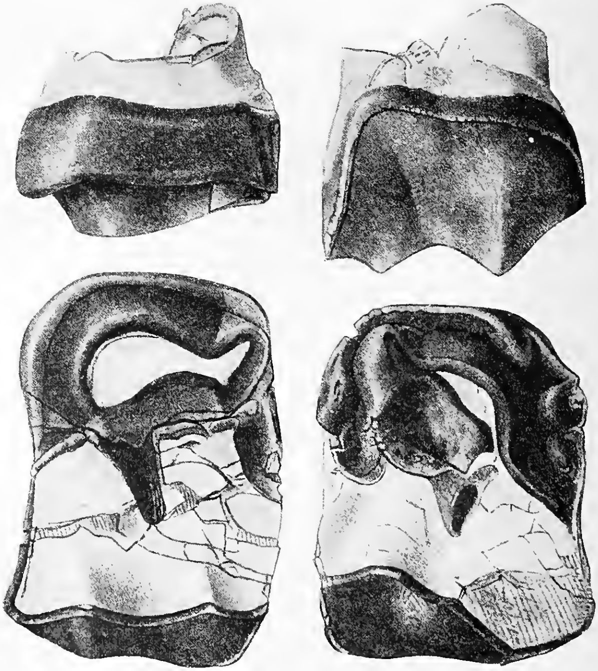

FIGURE 162.—Cotypes of *Rhinoceros americanus*

Two upper fourth premolars. After Leidy, 1853. Natural size.

possess a remarkably strong basal ridge and indicate an animal larger than any species of existing *Rhinoceros;* the greatest transverse diameter of the third premolar being 2½ inches; its anteroposterior diameter 1¾ inches. For the species the name *Rhinoceros americanus* is proposed.

Etymology.—americanus, in allusion to the then novel fact that a supposed rhinoceros had once inhabited America.

Present determination.—It does not seem possible to determine positively whether these isolated premolar teeth belong to *Allops* or to *Menodus;* the affinity to one or the other of these genera is indicated by the pronounced internal and external cingula and by the large tetartocone on p^4. In view of the doubt and the disappearance of the type, it seems best to regard "*Rhinoceros*" *americanus* as indeterminate.

Eotherium Leidy, 1853

Cf. *Menodus* Pomel, this monograph, page 522

Original reference.—Acad. Nat. Sci. Philadelphia Proc., vol. 6, p. 392, 1853 (Leidy, 1853.1).

Subsequent reference.—Leidy, The ancient fauna of Nebraska, pl. 17, figs. 1–7, 1853 (Leidy, 1854.1).

Type species (monotypic).—*Rhinoceros americanus* Leidy. (See above.)

Generic description.—Leidy says:

> Of the huge *Titanotherium proutii* there are numerous small fragments of bones and teeth and also several entire superior molars, which have served to remove some of the obscurity in regard to the characters of the animal. From the last-mentioned specimens it appears that those which have been described as probably indicating a new species of *Palaeotherium*, under the name *P. giganteum* (Ancient fauna of Nebraska, pl. 17, figs. 11–13), belong to *Titanotherium proutii*, while several superior molars (ib., figs. 1–7), attributed to the latter, belong to a new genus associating characters of *Rhinoceros* and *Palaeotherium.* For this genus and species, represented by Figures 1–7, Plate 17, in the Ancient fauna of Nebraska, I propose the name of *Eotherium americanum.*

Etymology.—ἠώς, dawn, *θηρίον,* beast; possibly in allusion to the relatively early geologic age of the animal.

Present determination.—The specimens indicated were first chosen the types of *Rhinoceros americanus.* (See above.) The very pronounced internal and external cingula of the type (fig. 162), however, appear to indicate that they belong generically to *Menodus.* The genus *Eotherium* was subsequently treated by Leidy as a synonym of *Titanotherium.* The name *Eotherium* was subsequently (1875) applied by Owen to a genus of sirenians.

Palaeotherium giganteum Leidy, 1854

(Indeterminate)

Original reference.—The ancient fauna of Nebraska: Smithsonian Contr. Knowledge, vol. 6, p. 78, pl. 17, figs. 11–13, 1853 (Leidy, 1854.1).

Type locality.—White River, "Nebraska" [South Dakota].

Types.—Portions of the ectoloph of five molars "in the collections of Mr. Culbertson and Dr. Owen."

Lectotypes (Osborn).—The fragmentary ectoloph figured in Plate 17, Figure 11, of Leidy's work. (See fig. 163.)

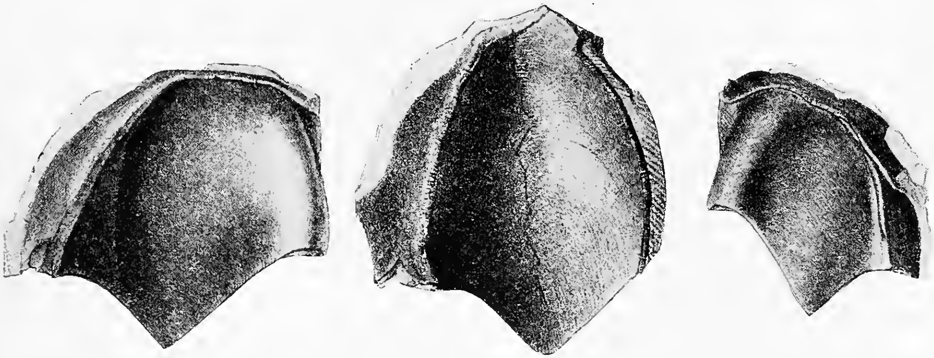

FIGURE 163.—Cotypes of *Palaeotherium giganteum*

Parts of the ectoloph of upper molars. After Leidy, 1853. Natural size.

Characters.—Leidy writes:

> The fragments, of which there are five, are only single external lobes of the upper molars. These, externally, correspond to the description of Cuvier of the teeth of *Palaeotherium.* A conjoined pair of the lobes, forming the outer part of a tooth, "present the external face strongly inclined inward in descending and divided by three salient ridges into two concavities, which are rounded toward the fangs and terminate in a triangular cusp at the masticating surface, the basal angles of which rest upon the termination of the salient ridges." The median ridge is a thick obtuse fold outward of the tooth, and the anterior and posterior ridges are acute, roughened offsets from the basal ridge, descending to the masticating surface.
>
> The measurements of the more perfect specimens are as follows:

	In.	lines
Length of the longest lobe	2	4
Length of a second specimen	2	
Breadth of the second specimen at the basal angles of the cusp	1	8
Length of the shortest lobe	1	7
Breadth of the shortest lobe at the basal angles of the cusp	1	3

Etymology.—*giganteum*, gigantic; in obvious allusion to the great size, which seems to have impressed all the early observers of *Titanotherium*.

Present determination.—Leidy himself subsequently (1854.1, p. 157) transferred this species to *T. proutii*. It is indeterminate.

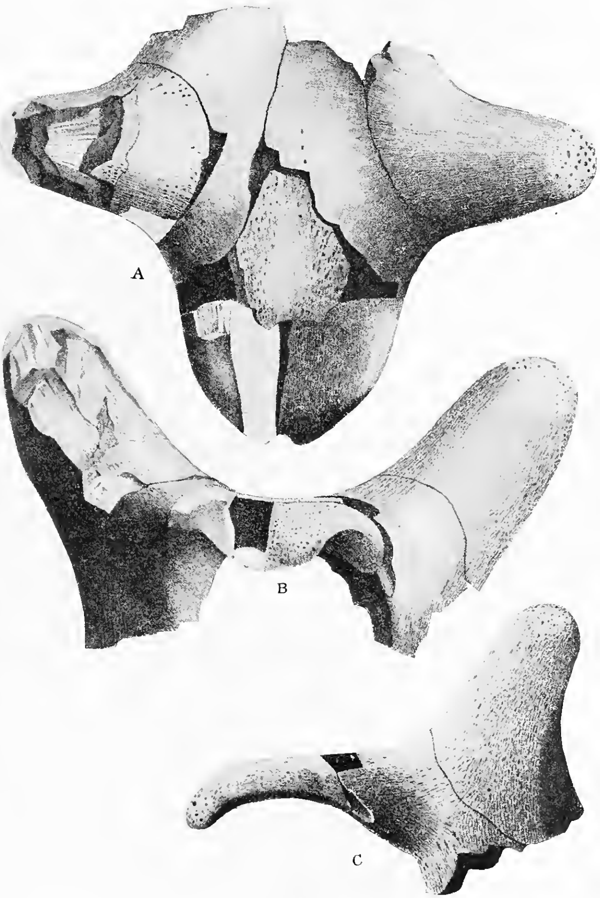

FIGURE 164.—Type (holotype) of *Megacerops coloradensis*. Nasals and "horns"

After Leidy, 1873. A, Top view; B, front view; C, view of left side. One-third natural size.

Leidyotherium Prout, 1860

(Indeterminate)

Original reference.—Acad. Sci. St. Louis Trans., vol. 1, pp. 699–700, 1860 (Prout, 1860.1).

Subsequent reference.—Leidy, Extinct Mammalia of Dakota and Nebraska, p. 390, 1869 (Leidy, 1869.1).

Type species.—None designated.

Type locality.—The specimen was reported to have been obtained near Abingdon, in Virginia, but was later stated by Leidy (op. cit., p. 390) to be "a fossil from the Mauvaises Terres of White River, Dakota."

Type.—"The fragment of a large molar tooth."

Generic characters.—Prout writes:

> The lobed or indented border of the enamel would seem to show that this animal was nearly allied to *Titanotherium*, while the great width and depth of the groove between the outer and what may have been the inner border of the tooth would separate it from this genus. * * * It is distinguished, moreover, from these [*Lophiodon*] by the greater length of the fangs and the comparative shortness of the enamel on the outer surface of the tooth. * * * It must have been a phytivorous pachyderm, as large if not larger than the *Titanotherium*.

Etymology.—Named in honor of Joseph Leidy.

Present determination.—No specific name is given. Leidy treated the genus as synonymous with *Titanotherium*. It is an indeterminate member of the family.

Megacerops Leidy, 1870

Cf. *Megacerops*, this monograph, page 541

Original reference.—Acad. Nat. Sci. Philadelphia Proc., vol. 22, p. 2, 1870 (Leidy, 1870.1).

Subsequent reference.—Leidy, Extinct vertebrate fauna of the Western Territories, p. 239, pl. 1, figs. 2, 3; pl. 2, fig. 2, 1873 (Leidy, 1873.1).

Type species.—*Megacerops coloradensis* Leidy.

Generic characters.—In the original reference a detailed description of the type specimen of *Megacerops coloradensis* is given, comparisons being made with the anterior horn cores and nasals of the Siwalik *Sivatherium*, with which it was thought possibly to be allied. Leidy concludes as follows:

> It is probable that the fossil may pertain to the same animal as the remains from the Mauvaises Terres of Nebraska, described under the name of *Titanotherium*, but in the state of extreme uncertainty as to its collocation, it may with equal probability be referred to other genera, perhaps to *Megalomeryx*, or it may have been an American species of the *Sivatherium*. Under the circumstances it may be referred to a new genus, with the name of *Megacerops coloradensis*.

Etymology.—μέγας, great; κέρας, horn; ὤψ, face.

Present determination.—Leidy's carefully executed figures of the type, in the opinion of the present writer (Osborn), reveal the generic relationship of this animal with that later described by Cope (1873.2, p. 4) as *Megaceratops acer*.

Megacerops coloradensis Leidy, 1870

Cf. *Megaccrops coloradensis*, this monograph, page 544

Original reference.—Acad. Nat. Sci. Philadelphia Proc., vol. 22, p. 2, 1870 (Leidy, 1870.1).

Subsequent reference.—Leidy, Extinct vertebrate fauna of the Western Territories, pp. 239–242, pl. 1, figs. 2, 3; pl. 2, fig. 2, 1873 (Leidy, 1873.1).

Type locality and geologic horizon.—Colorado; Chadron formation (*Titanotherium* zone), level not ascertained.

Type.—Fractured horns and nasals. The present location of this type has not been determined. It is not in the collection of the Philadelphia Academy, nor is any record of its loan to be found. (See fig. 164.)

Characters of type.—Leidy's description is too long to quote here. The specimen may be described briefly as follows: Seen from above the nasals are of moderate length and taper toward the extremities; from the side and front they appear decidedly long and thin and are strongly decurved at the tip, at which point there is a median notch. The horns project forward and outward and pass from an elongate oval section at the base to rounded, transversely oval tips. The greatest diameter of the horns at the base is anteroposterior, with flattened outer and convex inner faces. The following approximate measurements are taken from Leidy's descriptions and figures:

	Millimeters
Free width of nasals	108
Free length	104
Outside measurement of horns	140

Etymology.—coloradensis, in allusion to the type locality.

Present determination.—The type of *Megacerops coloradensis*, consisting of the osseous horns and nasals, is apparently distinct specifically from Cope's *M. acer, M. bucco.*

SPECIES DESCRIBED BY MARSH AND COPE IN 1873–1876

Brontotherium Marsh, 1873

Cf. *Brontotherium*, this monograph, pages 555–557

Original reference.—Am. Jour. Sci., 3d ser., vol. 5, p. 486, 1873 (Marsh, 1873.1).

Type species.—Brontotherium gigas Marsh. (See below.)

Generic characters.—Marsh writes:

> An examination of the remains, in the Yale Museum, of the huge mammals allied to *Titanotherium* has led to the discovery that two different animals have hitherto been referred to the species known as *T. prouti.* These animals are generically distinct and probably are from separate geological horizons. The one here described differs from *Titanotherium* in its dentition, having but three lower premolars, the series being as follows: Incisors 2, canine 1, premolars 3, molars 3. The animal was, moreover, a true perissodactyl, with limb bones resembling those of *Rhinoceros.* The genus is related to *Titanotherium,* and the two appear to form a distinct family, which may be called Brontotheridae. The present species is based on portions of three individuals, one of which has the lower jaws and entire molar series complete. They indicate an animal fully equal to *T. prouti* in size, and but little inferior in bulk to the elephant. The lower molars resemble those in the type specimen of *T. prouti*, but the jaw below them is not so deep, and its lower margin is more nearly straight, descending but very slightly toward the angle. The front part of the lower jaws is somewhat suilline in form. The incisors are quite small, and the two next to the symphysis are separated from each other. There is a short diastema between the canine and the first premolar. [This is followed by remarks on the skeleton based on the "other specimens."]

Etymology: βροντή, thunder; θηρίον, beast.

Present determination.—This was the most important contribution to the knowledge of the titanotheres made up to that time. The characters of the lower jaw and of the skeleton are correctly described, and the family is referred to the Perissodactyla. Subsequent research has shown that the genus *Brontotherium* is distinct from *Menodus* and *Megacerops; "Brontotherium ingens,"* as used in later publications by Marsh, referred to the skull, the type of *"B. ingens,"* and not to the jaw, the type of *Brontotherium gigas.*

Brontotherium gigas Marsh, 1873

Cf. *Brontotherium gigas*, this monograph, page 567

Original reference.—Am. Jour. Sci., 3d ser., vol. 5, p. 486, 1873 (Marsh, 1873.1).

Subsequent reference.—Principal characters of the Brontotheriidae: Am. Jour. Sci., 3d ser., vol. 11, pl. 12, figs. 1–3, 1876 (Marsh, 1876.1).

Type locality and geologic horizon.—Colorado; exact locality and level not published. Sargent, Griswold, and Marsh, collectors.

Type.—"The present species is based on portions of three individuals, one of which has the lower jaws and entire molar series complete [lectotype]." Yale Mus. 12009. (See fig. 165.)

Characters of type.—The specific characters were not separated by Marsh from the generic charcters. Measurements of the lower jaw were given, some of which (now verified) are as follows:

	Millimeters
Length of lower jaw, from condyle to front of symphysis	634
Depth of lower jaw, from top of coronoid process to angle	367
Length of last lower molar	117
Length of last lower premolar (Marsh gives this as 51)	[49]

Etymology.—γίγας, giant.

Present determination.—This valid species is fully discussed in Chapter VI of this monograph (p. 567).

Symborodon Cope, 1873

Cf. *Menodus*, this monograph, page 525

Original reference.—Pal. Bull. No. 15, p. 2, "issued August 20, 1873" (Cope, 1873.2).

Subsequent reference.—Cope, Report on the vertebrate paleontology of Colorado, pl. 2, fig. 1; pls. 3, 4, 1874 (Cope, 1874.2).

Type species.—Symborodon torvus Cope. (See below.)

Generic characters.—Cope writes:

> Dentition: I.? 0; C. 1; Pm. 3; M. 3; the canines slightly separated from each other, but not from the first premolar. Crowns of the premolars with L-shaped crescents as in *Rhinoceros;* of the molars with completed crescents; the last molar with third posterior crescent. Symphysis mandibuli coossified, crowns of canines not projecting, conic. * * * The genus differs from *Titanotherium* and *Brontotherium* in the absence of incisors and from the former in the presence of but three premolars. If there had been a deciduous incisor on each side I was unable to detect any trace of it.

Etymology.—σύν, together; βορός, devouring; ὀδούς, tooth; in reference to the approximation of the opposite canines toward the middle line.

Present determination.—Subsequent research has proved that this genus is a synonym of *Menodus.* It is fully described on page 522.

Symborodon torvus Cope, 1875

Cf. *Menodus torvus,* this monograph, page 525, Figure 166

Original reference.—Pal. Bull. No. 15, p. 2, "issued August 20, 1873" (Cope, 1873.2).

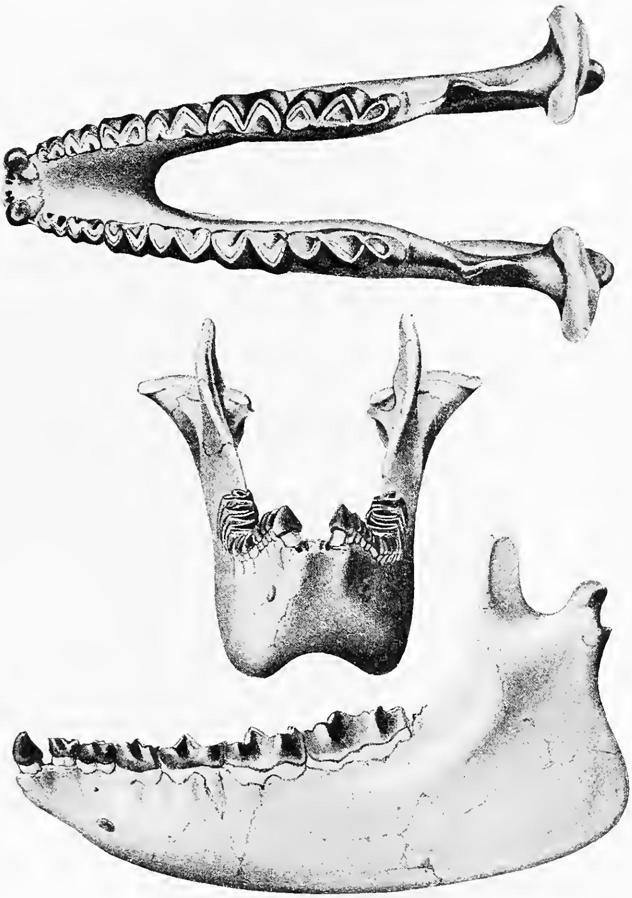

FIGURE 165.—Type (lectotype) of *Brontotherium gigas*

Lower jaw, with nearly complete dentition. Yale Mus. 12009. After Marsh, 1876. One-sixth natural size

Subsequent reference.—Report on the vertebrate paleontology of Colorado, p. 486, 1874. The jaw figured in Plate 2, Figure 1, is not the type of *torvus* (Cope, 1874.2).

Type locality and geologic horizon.—Horsetail Creek, Logan County, northeastern Colorado; Chadron formation (*Titanotherium* zone), level not ascertained.

Cotypes.—Cope writes: "The present genus is established on mandibular rami only, which can not be certainly associated with crania." These rami (Cope collection, Am. Mus. 6365, 6345) are accordingly cotypes. In his "Report on the vertebrate paleontology of Colorado" Cope says, "I append a description of the mandible, on which the species *Symborodon torvus* was established." Careful comparison of Cope's original and subsequent descriptions and measurements shows that the species was established largely upon the lower jaw (Am. Mus. 6365, fig. 166) which is accordingly regarded as the lectotype.

Etymology.—*torvus,* wild, grim.

Present determination.—The species is now regarded by Osborn as belonging in the genus *Menodus.* In size the type is intermediate between *M. heloceras* and *M. trigonoceras.*

Miobasileus Cope, 1873

(Indeterminate)

Original reference.—Pal. Bull. No. 15, p. 3, "issued August 20, 1873" (Cope, 1873.2).

Subsequent references.—On some extinct types of horned perissodactyls, p. 108, 1874 (Cope, 1874.1); Synopsis of new Vertebrata from the Tertiary of Colorado, p. 14, 1873 (Cope, 1873.3); Report on the vertebrate paleontology of Colorado, p. 490, 1874 (Cope, 1874.2); U. S. Geol. Survey Terr. Rept. for 1873, p. 490, 1874.

Type species.—*Miobasileus ophryas* Cope. (See below.)

Generic characters.—Not separated by Cope from specific characters. (See p. 201.)

Established on a cranium with nearly complete dentition but without mandibular ramus. Head elongate, concave in profile from the interorbital region to the supraoccipital crest. This is transverse and concave, the posterior borders of the temporal fossae extending behind it. These fossae leave a narrow flat vertex between them. Zygomatic arch stout and rather deep; a strong postglenoid process. Nasal bones very massive, their free portion elongate, hornless. A massive horn core rising from above each orbit, no superciliary angle or ridge. Orbit not inclosed behind. Of molar teeth only Pm. 2, M. 3, preserved, the M. with two, the Pm. with one inner cone, and two outer continuous crescents. The latter send inward to one side of the cones a transverse ridge. Incisors and canines unknown.

Char. specif.—Front concave transverse just behind between the horns. Latter massive and little compressed. Nasal bones convex longitudinally and transversely, slightly rugose. Transverse ridges of teeth with transverse expansions at their inner extremity, being thus T-shaped.

Measurements

	Millimeters
Length from apex of nasals to occipital condyles (axial)	684
Length from occipital condyles to femoris of palate	376
Length from occipital condyles to end of palatine lamina pteryzoidea	270
Length of four last molars	242
Length of three last molars	195
Length of last molar	68
Width of palate at nareal notch	116

Etymology.—*Mio*, Miocene; *βασιλεύς*, king—that is, monarch of the Miocene.

Present determination.—The genus is indeterminate. (See *M. ophryas.*)

Miobasileus ophryas Cope, 1873

(Indeterminate)

Original reference.—Pal. Bull. No. 15, p. 3, "issued August 20, 1873" (Cope, 1873.2).

Subsequent references.—Cope, On some extinct types of horned perissodactyls, p. 108, 1874 (Cope, 1874.1); Synopsis of new Vertebrata from the Tertiary of Colorado, p. 14, 1873 (Cope, 1873.3); Report on the vertebrate paleontology of Colorado, p. 490, 1874 (Cope, 1874.2).

Type locality and geologic horizon.—Cedar Creek, Logan County, Colo.; Chadron formation (*Titanotherium* zone), level not ascertained.

Type.—A cranium with incomplete dentition, without mandibular ramus. (In a later description Cope (1874.2, p. 490) remarks, "of molar teeth only pm 3–4, m 1, 2, 3, preserved.") This type was left in the field and is now lost.

Generic and specific characters (summarized from Cope).—Supraoccipital crest concave. Zygomatic arch stout and relatively deep. Nasal bones very massive, elongate, convex longitudinally and transversely; a massive horn core, little compressed, rising above each orbit. In a later communication Cope (1874.2, p. 491) gives the length from apex of nasals to occipital condyles as 664 millimeters and observes:

> The dental characters of this species ally it to the *S. trigonoceras*, but the form as well as the position of the horns is quite different. Instead of being triangular, a section of the base of these is elliptic. Extremity conical.

	Millimeters
Length from apex of nasals to occipital condyles	684
Length of three last molars	195
Length of last molar	68

Etymology.—*ὀφρύς*, eyebrow; possibly in allusion to the form of the orbit.

Present determination.—Owing to the loss of the type and the uncertain character of the description, this genus and species is indeterminate.

Megaceratops Cope, 1873

Original reference.—Pal. Bull. No. 15, p. 4, "issued August 20, 1873" (Cope, 1873.2).

Present determination.—This name *Megaceratops* was not proposed in order to denominate a new genus but was merely an emendation on etymologic grounds of Leidy's term *Megacerops*, of which it must be regarded as a synonym.

Megaceratops acer Cope, 1873

Cf. *Megacerops acer*, this monograph, page 545

Original reference.—Pal. Bull. No. 15, p. 4, "issued August 20, 1873" (Cope, 1873.2).

Subsequent reference.—Cope, Report on the vertebrate paleontology of Colorado, p. 488, pl. 7; pl. 8, fig. 3, 1874 (Cope, 1874.2).

Type locality and geologic horizon.—Horsetail Creek, northeastern Colorado; Chadron formation (*Titanotherium* zone), level not ascertained.

Type.—"A single cranium without under jaw." Am. Mus. 6348. (See figs. 167, 170.)

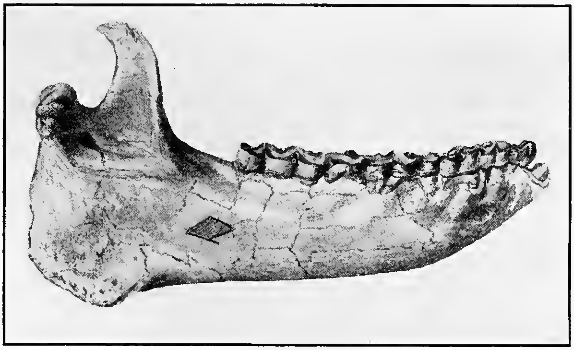

FIGURE 166.—Type (lectotype) jaw of *Symborodon torvus*
One-sixth natural size.

Specific characters.—Cope writes:

> Top of head flat, forming a narrow plane between the temporal fossae; latter produced backward. Orbit not inclosed behind, an overhanging superciliary ridge. Nasal exceedingly short and massive, each supporting a large acute horn core, which is connected with its fellow by a ridge at the base and diverges widely from it with an outward and forward curve to the acutely compressed apex. Each horn core about 1 foot long. The top of the head is plane between the orbits, and little concave fore and aft. The zygoma is very deep, and the postglenoid process well developed. End of nasal bones short and thick but flat.

Measurements

	Millimeters
Length of cranium (35 inches)	895
Length from posterior rim temporal fossa to middle of superciliary ridge	345
Width front between eyebrows	210
Length horn core on inner side (10 inches)	254

> The elemental origin of the horn cores is probably different in this genus from that which exists in *Miobasileus.*

Etymology.—*acer*, fierce, in allusion to the somewhat ferocious appearance.

Present determination.—This valid species, which pertains to the genus *Megacerops*, is fully described on page 545.

Megaceratops heloceras Cope, 1873

Cf. *Menodus heloceras*, this monograph, pages 524, 681

Original reference.—Pal. Bull. No. 15, p. 4, "issued August 20, 1873" (Cope, 1873.2).

Subsequent reference.—Cope, Report on the vertebrate paleontology of Colorado, pp. 487–488, 1874 (Cope, 1874.2).

Type locality and geologic horizon.—Horsetail Creek, northeastern Colorado; Chadron formation (*Titanotherium* zone), level not ascertained.

Type.—"A cranium * * * with nearly complete maxillary dentition," anterior teeth and part of frontals wanting. Am. Mus. 6360. (See fig. 168.)

Specific characters.—Cope writes:

> There is a prominent horizontal superciliary ridge without horns, and two short obtuse horn cores on the muzzle. These diverge outward, the outer sides being flattened and the summits contracted and truncate. They are mere rudiments of the horns seen in *M. aceronsor* [sic], *M. coloradoensis*. The molar teeth do not exhibit the T-shaped cross ridges seen in *Miobasileus*, and the two outer crescents are continuous with each other.

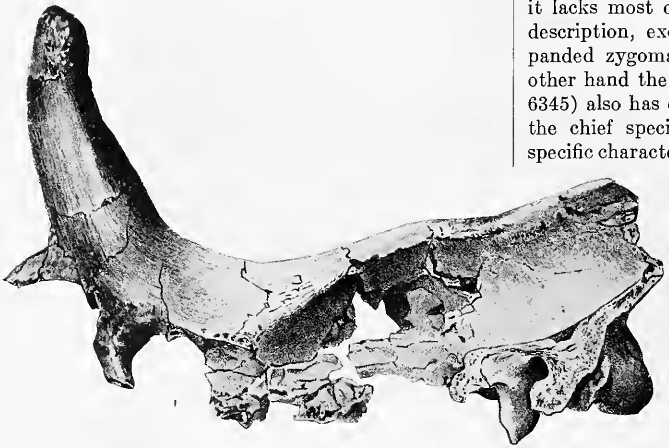

FIGURE 167.—Type (holotype) skull of *Megaceratops acer*

Am. Mus. 6348. After Cope, 1874. One-sixth natural size.

Measurements

	Millimeters
Length from posterior rim of temporal fossa to middle of osseous eyebrow	472
Least width of parietal plane	104
Superciliary width	260
Elevation of horn core	50

Etymology.—ἧλος, wart; *κέρας*, horn; in allusion to the wartlike appearance of the horn.

Present determination.—The species is valid but referable to the genus *Menodus*. (See p. 524.)

Symborodon bucco Cope, 1873

Cf. *Megacerops bucco*, this monograph, page 544

Original reference.—Synopsis of new Vertebrata from the Tertiary of Colorado, p. 11, 1873 (Cope, 1873.3).

Subsequent reference.—Cope, Report on the vertebrate paleontology of Colorado, pp. 484, 485, pls. 2–4. 1874 (Cope, 1874.2).

Type locality and geologic horizon.—Horsetail Creek, northeastern Colorado; Chadron formation (*Titanotherium* zone), level not ascertained.

Cotypes.—In the original description Cope says the species is represented "by an imperfect cranium; by a cranium almost perfect, including very probably both mandibular rami, with entire dentition; a fragmentary skeleton, including parts of cranium, teeth, and vertebrae; and by a series of cervical and dorsal vertebrae." Which of these cotype individuals thus mentioned shall we select as the lectotype? If we should take the first specimen mentioned, namely, the imperfect cranium (known to be Am. Mus. 6346), we find that since it consists of only the posterior portion it lacks most of the characters given in the specific description, except the single one of possessing expanded zygomata (hence the name *bucco*). On the other hand the "cranium almost perfect" (Am. Mus. 6345) also has expanded zygomata and was evidently the chief specimen, since it furnished most of the specific characters and measurements given in the original description; moreover, in Cope's fuller report (1874.2) it was figured in Plates 2, 3, 4, under the name *Symborodon bucco*, and in the key to the species (p. 484), in which *S. bucco* is contrasted with *S. altirostris*, the diagnostic characters (referring to the horns, premolars, nasals, depressed cranium) are evidently from the "cranium almost perfect" (No. 6345) rather than from the "imperfect cranium."

Lectotype.—From these clear indications of the author's intention the skull (Am. Mus. 6345) may therefore be regarded as the lectotype. (See figs. 169, 170.)

Specific characters.—Cope mentions especially the enormous buccal expansion of the zygomata, the characters of the horns, nasals, skull top, orbits, etc. Specific characters are fully given on page 544.

Etymology.—*bucco*, one having extended cheeks.

Present determination.—This species is provisionally regarded as a valid one.

Symborodon altirostris Cope, 1873

Cf. *Megacerops acer*, this monograph, page 545

Original reference.—Synopsis of new Vertebrata from the Tertiary of Colorado, p. 12, 1873 (Cope, 1873.3).

Subsequent references.—Cope, Report on the vertebrate paleontology of Colorado, p. 486, pls. 5, 6, 8, fig. 1, 1874 (Cope, 1874.2); The Perissodactyla, pl. 33, fig. a, opposite p. 1062, 1887 (Cope, 1887.1).

Type locality.—Cedar Creek, Logan County, Colo.

Type.—A cranium with premolar-molar teeth, zygomatic arches fractured (Am. Mus. 6350). (See figs. 170, 171.)

Characters of type (summarized from Cope).—Nasal bones very short, broad, obtuse, massive, and "standing on a plane above that of the front." Orbit very far forward. Horns straight, with approximated bases and moderately divergent, subcylindrical at base and compressed inward and forward at the narrow apex. "The first premolar and two incisors are very insignificant; canines with short stout crowns." The premolars with two smooth cones. Many other characters are given.

Etymology.—*altus*, high; *rostris*, beak, snout; in allusion to the high position of the nasals.

Present determination.—As shown (p. 545), there are reasons for regarding the type of *S. altirostris* as representing a female skull of *Megacerops acer*.

Symborodon trigonoceras Cope, 1873

Cf. *Menodus trigonoceras*, this monograph, page 528

Original reference.—Synopsis of new Vertebrata from the Tertiary of Colorado, p. 13, 1873 (Cope, 1873.3).

Subsequent references.—Cope, Report on vertebrate paleontology of Colorado, 1874, p. 488, 1874 (Cope, 1874.2); The Perissodactyla, p. 1065, figs. 29, 30, 1887 (Cope, 1887.1).

Type locality and geologic horizon.—Horsetail Creek, northeastern Colorado; Chadron formation (*Titanotherium* zone), level not ascertained.

FIGURE 168.—Type (holotype) skull of *Megaceratops heloceras*

Am. Mus. 6360. After Cope. One-fifth natural size.

Cotypes.—Skull (Am. Mus. 6355) lacking all the teeth except m^2; Am. Mus. 6356, anterior-inferior portion of skull, including horns, nasals, right zygoma, and teeth. Of these two cotypes we may regard No. 6355 as the lectotype. (See fig. 172.)

Specific characters (summarized from Cope).—A strong basal cingulum, on the inner side of the premolars, which is continued in a less prominent form between the bases of the cones of the molars. Bases of cones of premolars strongly plicate. Horns triquetrous, directed outward and upward. Squamosals not expanded, nasals elongate transversely plane.

FIGURE 169.—Type (lectotype) skull of *Symborodon bucco*

Am. Mus. 6345. After Cope, 1874. One-ninth natural size. The mandible in the upper figure probably does not belong with the skull.

Etymology.—τρίς, three; γωνία, angle; κέρας, horn; in allusion to the three-sided section of the horn.

Present determination.—This is a valid species, described on page 528, referable to *Menodus.*

Brontotherium ingens Marsh, 1873

Cf. *Menodus giganteus*, this monograph, page 530

Original reference.—Am. Jour. Sci., 3d ser., vol. 7, pp. 85, 86, pls. 1, 2, January, 1874; "published Dec. 30, 1873" (Marsh, 1874.1).

Subsequent reference.—Marsh, The principal characters of the Brontotheridae, p. 335, text figs. 1, 2, pls. 10, 11, 1876 (Marsh, 1876.1).

Type locality and geologic horizon.—Colorado; Chadron formation (*Titanotherium* zone); exact locality and level not recorded.

Type.—A complete skull; premaxillaries with incisors and canines wanting; nasals and horns partly restored. Yale Mus. 2010. (See fig. 173.)

Characters.—Marsh says:

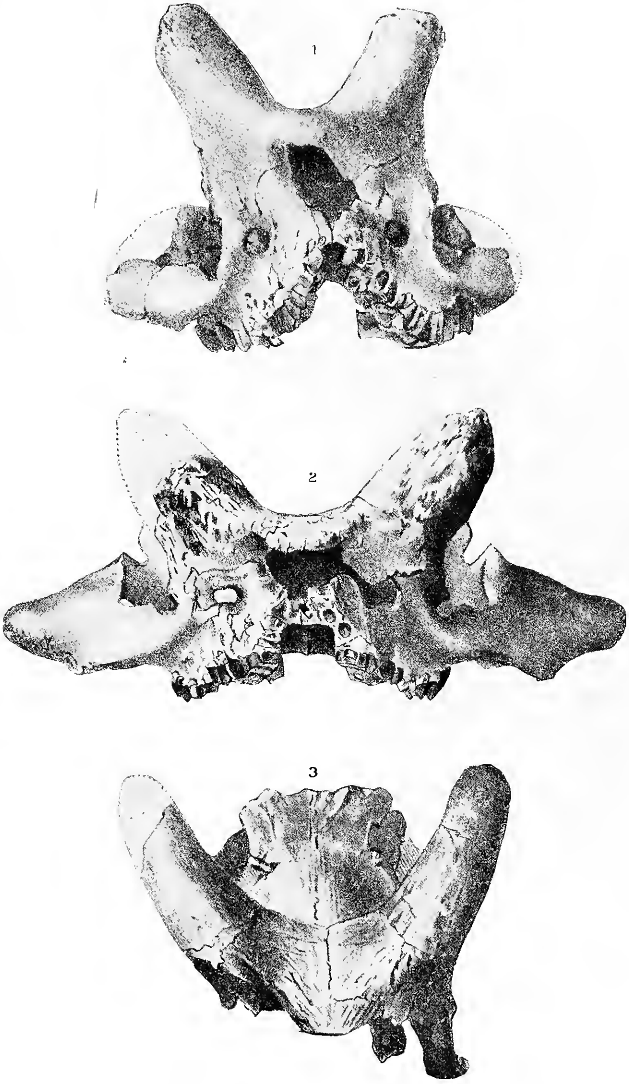

FIGURE 170.—Type skulls of *Symborodon altirostris* (1), *S. bucco* (2), and *Megacerops acer* (3)

Front views. After Cope, 1874. One-sixth natural size.

The most striking peculiarity of this cranium is the pair of huge horn cores on the nasals. They are about 8 inches in length and extend upward and outward. They are triangular at the base, with the broadest face external. The two inner faces of each core are separated by a ridge, which is continued to the median line. The upper part of the horn cores is rugose, and the base contains large air cavities. The free extremities of the nasals are coossified and much elongated. They are rounded in front, slightly decurved, and the surface at the end is rugose. [Many other characters are listed.]

	Millimeters
Length of skull from occipital condyles to end of nasals (36 inches)	915
Distance on median line from occipital crest to end of nasals	762

	Millimeters
Expanse of zygomatic arches	558
Least distance across vertex	157
Space occupied by four upper premolars	162
Space occupied by three upper true molars	266
Space occupied by molar-premolar series	428

Etymology.—*ingens*, vast.

Present determination.—The species is a synonym of *Menodus giganteus* Pomel.

Symborodon hypoceras Cope, 1874

Cf. *Brontotherium hypoceras*, this monograph, page 562

Original reference.—U. S. Geol. and Geog. Survey Terr. Ann. Rept. for 1873 (Hayden), p. 491 [no figure], 1874 (Cope, 1874. 2).

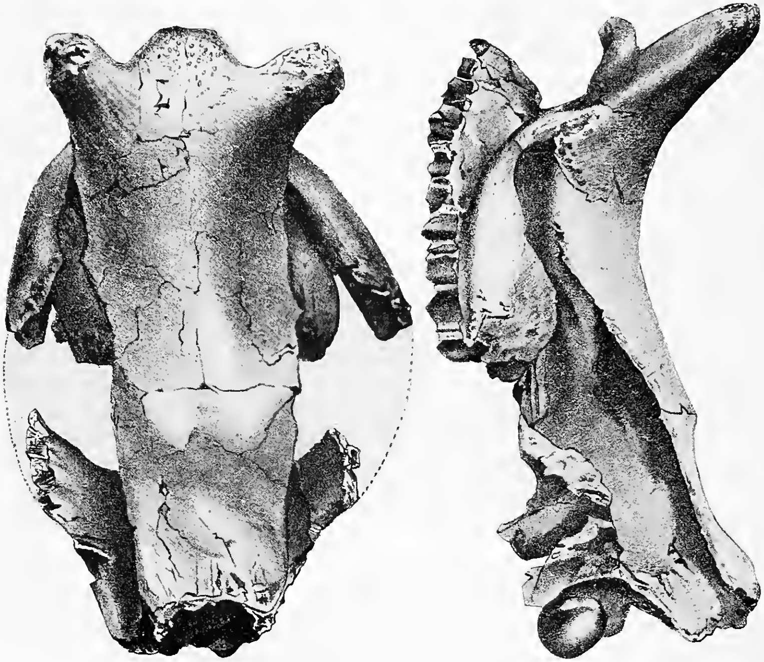

FIGURE 171.—Type (holotype) skull of *Symborodon altirostris*

Am. Mus. 6350. After Cope, 1874. One-sixth natural size.

Type locality.—?Cedar Creek, Logan County, Colo.

Type.—Cope writes:

> This species reposes on a fragmentary cranium only, which embraces nasal, maxillary, frontal, malar bones, etc., both zygomata, premolar, and parts of molar teeth. These fragments were taken out of the matrix by the writer and were found in juxtaposition. They represent parts of the same skull and, as no other was found in the same bank, are probably without admixture.

The only remains representing this type which are now preserved in the American Museum of Natural History (Am. Mus. 6361) include two portions of the malar bones, a fragment of the orbit and infraorbital canal, a fragment of the alveolar region, and two horn cores of very different shape described below. (See fig. 174.)

Specific characters.—Infraorbital foramen "flat with a wide external face, instead of being a cylindric column as in *S. acer*, *altirostris*, *bucco*, and *ophryas*." One of the horn cores "consists of the extremital part. * * * Its section is a compressed oval narrowed in front; its profile with parallel outlines and a little recurved and not very rugose. Its size as compared with the rest of the skull is the smallest in the genus, and not more than half the proportions of the *S. altirostris*." Another fragment Cope determined as a portion of the frontal bearing a "large osseous tuberosity, which consists of a mass of bone coossified with the upper surface as in the horn of the giraffe." Cope concluded that "it is probable that this species possessed two pairs of osseous processes or cores on each side, the one on the nasal, the other on the frontal bone." The name "*hypoceras*" doubtless referred to the supposed presence of the second horn core (the rounded tuberosity) behind and below the oval-sectioned horn on the nasals. Cope gives 14 measurements, including the following:

	Millimeters
Length from front of orbit to glenoid fossa (axial)	365
Depth of malar below orbit	20
Length of molars and last three premolars	293
Length of last three premolars	110
Diameter of horn core, transverse	38

Fixation of lectotype.—Cope's conclusion that the above-mentioned fragments "are probably without admixture" appears open to doubt. The "frontal tuberosity" referred to is shown by comparison with well-preserved material to be the horn core of the left side of an immature individual resembling *Allops marshi*, a reference favored by Cope's observation of the wide bridge over the infraorbital foramen, which contrasts with the narrow columnar bridge in *Brontotherium* and *Symborodon.* The oval-sectioned horn core which Cope supposed to be borne on the nasals is a right horn core of very different shape, agreeing closely with that in skull No. 4702, U. S. National Museum, which Osborn selected (1902.208, p. 106) as the neotype of this species. The oval-sectioned horn core may, therefore, be regarded as the *lectotype.*

Etymology.—*ὑπό*, below; *κέρας*, horn; in allusion to the supposed presence of a low horn swelling on the frontal, behind the one on the nasal.

Present determination.—As thus interpreted, *hypoceras* is a valid species of the genus *Brontotherium.*

Anisacodon Marsh, 1875

Cf. *Menodus*, this monograph, page 522

Original reference.—Am. Jour. Sci., 3d ser., vol. 9, p. 246, March, 1875 (Marsh, 1875.1).

Type species.—*Anisacodon montanus* Marsh (see below).

Generic characters (Marsh).—"Dentition: Incisors $\frac{0}{1}$; canines $\frac{1}{1}$; premolars $\frac{4}{3}$; molars $\frac{3}{3}$. No superior diastema. Strong inner basal ridge on upper premolars. Last upper molar with two inner cones. No postorbital process."

Etymology.—*ἄνισος*, unequal; *ἀκη*, point; *ὀδούς*, tooth. Possibly in allusion to the unequal development of the two inner cones on the third upper molar.

Present determination.—In view of the strong similarities to *Menodus* in the vestigial condition of the incisors, in the strong internal cingulum in the premolars, in the shape of the nasals, and in the second internal cone of the third molar, this genus is now regarded as a synonym of *Menodus.*

Anisacodon montanus Marsh, 1875

Cf. *Menodus giganteus?*, this monograph, page 537

Original reference.—Am. Jour. Sci., 3d ser., vol. 9, p. 246, March, 1875 (Marsh, 1875.1).

Type locality and geologic horizon.—"Northern Nebraska" (Big Badlands, White River, S. Dak.); Chadron formation (*Titanotherium* zone); exact locality and level not recorded.

Type.—A fragmentary skull including the maxillaries and fragmentary molar teeth. Yale Mus. 10022. (See fig. 175.)

Specific characters.—Marsh writes:

> This species is especially distinguished by the emargination of the extremity of the nasals, the short premaxillaries, and the rectangular form of the last upper molar. The inner posterior cone of this molar is smaller than the one in front, and quite distinct from the posterior basal ridge.

Measurements [selected from Marsh]

	Millimeters
Width of nasals above end of premaxillaries	95
Anteroposterior diameter of last upper premolar	43
Anteroposterior diameter of penultimate upper molar	77
Anteroposterior diameter of last upper molar	84

Etymology.—*montanus*, dwelling in the mountains. Exact allusion uncertain, unless the badland topography of South Dakota is thought of as mountainous.

FIGURE 172.—Type (holotype) skull of *Symborodon trigonoceras*

Am. Mus. 6355. One-ninth natural size.

Present determination.—In the form of its premolars and third molar as well as in its vestigial incisors this animal resembles *Menodus giganteus;* the emarginate nasals with processes on either side of the median notch also recall female *Menodus* skulls. *Anisacodon (Diconodon) montanus* is probably referable to *Menodus* cf. *M. giganteus.*

"Diconodon non Anisacodon" Marsh, 1876

Cf. *Menodus giganteus*, this monograph, page 530

Original reference.—Am. Jour. Sci., 3d ser., vol. 11, p. 339, April, 1876 (Marsh, 1876.1). In this paper Marsh gives diagnosis of four genera of Brontotheridae. No. 4 is called "*Diconodon* Marsh (*Anisaco-*

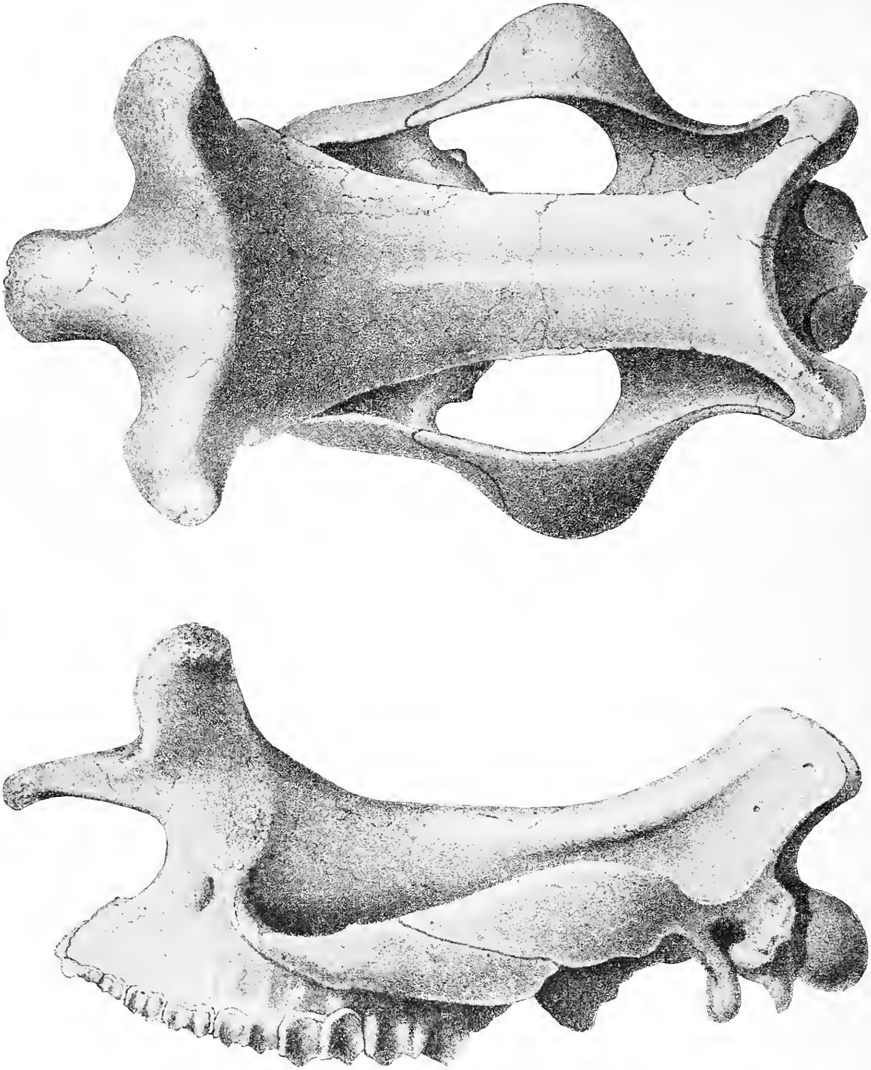

FIGURE 173.—Type (holotype) skull of *Brontotherium* (=*Menodus*) *ingens*

Yale Mus. 2010. After Marsh, 1874. About one-sixth natural size.

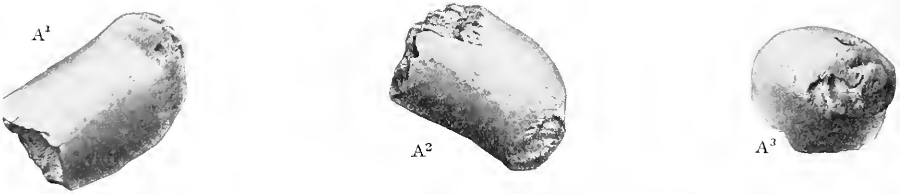

FIGURE 174.—Type (lectotype) of *Symborodon* (=*Brontotherium*) *hypocĕras*

Am. Mus. 6361. One-half natural size. Fragment of right horn core: A^1, front view; A^2, rear view; A^3, top view.

don). * * * Type *D. montanus* Marsh." The term *Anisacodon* had been preoccupied by *Anisacodon* Marsh, 1872, a genus of insectivores.

Etymology.—δὶς, double; κῶνος, cone; ὀδοὺς, tooth.

Present determination.—See remarks under *Anisacodon*, above.

FIRST NOTICE OF CANADIAN TITANOTHERES BY COPE, 1886

Menodus angustigenis Cope, 1886

Cf. *Megacerops angustigenis*, this monograph, page 482, fig. 176, C_1

Original reference.—Canada Geol. Survey Ann. Rept., new ser., vol. 1, p. 81, 1886 (Cope, 1886.1).

Subsequent references.—"*Haplacodon angustigenis*," The Vertebrata of the Swift Current River, II, p. 153, 1889 (Cope, 1889.1); On Vertebrata from the Tertiary and Cretaceous rocks of the Northwest Territory, I, p. 13, pl. 5, figs. 1, 2; pl. 6, figs. 2, 2a; pl. 7, figs. 1, 1a, 1a [bis], 1891 (Cop, 1891.2).

Type locality and geologic horizon.—Swift Current River, Assiniboia, Canada; Cypress Hills beds, level not determined. McConnell and Weston, collectors.

Cope's cotypes.—Cope writes:

> This large mammal is represented by numerous specimens. I select for present description two maxillary bones from the same skull [fig. 176, A] [Cope, 1891.2, pl. 5, figs. 1, 2], each of which contains the first [fourth] premolar and the true molars; and two lower jaws from second and third individuals [fig. 176, B]. One of these [op. cit., pl. 7, figs. 1, 1a, 1a [bis], our fig. 176 C, now regarded as the lectotype] consists of little more than the symphysis. The other [op. cit., pl. 5, fig. 2; pl. 6, figs. 2, 2a] includes part of the symphysis and the left ramus, which contains all the molar teeth except the first and last. [See fig. 176.]

Lectotype.—Of these semingly coequal types or cotypes, which is to be regarded as the lectotype? The one mentioned first is "the two maxillary bones from the same skull," but the mandibular symphysis (op. cit., pl. 7, figs. 1, 1a, 1a [bis]), from which the species evidently takes its name (meaning narrow chin), is certainly to be selected as the lectotype.

Specific characters.—Cope's description is too long to quote here. He compared *Menodus angustigenis* with "*Symborodon trigonoceras*" and other species and gave numerous measurements. Among the chief characters noted are the contracted shape of the mandibular symphysis and the square outline of the molars.

Etymology.—*angustus*, narrow; *gena*, chin.

Present determination.—As defined from the lectotype the species is provisionally referred to *Megacerops*, although its generic reference is uncertain.

The maxilla with the dentition belongs to a very different animal. It is apparently referable to *Allops* sp. (See below.) The lower jaw appears to be referable to *Menodus* cf. *M. proutii.*

SPECIES DESCRIBED BY SCOTT AND OSBORN IN 1887

Menodus tichoceras Scott and Osborn, 1887

Cf. *Brontotherium tichoceras*, this monograph, page 565

Original reference.—Mus. Comp. Zoology Bull., vol. 13, No. 5, p. 159, text figs. 3, 2; 5, 2; 6, 2, 1887 (Scott and Osborn, 1887.1).

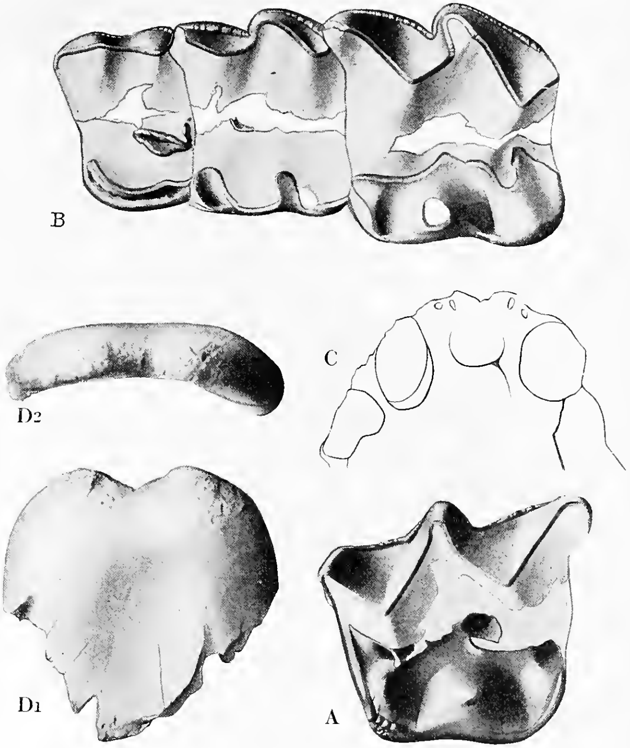

FIGURE 175.—Type (holotype) of *Anisacodon montanus*

Yale Mus. 10022. A, Third right upper molar; B, fourth upper premolar and first and second molars; C, alveoli of upper canines and incisors; D_1, nasals, top view; D_2, nasals, front view. All one-half natural size.

Type locality and geologic horizon.—Big Badlands, South Dakota; exact locality and horizon not recorded. S. Garman, collector.

Type.—Scott and Osborn describe the type as "a large skull with the dentition complete, lacking the upper part of the horns and the crest of the occiput." Now in the Museum of Comparative Zoology at Cambridge, Mass. (See fig. 177.)

Characters (abbreviated from Scott and Osborn). Dentition: I 2, C 1, P 4, M 3. The skull is described as 29 inches [736 mm.] in length; with a narrow and elevated anterior portion; nasals of medium length, with short, obliquely placed horns, zygomatic arch very massive, presenting a bulge in the posterior half which is much less prominent than in *S. bucco*.

Etymology.—τεῖχος, wall; κέρας, horn; possibly in allusion to the high connecting crest.

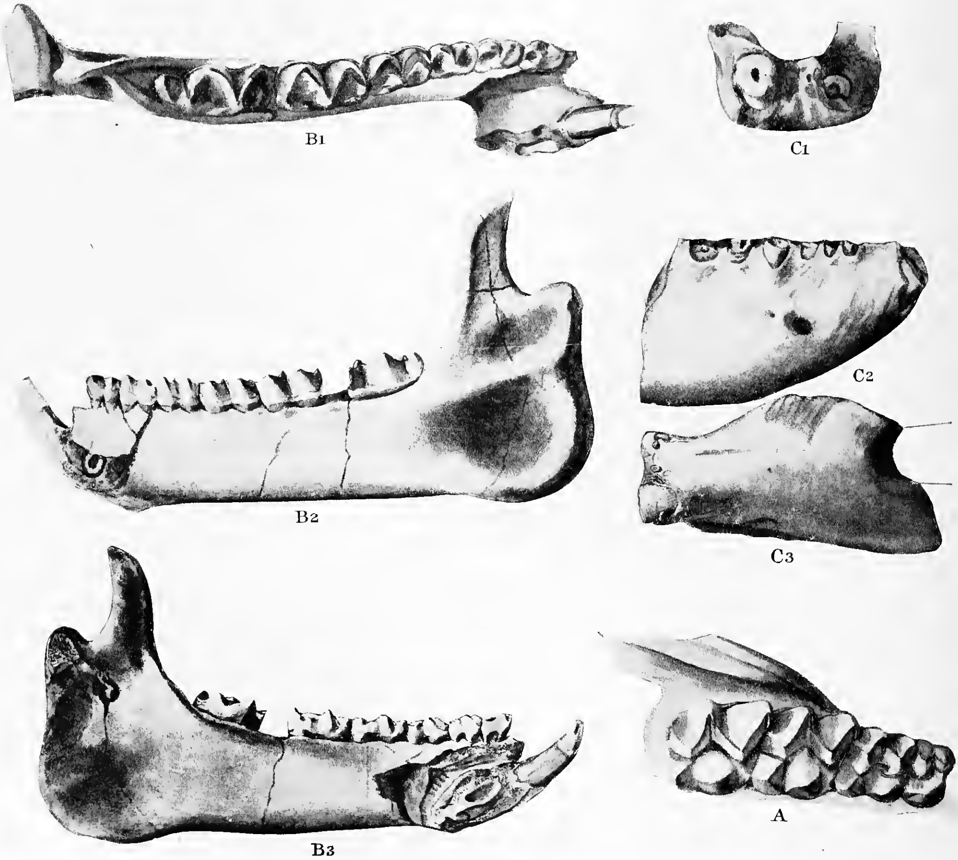

FIGURE 176.—Cope's cotypes of *Menodus angustigenis*

A, Right maxilla (subsequently made the type of *Haplacodon angustigenis*), three-sixteenths natural size; B, left half of a lower jaw (now referred to *Menodus* sp.), three-sixteenths natural size; C, symphysis mandibulae (leetotype), one-third natural size (C_1, front; C_2, right side; C_3, under side).

Present determination.—This species is provisionally referred to *Brontotherium*, but its exact position in that phylum is uncertain. (See p. 565.)

Menodus dolichoceras Scott and Osborn, 1887

Cf. *Brontotherium dolichoceras*, this monograph, page 572

Original reference.—Mus. Comp. Zoology Bull., vol. 13, No. 5, p. 160, figs. 3, 3; 5, 3; 6, 3, 1887 (Scott and Osborn, 1887.1).

Type locality and geologic horizon.—South Dakota; Chadron formation (*Titanotherium* zone); exact locality and level not recorded.

Type.—A skull incomplete in the supraoccipital region; zygomatic arch fragmentary; maxillary, palatine, and basioccipital regions much distorted. Now in the Museum of Comparative Zoology, Harvard University. (See fig. 177.)

Characters.—Scott and Osborn write:

Dentition: I ?, $C^{\underline{1}}$, $P^{\underline{4}}$, $M^{\underline{3}}$. Upper premolars with a faint internal cingulum. Nasal bones extremely short and obtuse. Horns extremely long and powerful, directed obliquely forward and outward, projecting beyond the nasals in side view. The section is suboval at the base, with the long axis obliquely transverse. Cranium very broad and saddle-shaped above the orbits, narrowing somewhat posteriorly. A prominent and overhanging superciliary ridge. Postglenoid and post-tympanic processes united for a short distance. The skull which we have made the type of this species is much larger and more powerful than Professor Cope's type of *S. acer*. The horns are longer and more widely divergent at the base. The angle of inclination of the horns and the diminutive proportions of the nasals, as well as the form of the top of the cranium, all bring this specimen near *S. acer* and separate it from other known species. Unlike *S. acer,* the horns are not united by a ridge. [This is an error.] The specimen is incomplete in the supraoccipital region, the zygomatic arch is fragmentary, and the maxillary, palatine, and basioccipital regions are much distorted.

Menodus platyceras Scott and Osborn, 1887

Cf. *Brontotherium platyceras,* this monograph, page 578

Original reference.—Mus. Comp. Zoology Bull., vol. 13, No. 5, pp. 160, 161, fig. 4, 1887 (Scott and Osborn, 1887.1).

Subsequent reference.—The cranial evolution of *Titanotherium,* p. 186, fig. 7A, 1896 (Osborn, 1896.110). The specimen figured is not the type.

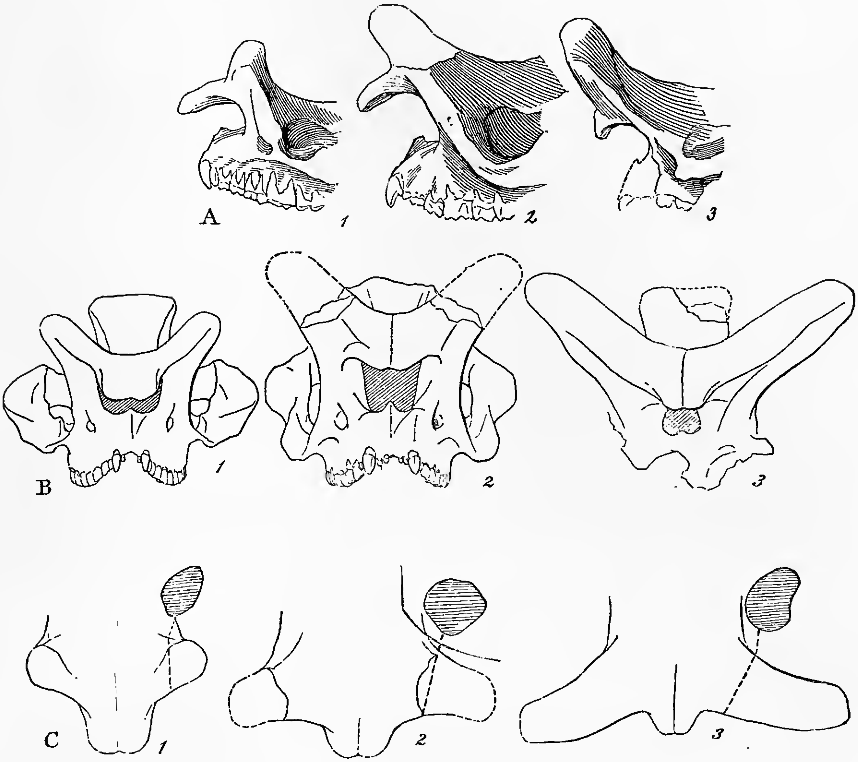

FIGURE 177.—Anterior part of skulls of (1) "*Megacerops coloradensis*" (not the type), now referred to *Allops marshi;* (2) *Menodus tichoceras* (type) (present determination, *Brontotherium tichoceras*); and (3) *Menodus dolichoceras* (type) (present determination, *Brontotherium dolichoceras*)

Specimens in the Museum of Comparative Zoology, Harvard University. After Scott and Osborn, 1887. Greatly reduced in size. A, Side views; B, front views, showing the variations in the horns, nasals, and anterior nares; C, top views, showing the nasals and horns, and sections of the bases of the horns.

Revised measurements

	Millimeters
Occipital condyles to nasal tips	690
Free length of nasals	45
Free breadth of nasals	90
Outside measurement of horns	310
Anteroposterior diameter of horns	85
Transverse diameter of horns	125

Etymology.—δολιχός, long; κέρας, horn.

Present determination.—As shown in Chapter VI the present species probably pertains to *Brontotherium* rather than to *Symborodon.*

Type locality and geologic horizon.—Big Badlands, South Dakota; Chadron formation (*Titanotherium* zone, Chadron C); exact locality and level not recorded. S. Garman, collector.

Type.—A pair of horns with the nasal bones attached. Now in the Museum of Comparative Zoology at Cambridge, Mass. (See fig. 178.)

Neotype.—Skull (Am. Mus. 1448).

Characters.—Scott and Osborn write:

Nasal bones extremely short and obtuse, as in *M. dolichoceras* and *M. acer.* The inner [posterior] contour of the horns

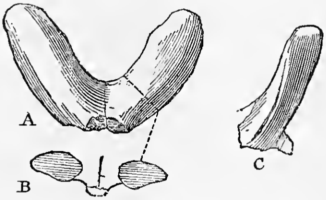

Figure 178.—Type (holotype) horns of *Menodus platyceras*

In the collection of the Museum of Comparative Zoology, Harvard University. After Scott and Osborn, 1887. Greatly reduced. A, Front view; B, cross section; C, side view.

is concave; they are greatly flattened anteroposteriorly, with a ridgelike outer margin, and connected by a well-raised median ridge. The posterior face is nearly plane, the anterior is convex, so that the section of the horn is plano-convex from base to tip. In side view the horns completely overhang the nasals and are slightly recurved. The long axis of the horn section is [almost or quite] directly transverse.

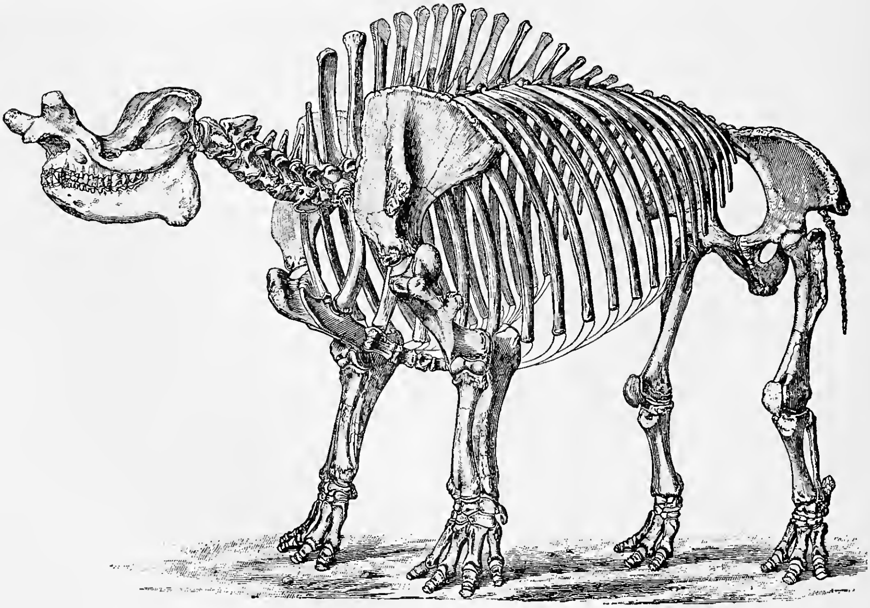

Figure 179.—Type (holotype) skeleton of *Brontops robustus*

Yale Mus. 12048. After Marsh, 1889. One twenty-fourth natural size.

Measurements

	Millimeters
Outside length of horns	315
Transverse diameter of horns	125
Anteroposterior diameter of horns	67

The type probably belongs to a young male in which the horns are not fully developed, because the horns increase in width and flatness and the basal section becomes more truly transverse, with age.

Etymology.—πλατύς, flat; κέρας, horn.

Present determination.—This valid species, described on page 578, belongs in the genus *Brontotherium*.

SPECIES DESCRIBED BY MARSH IN 1887

Brontops Marsh, 1887

Cf. *Brontops*, this monograph, page 482

Original reference.—Am. Jour. Sci., 3d ser., vol. 34, p. 326, October, 1887 (Marsh, 1887.1).

Type species.—*Brontops robustus* Marsh. (See below.)

Generic characters.—Marsh writes:

> The present genus is quite distinct from any of the forms previously described. * * * The skull is large and massive, with widely expanded zygomatic arches, and short and robust horn cores, projecting well forward. In general form it resembles the skull of *Brontotherium* but may be readily distinguished from it by the dental formula, which is as follows: Incisors $\frac{2}{1}$; canines $\frac{1}{1}$; premolars $\frac{4}{4}$; molars $\frac{3}{3}$.
>
> The presence of four premolars in each ramus of the lower jaw is a distinctive feature in this genus. This character, with the single, well-developed incisor, marks both the known species [*B. robustus*, *B. dispar*].

Etymology.—*Brontotherium;* ὤψ, face, "having the face or appearance of"; resembling *Brontotherium.*

Present determination.—In 1902 Osborn (1902.208) treated *Brontops* as a synonym of *Megacerops* Leidy, but renewed examination of Leidy's figure of *M. coloradensis* indicates that it is not congeneric with *Brontops*, which is here regarded as a valid genus.

Brontops robustus Marsh, 1887

Cf. *Brontops robustus*, this monograph, page 492

Original reference.—Am. Jour. Sci., 3d ser., vol. 34, p. 326, October, 1887 (Marsh, 1887.1).

Subsequent references.—Restoration of *Brontops robustus:* Am. Jour. Sci., 3d ser., vol. 37, pp. 163–165, pl.

6, 1889 (Marsh, 1889.1); skeleton and restoration, this monograph, Plates XCVI–CIII, CXCV–CCXXIX.

Type locality and geologic horizon.—"Near the White River in northern Nebraska." "The geological horizon is in the upper part of the *Brontotherium* beds [Chadron formation, *Titanotherium* zone]" (Marsh). "Upper levels of middle beds at least 60 feet below the top of the upper beds" (Hatcher, 1901).

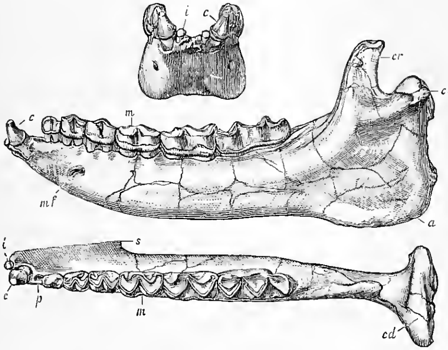

FIGURE 180.—Type (holotype) lower jaw of *Brontops dispar*
Nat. Mus. 4941. After Marsh, 1887. One-eighth natural size.

Type.—A skull and skeleton, Yale Mus. 12048. (See fig. 179.)

Specific characters.—Marsh did not formally separate the specific from the generic characters. He records the fact that the skull is large and massive, with widely expanding zygomatic arches and stout, robust horn cores, projecting well forward.

Etymology.—*robustus*, robust (that is, strong as an oak, *robur*).

Present determination.—The genus and species are valid. The species is described also on pages 492–499.

Brontops dispar Marsh, 1887

Cf. *Brontops dispar*, this monograph, page 488

Original reference.—Am. Jour. Sci., 3d ser., vol. 34, pp. 327, 329, figs. 7, 8 (jaw); not figs. 5, 6 (skull), October, 1887 (Marsh, 1887.1).

Type locality and geologic horizon.—Found on Hat Creek, Sioux County, Nebr., by J. B. Hatcher, May 14, 1886; Chadron formation (*Titanotherium* zone), middle level.

Type.—"A nearly complete skull with lower jaws and entire dentition." (Marsh.) Nat. Mus. 4941 (skull D). (See fig. 180.)

Characters.—Marsh writes: "The skull is less massive and proportionately more elongate than in the type species, and the lower jaw more slender." In the same brief passage Marsh described a young skull (Nat. Mus. 4258) as belonging to the same species; this is a somewhat more primitive type (*Brontops brachycephalus*) belonging to a younger individual (p. 483).

Etymology.—*dispar*, uneven, probably in allusion to the asymmetrical distortion of the type skull.

Present determination.—The species is valid and is now referred to *Brontops*.

Menops Marsh, 1887

Cf. *Menodus*, this monograph, page 522

Original reference.—Am. Jour. Sci., 3d ser., vol. 34, p. 328, October, 1887 (Marsh, 1887.1).

Type species.—*Menops varians.* (See below.)

Generic characters.—Marsh writes:

> The present genus is most nearly related to *Diconodon* and in its molar teeth agrees with that form. It differs in the presence of two upper incisors on each side. The superior dentition is as follows: Incisors, 2; canine, 1; premolars, 4; molars, 3.

Etymology.—*Menodus; ὤψ*, face; resembling *Menodus* (cf. *Brontops*, above).

Present determination.—The incisors are vestigial, the alveoli being very small. The skull presents resemblance to both *Menodus* and *Allops*. The generic reference is to *Menodus*.

Menops varians Marsh, 1887

Cf. *Menodus varians*, this monograph, page 535

Original reference.—Am. Jour. Sci., 3d ser., vol. 34, p. 328, fig. 9, October, 1887 (Marsh, 1887.1).

Type locality and geologic horizon.—"*Brontotherium* beds of Dakota" (Chadron formation, *Titanotherium* zone); exact locality and level not stated. George A. Clarke, collector.

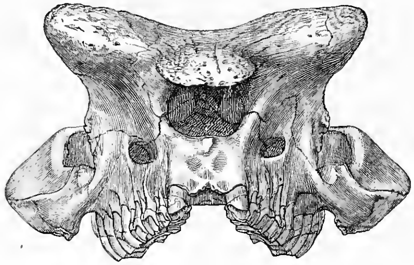

FIGURE 181.—Type (holotype) skull of *Menops varians*
Yale Mus. 12060. Front view. One-eighth natural size.

Type.—A well-preserved skull (Yale Mus. 12060). (See fig. 181.)

Specific characters.—Not separated by Marsh from generic characters. (See above.)

Etymology.—*varians*, variant; allusion doubtful, but possibly to the somewhat aberrant character of the type skull.

Present determination.—The species is valid and is referred to *Menodus*.

Titanops Marsh, 1887

Cf. *Brontotherium*, this monograph, page 555

Original reference.—Am. Jour. Sci., 3d ser., vol. 34, p. 330, October, 1887 (Marsh, 1887.1).

Type species.—Titanops curtus. (See below.)

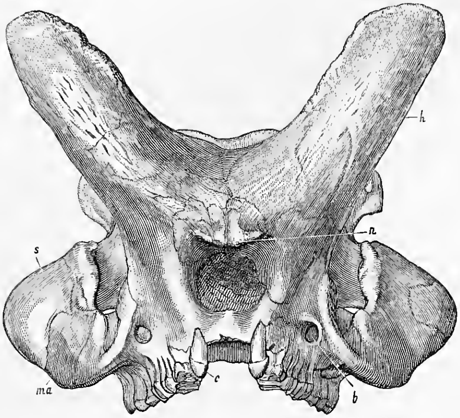

FIGURE 182.—Type (holotype) skull of *Titanops curtus*
Front view. Yale Mus. 12013. After Marsh, 1887. One-eighth natural size.

Generic characters.—Marsh writes:

> This genus contains the largest members of the Brontotheridae and some of the last survivors of the group. They are distinguished from all the other known types by the long, narrow skulls, lofty, flat horn cores, and short nasals. The upper dentition corresponds nearly to that of *Brontotherium*, but the upper molars have all two inner cones. * * * The nasals are the shortest known in the group.

Etymology.—Titanotherium; ὤψ, face—that is, like *Titanotherium.*

Present determination.—The genus is a synonym of *Brontotherium* Marsh.

Titanops curtus Marsh, 1887

Cf. *Brontotherium curtum*, this monograph, page 574

Original reference.—Am. Jour. Sci. 3d ser., vol. 34, p. 330, fig. 11, October, 1887 (Marsh, 1887.1).

Type locality and geologic horizon.—Colorado; exact locality not stated but recorded by Hatcher (1901) as from the upper *Titanotherium* zone [of Chadron formation].

Type.—A complete skull with teeth (Yale Mus. 12013). (See fig. 182.)

Specific characters.—Not separated from generic characters by Marsh.

Etymology.—curtus, short; in allusion to the short nasals.

Present determination.—The species is valid and is referred to *Brontotherium.*

Titanops elatus Marsh, 1887

Cf. *Brontotherium gigas*, this monograph, page 567

Original reference.—Am. Jour. Sci., 3d ser., vol. 34, p. 330, fig. 12, October, 1887 (Marsh, 1887.1).

Type locality and geologic horizon.—"Upper *Titanotherium* zone, South Dakota" (Chadron formation).

Type.—A skull and jaw (Yale Mus. 12061). (See fig. 183.)

Specific characters.—Marsh writes:

> The nasals are much longer, and the occipital crest much higher, than in the type species [*T. curtus*]. The zygomatic arches are unfortunately wanting, but the lower jaw is present, nearly in place. It shows no marked characters different from that of *Brontops.*

Etymology.—elatus, lofty; possibly in allusion to the high stage of specialization.

Present determination.—The species is synonymous with *Brontotherium gigas* Marsh.

Allops Marsh, 1887

Cf. *Allops*, this monograph, page 506

Original reference.—Am. Jour. Sci., 3d ser., vol. 34, p. 331, October, 1887 (Marsh, 1887.1).

Type species.—Allops serotinus. (See below.)

Generic and specific characters.—Marsh writes:

> This skull in its general form resembles that of *Brontotherium*, but differs in having only a single upper incisor, and the last molar has the posterior inner cone more strongly developed.
>
> The superior dentition is as follows: Incisor, 1; canine, 1; premolars, 4; molars, 3.
>
> In the type specimen the canine is small, extending but little below the premolars. There is no diastema. The upper premolars have a very strong inner basal ridge. The nasals are wide, expand forward in the free portion, and are notched in front. The entire length of the skull is 31 inches (79 centimeters), the distance across the zygomatic arches 21 inches (53 centimeters), and the length of the horn cores about 10 inches (25 centimeters).

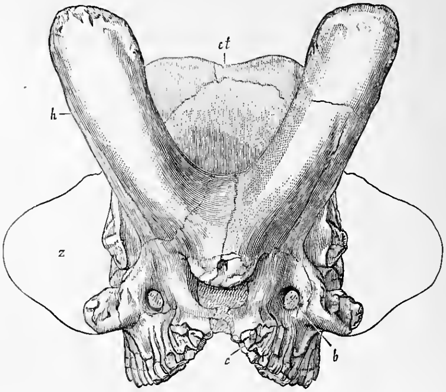

FIGURE 183.—Type (holotype) skull of *Titanops elatus*
Front view. Yale Mus. 12061. After Marsh, 1887. One-eighth natural size.

Etymology.—ἄλλος, strange; ὤψ, face.

Present determination.—Allops is intermediate between *Menodus* and *Brontops* and is here regarded as a valid genus. (See p. 506.)

Allops serotinus Marsh, 1887

Cf. *Allops serotinus*, this monograph, page 515

Original reference.—Am. Jour. Sci., 3d ser., vol. 34, p. 331, October, 1887 (Marsh, 1887.1).

Type locality and geologic horizon.—Quinn Draw, South Dakota, "near the top of the *Brontotherium* beds," Chadron formation (*Titanotherium* zone).

FIGURE 184.—Type (holotype) skull of *Allops serotinus*
After Marsh. Nat. Mus. 4251. One-seventh natural size.

Type.—"A well-preserved skull and various other remains." U. S. Nat. Mus. 4251. J. B. Hatcher, collector. (See fig. 184.)

Specific characters.—Not separated from generic characters in original description.

Etymology.—*serotinus*, from *sero*(?), to bind, connect; possibly because the characters appeared to be more or less annectant with those of other species.

Present determination.—The species is valid. It is described on page 515.

CANADIAN SPECIES DESCRIBED BY COPE IN 1889

Haplacodon Cope, 1889

Cf. *Allops*, this monograph, page 506

Original reference.—Am. Naturalist, vol. 23, p. 153, March, 1889 (Cope, 1889.1). (See p. 202.)

Type species.—*Menodus angustigenis* Cope. The genus was founded on the characters of one of the several "types" of *Menodus angustigenis*, namely, a maxilla containing the fourth upper premolar and the three molars.

Generic characters.—Cope writes:

> It differs from all the genera of the Menodontidae in the presence of but a single internal cusp of the first (posterior) superior premolar, a fact which renders it highly probable that the premolars which precede it in the maxillary bone were similarly constituted. It differs from all other genera of Lambdotheriidae and also from *Diplacodon*, to which it is allied, in the presence of but two inferior incisors on each side. It is not certain whether it possesses horns or not.

Comparative measurements of the type of "Haplacodon" Cope, in millimeters

	Paratype	Allops walcotti (type)
M^1–m^3	187	169
P^4, ap. by tr	38 × 52	35 × 51
M^1, ap. by tr	50 × 52	45 × 51
M^2, ap. by tr	66 × 62	61 × 61
M^3, ap. by tr	65 × 62	60 × 61

Etymology.—ἀπλόος, simple; ἀκή, cone; ὀδούς, tooth; in allusion to the "single internal cusp" of the fourth upper premolar.

Present determination.—The upper teeth agree closely in general characters with those of *Allops* and are intermediate in size between *Allops walcotti* and *Allops marshi.*

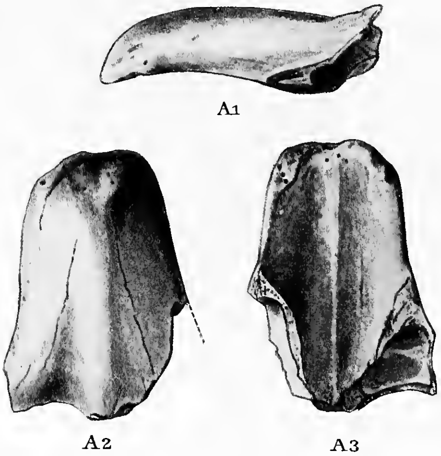

FIGURE 185.—Type of *Menodus selwynianus*
Coossified nasal. A_1, Left side; A_2, upper side; A_3, under side. Three-eighths natural size.

Menodus selwynianus Cope, 1889

Cf. *Diploclonus selwynianus*, this monograph, page 502

Original reference.—Am. Naturalist, vol. 23, p. 628, July, 1889 (Cope, 1889.2).

Subsequent reference.—On Vertebrata from the Tertiary and Cretaceous rocks of the Northwest Territory, I, p. 17, pl. 5, figs. 3, 3a, 3b, 1891 (Cope, 1891.2).

Type locality and geologic horizon.—Swift Current River, Assiniboia, Canada; Cypress Hills beds, level not recorded.

Type.—Coossified nasal bones detached from skull. Ottawa Mus. (See fig. 185.)

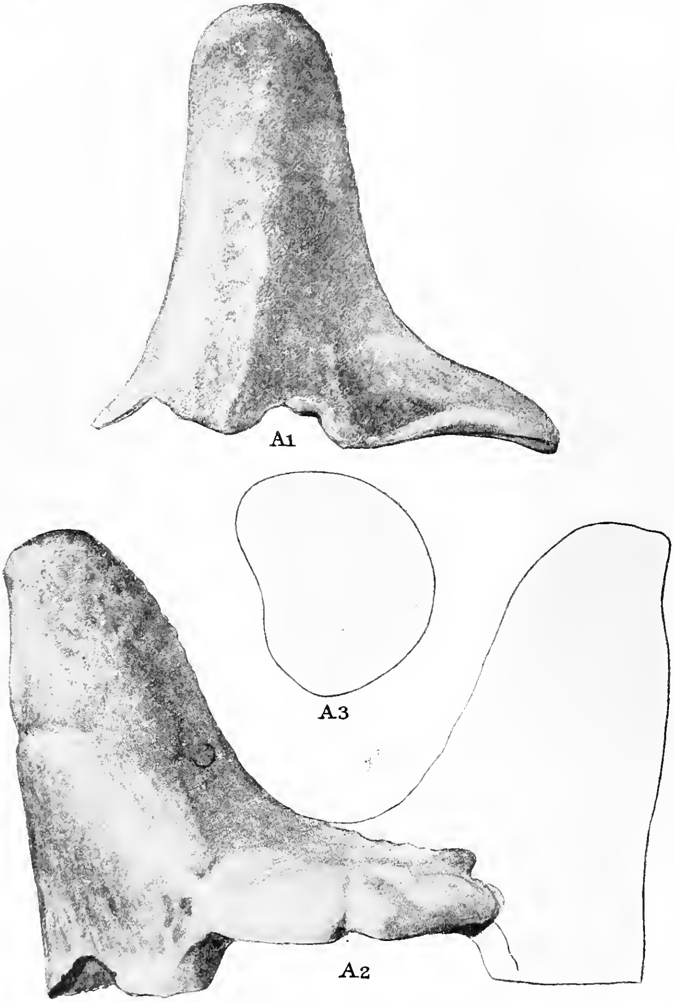

FIGURE 186.—Type of *Menodus syceras*

Coossified nasal and left horn core. After Cope. A1, Left side; A2, front; A3, section of left horn. One-half natural size.

Characters of type.—Cope writes:

> Represented by a nasal process, which consists of the coossified nasal bones, of peculiar form. They are elongate as compared with their width and are vaulted. The lateral borders are nearly parallel, and the extremity viewed from above is rounded. Owing to the thickness of the body, the profile descends abruptly at the extremity, and the convex surface is roughened as though for the attachment of some fixed body, tegumentary or muscular. From this tuberosity the surface descends steeply to a thin border. A short distance posterior to the extremity the lateral margins are decurved, forming the lateral walls of a deep longitudinal median gutter-like nasal meatus, which is deeper than in any other species. The horns are broken off, but the median inferior surface is so little recurved laterally that it is evident that the former were not only small but laterally placed. Length of fragment above, millimeters, 130; length of nasal border, 70; width at nasal notch, 80; width near extremity, 65; depth at apical tuberosity, 26.

Additional observations.—The lower surface of the horns in the type exhibits a portion of the frontal sinus. The nasals are shorter than in the type of *M. coloradensis.* The measurements are as follows:

	Millimeters
Free length of nasals	80
Free width of nasals	101
Outside measurement of horns	67
Anteroposterior measurement of horns	79

Etymology.—"This species is dedicated to Dr. A. R. C. Selwyn, the accomplished Director of the Survey of Canada." (Cope.)

Present determination.—The species is probably allied to *Diploclonus bicornutus* (Osborn).

Menodus syceras Cope, 1889

Cf. *Megacerops syceras,* this monograph, page 549

Original reference.—Am. Naturalist, vol. 23, pp. 628–629, July, 1889 (Cope, 1889.2).

Subsequent reference.—Cope, On Vertebrata from the Tertiary and Cretaceous rocks of the Northwest Territory, I, p. 18, pls. 7, fig. 2; 8, figs. 4, 5, 1891 (Cope, 1891.2).

Type locality and geologic horizon.—Swift Current River, Assiniboia, Canada; Cypress Hills beds, level not recorded.

Cotypes.—"The nasal bones of three individuals present the characters above given." Of these we may select as the lectotype the specimen figured by Cope (1891.2, pl. 8) that shows the character from which the name *syceras* is derived, in reference to the approximation of the horns at their bases. Portion of right frontal, coossified nasals, and right horn. (See fig. 186.)

Characters of type.—Cope writes:

> It differs from the two species of that group now known, the *M. proutii* Leidy and the *M. tichoceras* S. and O., in the very close approximation of the basis of the horns and the presence of a strong angle or ridge connecting them, so that the nasal bones are in a different plane from that of the front. The entire width of the skull at the basis of the horns is not greater than the length of each horn above the nasal notch. The horns are not long, and the section of their base is a longitudinal oval, flattened on the external side. Summit subround. The nasal bones are flat, with broadly rounded extremity, and are much wider than long.
>
> The width of the nasals at the base of the horns is 116 millimeters; length of do. from do., 70; diameters of bases of horns; anteroposterior, 94; transverse, 67; length of horn from nasal notch, 160; width of muzzle at bases of horns inclusive, 160.

Etymology.—*σύν*, together; *κέρας*, horn; because the horns were set very near to each other at the base.

Present determination.—*M. syceras* is at present indeterminate or possibly a synonym of *M. angustigenis*, both are provisionally referred to the genus *Megacerops*.

LAST FIVE SPECIES DESCRIBED BY MARSH, 1890–91

Diploclonus Marsh, 1890

Cf. *Diploclonus*, this monograph, page 499

Original reference.—Am. Jour. Sci., 3d ser., vol. 39, p. 523, June, 1890 (Marsh, 1890.1).

Type species.—*Diploclonus amplus.* (See below.)

Characters.—Marsh writes:

> One of the most marked features is seen in the horn cores, which are high, compressed transversely, and have a prominent knob on the inner superior margin about one-third of the distance to the summit. Seen from the front the horn cores thus appear to be branched. It is probable that in life this feature was still more evident, and the covering of the horn core may have shown an actual division, but this can not be determined from the present specimen. There is a sharp ridge at the base of the horn cores on the outside. The nasals project but very little in front of the horn cores. The zygomatic arches are especially strong and widely expanded. The posterior nares have their front margin opposite the back of the last upper molars.
>
> There were apparently but two upper incisors—that is, one on each side—and no diastema exists behind the canines. The premolars have a strong inner basal ridge, and the last upper molar has two inner cones. This genus appears to be most nearly related to *Titanops*, but the horn cores will distinguish it readily from all known forms of the Brontotheridae.

Etymology.—*διπλόος*, double; *κλών*, a twig; in allusion to the branched appearance of the "horn core."

Present determination.—The genus is now regarded as valid by Osborn.

Diploclonus amplus Marsh, 1890

Cf. *Brontops amplus*, this monograph, page 504

Original reference.—Am. Jour. Sci., 3d ser., vol. 39, p. 523, June, 1890 (Marsh, 1890.1).

Type locality and geologic horizon.—South Dakota; "*Brontotherium* beds" (= Chadron formation, or *Titanotherium* zone).

Type.—"Nearly complete skull, in good preservation, but without the lower jaws." Yale Mus. 12015a. (See fig. 187.)

Specific characters.—Marsh writes:

> The skull measures 28 inches from the front of the nasals to the back of the occipital condyles and 24 inches in greatest width across the zygomatic arches. The space occupied by the upper dental series is 13½ inches, and by the true molars 8 inches.

Etymology.—*amplus*, broad, in allusion to the great breadth of the skull.

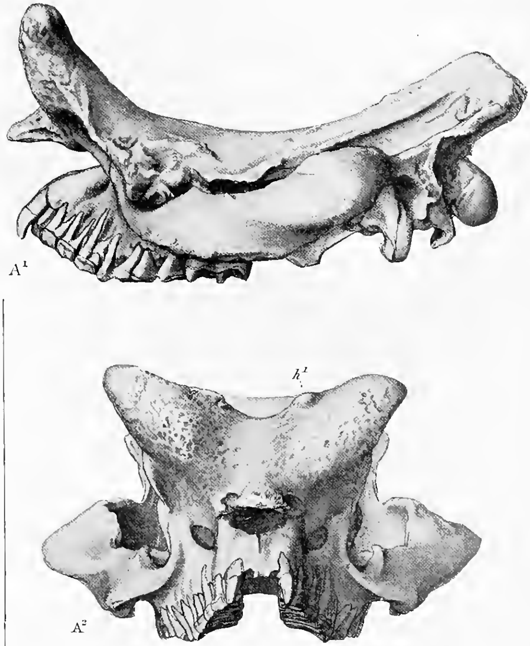

FIGURE 187.—Type skull of *Diploclonus amplus*

After Marsh. One-eighth natural size. A¹, Side view; A², front view

Present determination.—This species is either an aberrant stage in the evolution of *Brontops*—that is, a sport—or a lateral phylum of *Brontops*.

Teleodus Marsh, 1890

Cf. *Teleodus*, this monograph, page 481

Original reference.—Am. Jour. Sci., 3d ser., vol. 39, p 524, June, 1890 (Marsh, 1890.1).

Type species.—*Teleodus avus* Marsh. (See below.)

Generic characters.—Marsh writes:

> The present genus is allied to *Brontotherium* but differs from it in having six lower incisors instead of four. It has the same number of inferior premolars and molars, and these teeth are similar in the two genera. From *Diplacodon* of the upper

Eocene the present genus may be distinguished by having only three lower premolars on a side instead of four. * * * Of the three lower incisors in place on each side, the middle one is the largest. There is a short diastema behind the lower canine, but no first premolar. The dental formula of the lower jaws is as follows: Incisors, 3; canine, 1; premolars, 3; molars, 3.

The space occupied by the lower dental series is 14½ inches, and by the last three molars 8½ inches.

Etymology.—τέλεος, distant; ὀδούς, tooth; in allusion to the peculiar character of the incisors.

Present determination.—The genus may either be valid or synonymous with an early stage in the evolution of *Brontops.*

Teleodus avus Marsh, 1890

Cf. *Teleodus avus*, this monograph, page 481

Original reference.—Am. Jour. Sci., 3d ser., vol. 39, pp. 523, 524, June, 1890 (Marsh, 1890.1).

Type locality and geologic horizon.—"*Brontotherium* beds of Dakota" (=Chadron formation, or *Titanotherium* zone); exact geologic level not recorded but probably lower beds (Chadron A).

Type.—A lower jaw. Yale Mus. 10321. (See fig. 188.)

Specific characters.—Not separated by Marsh from the generic characters. (See p. 481.)

Etymology.—*avus*, grandfather; in allusion to the primitive character of the animal.

Present determination.—The species is probably valid.

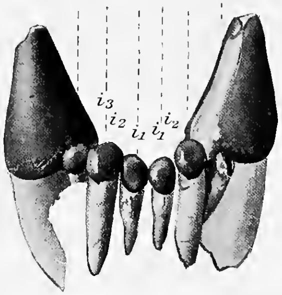

FIGURE 188.—Type of *Teleodus avus*

Lower incisors and canines. Two-thirds natural size.

Allops crassicornis Marsh, 1891

Cf. *Allops crassicornis*, this monograph, page 517

Original reference.—Am. Jour. Sci., 3d ser., vol. 42, p. 268, September, 1891 (Marsh, 1891.1).

Type locality and geologic horizon.—"*Brontotherium* beds of South Dakota" (=Chadron formation, or *Titanotherium* zone). Geologic level as recorded by J. B. Hatcher, collector, is the lower portion of the upper *Titanotherium* zone (Chadron C).

Type.—A "nearly perfect skull of an adult but not old animal." Nat. Mus. 4289. (See fig. 189.)

Specific characters.—Marsh writes:

> The skull is of medium size, with the zygomatic arches moderately expanded. The nasal bones do not project beyond the premaxillaries. The horn cores are very short and massive, with rounded summits, and thus form one of the striking features of the skull. The dentition is complete and in fine preservation. The single incisor is quite small and situated close to the canine. The latter is of moderate size and projects but little above the rest of the dental series. There is no diastema between the canine and the first premolar, which is small and has its inner face on a line between the canine and the second premolar. The second, third, and fourth premolars are large and have a strong inner basal ridge. The last molar has its anterior margin somewhat in advance of the front border of the posterior nares.
>
> The length of this skull on the median line is about 30 inches, and the width across the zygomatic arches 23 inches. The width across the horn cores is 14 inches. The extent of the superior dental series is 16 inches.

Etymology.—*crassus*, thick; *cornus*, horn.

Present determination.—The species is valid. It is fully described on page 517.

Brontops validus Marsh, 1891

Cf. *Brontops dispar*, this monograph, pages 230, 488

Original reference.—Am. Jour. Sci., 3d ser., vol. 42, p. 269, September, 1891 (Marsh, 1891.1).

Type locality and geologic horizon.—The geologic level as recorded by J. B. Hatcher, collector, is the "middle portion of the middle *Titanotherium* beds, White River, S. Dak." (Chadron formation, horizon Chadron B).

Type.—A "skull in fine preservation." Nat. Mus. 4290 (skull K). (See fig. 190.)

Specific characters.—Marsh writes:

> [The skull] agrees in its main characters with the other species of the genus but is particularly short and robust. The zygomatic arches are widely expanded, almost as much as in any skull of this group. The nasal bones have only a moderate extension in front and do not reach the end of the premaxillaries. The free portion is broad and massive. The horn cores are of moderate size, nearly round in section, and have their obtuse summits directed somewhat backward. The occipital crest slopes forward and is expanded transversely. The length of this skull on the median line is about 26 inches. The greatest transverse diameter across the zygomatic arches is 22 inches, and across the summits of the horn cores 14 inches.

Etymology.—*validus*, stout, brave.

Present determination.—As shown on page 202, this species is probably synonymous with *Brontops dispar.*

Titanops medius Marsh, 1891

Cf. *Brontotherium medium*, this monograph, page 573

Original reference.—Am. Jour. Sci., 3d ser., vol. 42, p. 269, September, 1891 (Marsh, 1891.1).

Type locality and geologic horizon.—"Near the top of the *Brontotherium* beds of South Dakota" (Chadron formation, *Titanotherium* zone). J. B. Hatcher, collector.

Type.—"One skull in fair preservation with the horn cores and dentition complete." Nat. Mus. 4256. (See fig. 191.)

Specific characters.—Marsh writes:

> The free portion of the nasals is very small and projects but slightly beyond the anterior line of the horn cores. The latter are compressed anteroposteriorly and project laterally nearly

at right angles to the median line of the skull. The two incisors on each side are quite small and separated from each other and from the canine. There is a slight diastema behind the canine. The first premolar is small and triangular in outline. The second premolar is of moderate size, and the third and fourth premolars have only an incomplete inner basal ridge.

The width of this skull across the horn cores is 23 inches, and the distance from the end of the nasals to the front of the posterior nares is 16 inches. The extent of the upper dental series is 17 inches.

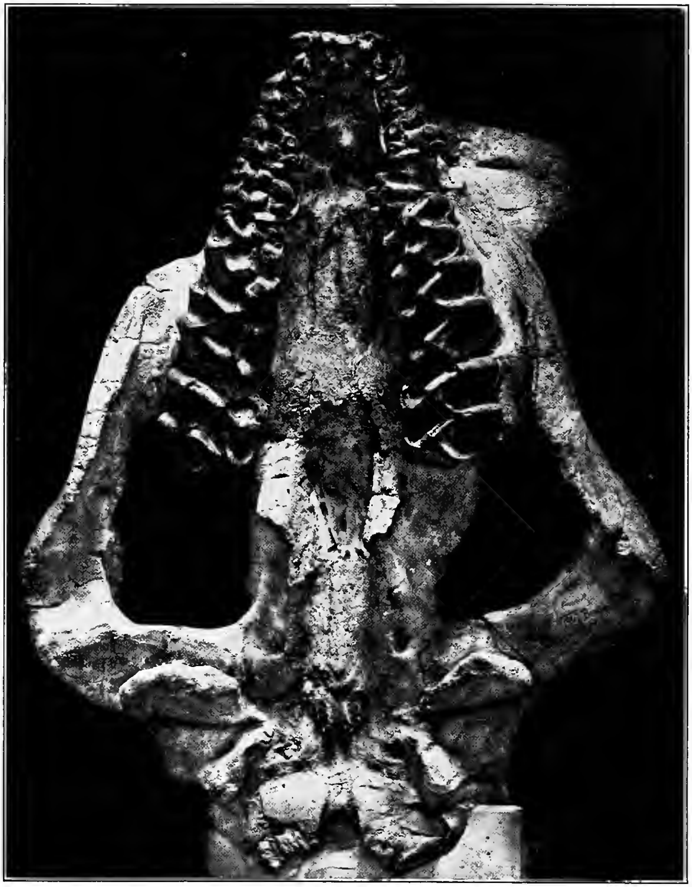

Figure 189.—Type skull of *Allops crassicornis*

Palatal view. Nat. Mus. 4289. After Marsh. One-fifth natural size.

Etymology.—*medius*, middle; in allusion to the intermediate character (between the species *elatus* and *curtus*) of this form.

Present determination.—The species is probably valid and is referable to *Brontotherium.*

LAST SPECIES DESCRIBED BY COPE, 1891

Menodus peltoceras Cope, 1891

Cf. *Brontotherium curtum*, this monograph, page 574

Original reference.—Am. Naturalist, vol. 25, p. 48, January, 1891 (Cope, 1891.1).

Type locality and geologic horizon.—"*Titanotherium* beds of northern Nebraska" (Chadron formation).

Type.—"Represented by the nasal region and the horn cores; the apex of one of the latter being broken away." Am. Mus. 10719. Dr. Hobart Hare, collector, Nebraska. Presented by the Museum of the University of Pennsylvania. (See fig. 192.)

Specific characters.—Cope writes:

> The peculiarity of the species consists in the immense transverse extent of the horn cores and their complete fusion into an osseous wall which extends across the muzzle, forming a huge plate or shield. The superior border of this shield is moderately concave, a protuberant angle on each side representing the apex of each horn core. The nasal bones form a flattened protuberance much wider than long, which overhangs the nares. * * * Measurements: Elevation of horn-core plate at middle line behind, 180 millimeters; do. at lateral apex, 190 millimeters; total width of do. at middle, 300 millimeters. Projection of nasal bones beyond lateral base of horn-core plate, 20 millimeters; width of nasal meatus at base of nasal bones, 65 millimeters; width of base of horn-core plate outside of nasal meatus, 90 millimeters. Anteroposterior diameter of base of horn core above side of and parallel to nasal meatus, 85 millimeters. This species is nearest the *M. platyceras* S. and O., which has transverse compressed horn cores. They are, however, distinct from each other, and not nearly so expanded transversely as in the present form. The *M. peltoceras*, in fact, carried a transverse shield on the end of its nose, which must have given it an extraordinary appearance.

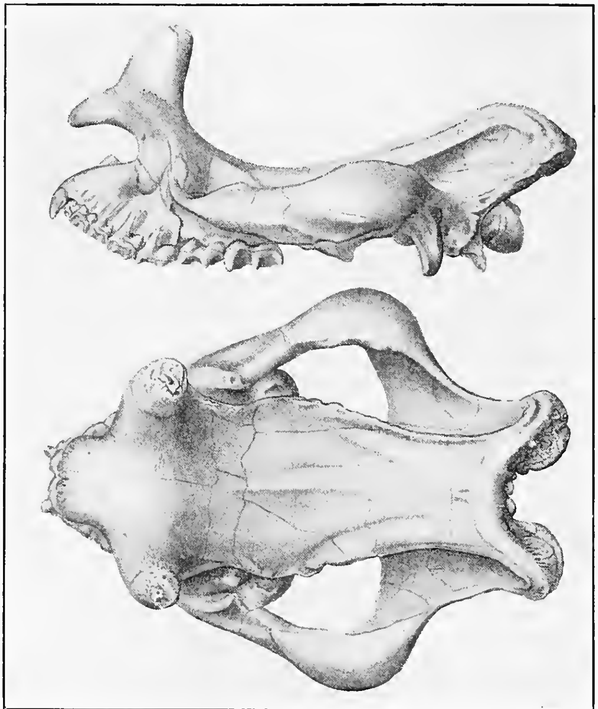

FIGURE 190.—Type (holotype) skull of *Brontops validus*

After Marsh. Nat. Mus. 4290. One-eighth natural size.

Etymology.—πέλτη, small shield; κέρας, horn; because the bases of the horns formed together a "huge plate or shield" extending across the muzzle.

Present determination.—The type specimen (fig. 192) possibly represents a female of one of the long-horned species of *Brontotherium*, perhaps *B. curtum*, *B. platyceras*, or *B. ramosum*. The species is therefore practically indeterminate at present.

FIRST EUROPEAN OLIGOCENE SPECIES, DESCRIBED BY TOULA, 1892

Menodus? rumelicus Toula, 1892

Cf. *Brontotherium rumelicum*, this monograph, pages 560, 941

Original reference.—Akad. Wiss. Wien, Math.-nat. Classe, Sitzungsber., Band 101, Abt. 1, pp. 608–615, 1 pl., May, 1892 (Toula, 1892.1).

Subsequent reference.—Ueber einen neuen Rest von *Leptodon?* (*Titanotherium?*) *rumelicus* Toula spec., pp. 922–924, 1896 (Toula, 1896.1).

Type locality and geologic horizon.—Near the railroad on the Jambol line near Kajali, northwest of Burgas, eastern Rumelia. Level, lower Oligocene (?). The formation from which the type was recorded was correlated by Toula with the "Belvedereschotter."

On account of the extreme rarity of titanotheres in Europe it seems important to note the published evidence concerning the provenience of the type and referred specimens of this species. According to Toula the specimens were received from his friend G. N. Zlatarski in Sofia. Toula does not state that Zlatarski himself collected the specimens. He states only that they must have come from near the railroad at Kajali, from the great heaps of material which had been dug up in the search for usable rubble ("tauglichem Schotter"), and that these "Schottermassen" should correspond at best with that isolated remnant of a formation at Lidscha, northwest of Burgas, of which he had already spoken in his first report on the geology of the eastern Balkans. He writes: "I have referred to these 'Schotter' as Belvedereschotter, and I believe, from the condition of preservation of the specimens from Kajali, and especially from the rusty sand grains still adhering to them, that they must be referred to the same kind of rock." Besides the specimens of titanotheres Toula records a lower molar and a canine of a "middle-sized rhinoceros" from the same locality. Later he received from the same locality, this also from Zlatarski, a fragment of the lower jaw of a titanothere that included the symphyseal region (Toula, 1896.1, pp. 922–924). But Toula has not disproved the possibility that these specimens may have been imported from America, perhaps by laborers returning home from the western United States. (See p. 560.)

Lectotype.—Third right lower molar and part of the right ramus of the lower jaw. (See fig. 193.)

Paratypes.—A second right lower molar and a canine.

Referred specimen.—The symphyseal region of the jaw with the roots of p_1, p_2, p_3, and the worn p_4, in place.

Specific characters.—Toula's description is too long to quote here. The principal characters revealed by his figures are, symphysis massive, canines (?) large, four lower premolars, lower molars with faint external cingula, hypoconulid of m_3 without strong internal crest.

Etymology.—*rumelicus*, in allusion to Rumelia, the region in Hungary where the type was discovered.

Present determination.—The species is probably valid, and its generic reference is probably to *Brontotherium*.

SPECIES DESCRIBED BY OSBORN IN 1896 AND 1902

Titanotherium ramosum Osborn, 1896

Cf. *Brontotherium ramosum*, this monograph, page 577

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 8, p. 1941, pl. 4, text fig. 13, 1896 (Osborn, 1896.110).

Type locality and geologic horizon.—"Upper *Titanotherium* beds, South Dakota." Chadron formation, Quinn Draw, Big Badlands, S. Dak.

Type.—A complete male skull lacking incisive border. Am. Mus. 1447. (See fig. 194.)

Characters of type.—Osborn writes:

> The distal spreading or branching of the horns is the character by which this species is designated. It differs from *T. elatum* in this character, but more especially in the great depth of the "connecting crest" and the extreme flattening of the horns, the section, as shown in diagram 1, being intermediate between that of the *T. elatum* and of *T. platyceras*. It is remarkable that the teeth in this large skull are relatively of small size; the last upper molar has no second cone.

Etymology.—*ramosum*, branched, in allusion to the "distal spreading or branching of the horns."

Present determination.—The species is probably valid.

Megacerops brachycephalus Osborn, 1902

Cf. *Brontops brachycephalus*, this monograph, page 483

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 16, pp. 97–98, fig. 3 (not the type), 1902 (Osborn, 1902.208).

Type locality and geologic horizon.—Big Badlands, S. Dak.; Chadron formation, Chadron A, base or level A of lower *Titanotherium* zone.

Type.—A complete skull (Nat. Mus. 4261, skull a), collected by J. B. Hatcher in 1887. (See fig. 195.)

Specific characters.—Osborn writes:

> The type of this species is No. 4261, U. S. Nat. Mus. It includes very small, broad-skulled titanotheres with very rudimentary second internal cones upon the upper premolars; nasals elongate, narrowing anteriorly, as in *Palaeosyops*. Horns of anteroposterior oval section placed above orbits. It is represented in the National Museum by numerous skulls besides the type, all collected and recorded by Hatcher. One of these skulls was provisionally referred by him to *Teleodus avus*, from which this species is quite distinct.

Etymology.—βραχύς, short; κεφαλή, head, in allusion to the brachycephalic form of the skull.

Present determination.—The species is probably valid.

Megacerops bicornutus Osborn, 1902

Cf. *Diploclonus bicornutus*, this monograph, pages 234, 501

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 16, p. 99, fig. 5, 1902 (Osborn, 1902.208).

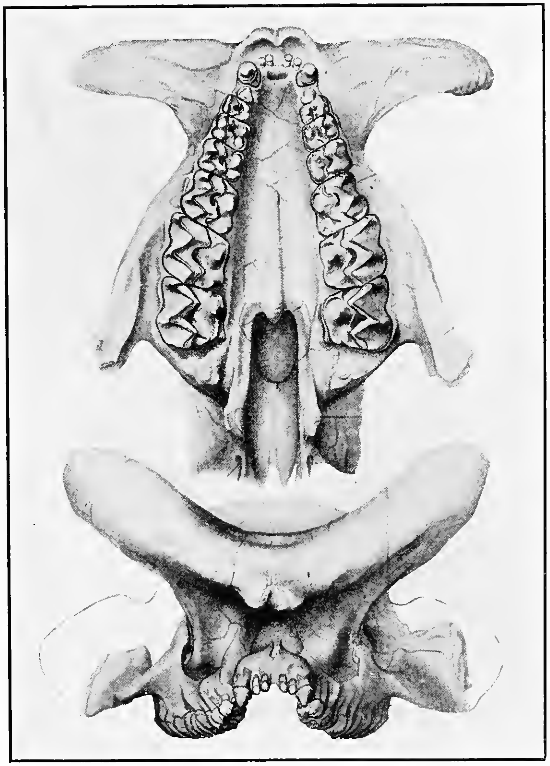

FIGURE 191.—Type (holotype) skull of *Titanops medius*

After Marsh. Nat. Mus. 4256. One-eighth natural size.

Type locality and geologic horizon.—Quinn Draw, White River, S. Dak.; exact level not recorded. Collected by J. W. Gidley, 1896.

Type.—Skull and lower jaws (Am. Mus. 1476). (See fig. 196.) Paratype, skull (Am. Mus. 1081). One of these skulls (No. 1081) was first described by Osborn (1896.110, p. 176) as *Titanotherium torvum* or *robustum*.

Specific characters.—Osborn writes:

> Horns directed anteriorly. Hornlets upon the inner and anterior midportion of the horn. Basal section of the horn slightly oval, subtransverse. Nasals narrow and relatively elongate. Sharp malar bridge in front of orbit. Orbit large.

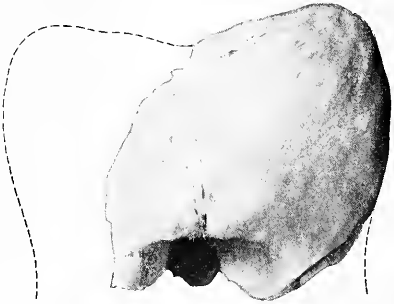

FIGURE 192.—Type (holotype) nasofrontal shield of *Menodus peltoceras*

Am. Mus. 10719. One-fourth natural size.

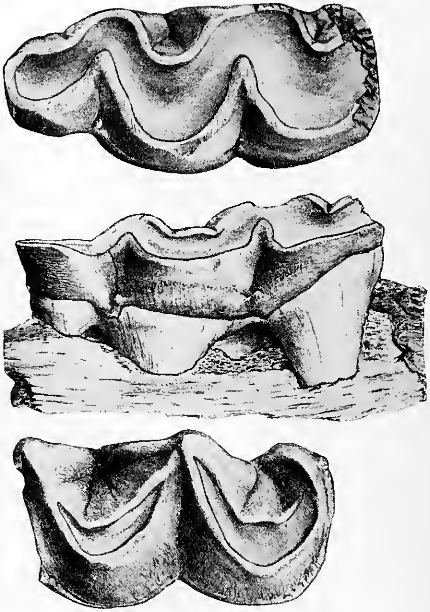

FIGURE 193.—Cotypes of *Menodus? rumelicus*

After Toula, 1892. Two-thirds natural size. The right lower molar (two upper figures) is the lectotype.

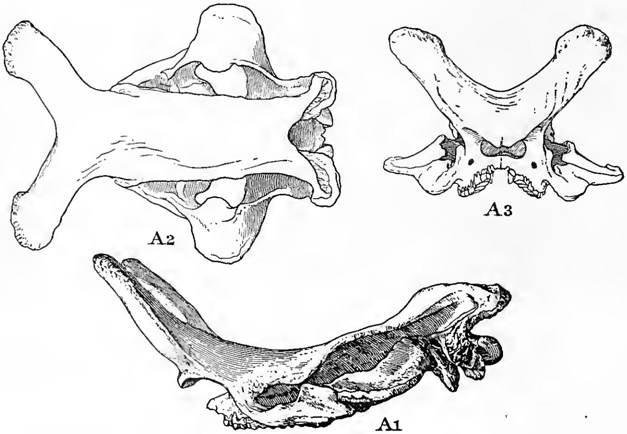

FIGURE 194.—Type (holotype) skull of *Titanotherium ramosum*

After Osborn, 1896. Am. Mus. 1447. A_1, Side view, one-twelfth natural size; A_2, top view, one-thirteenth natural size; A_3, front view, one-thirteenth natural size.

This animal stands nearest *M. selwynianus*, though distinguished by the greater size and slightly greater width of the nasals. The sharp malar bridge is the most absolute character. The two hornlets are possibly variations.

Type locality and geologic horizon.—Big Badlands (probably Cheyenne River badlands), S. Dak.; Chadron formation (*Titanotherium* zone), exact level not determined.

FIGURE 195.—Type skull of *Megacerops brachycephalus*

Nat. Mus. 4261. One-fourth natural size.

Etymology.—*bis*, twice; *cornutus*, horned; in allusion to the presence of small accessory horn swellings.

Present determination.—The species is probably valid.

Megacerops marshi Osborn, 1902

Cf. *Allops marshi*, this monograph, pages 511–515

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 16, pp. 100–101, fig. 6, 1902 (Osborn, 1902.208).

Type.—A complete skull (Am. Mus. 501). (See fig. 197.)

Paratype.—Skull (Am. Mus. 1445). Collected by American Museum expedition, 1892.

Specific characters.—Osborn writes:

Type, skull No. 501; cotype, skull No. 1445, Am. Mus. Nasals elongate and square distally, horns short, of oblique oval basal section, overhanging the maxillae, or projecting forward or outward. Incisors, ?$\frac{2}{2}$. Canines short, tetartocones of premolars moderately developed. These skulls were previously confused by the writer with *T. trigonoceras*, from which they are readily separated by the horn section, which relates them to some of the primitive types of *M. brachycephalus* and equally to *M. robustus*. The canines are more obtuse than in *M. dispar*, and the superior incisors resemble those in *Brontotherium* rather than in *M. robustus*.

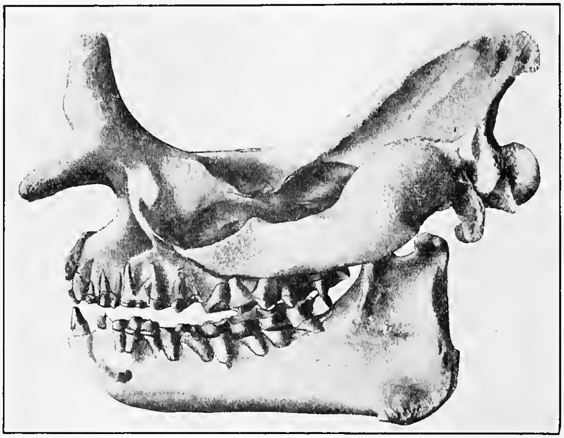

FIGURE 196.—Type (holotype) skull and lower jaw of *Megacerops bicornutus*

Am. Mus. 1476. After Osborn, 1902. One-eighth natural size.

Etymology.—Named in honor of the late Prof. O. C. Marsh, who established the remarkable collections of titanotheres in the Yale and National Museums, proposed the family name Brontotheridae, gave names to many of the genera and species, and projected the present monograph.

Present determination.—The species is probably valid.

Brontotherium leidyi Osborn, 1902

Cf. *Bronthotherium leidyi*, this monograph, page 558

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 16, pp. 105–106, figs. 9, 10, 1902 (Osborn, 1902.208).

Type locality and geologic horizon.—Big Badlands, S. Dak.; Chadron formation, lower levels of lower *Titanotherium* zone (Chadron A).

Type.—A complete skull (Nat. Mus. 4249, skull R) collected by J. B. Hatcher in 1887. (See figs. 198, 199.)

Specific characters.—Osborn writes:

> Nasals elongate, narrowing anteriorly. Horns very short, slightly recurved, of transverse oval section. Canines stout and blunt. Premolars noncingulate, with rounded contours and well-developed tetartocones. Incisors$\frac{2}{1}$.

Etymology.—Named in honor of Joseph Leidy, the first of the three great founders of American vertebrate paleontology, describer of *Titanotherium*, *Megacerops*, *Palaeosyops*, author of "The ancient fauna of Nebraska" and of "The extinct mammalian fauna of Dakota and Nebraska."

Present determination.—The species is probably valid.

SPECIES DESCRIBED BY LULL IN 1905

Megacerops tyleri Lull, 1905

Cf. *Diploclonus tyleri*, this monograph, page 502.

Original reference.—Jour. Geology, vol. 13, No. 5, pp. 443–456, pls. 3, 4, August, 1905 (Lull, 1905.1).

Type locality and geologic horizon.—North side of Spring Draw Basin, about 10 miles from the mouth of Bear Creek, a tributary of Cheyenne River, S. Dak. Type specimen found 35 feet above the base of 200 feet of the Chadron formation (*Titanotherium* zone) lying upon Pierre deposits, "hence in the upper part of the lower division," as defined by Hatcher in 1893 (1893.1, p. 218).

Type.—Skull, limbs, and many vertebrae of a single individual (Amherst Mus. 327). (See figs. 200 and 201.) Found by T. C. Brown, of the Amherst College paleontologic expedition of 1903.

Specific characters.—Lull writes:

> Horns well in front of orbits, directed somewhat forward and outward, an elongate oval in basal section with the long axes in line, rounded oval at the summit. Hornlets quite conspicuous, on the inner face of the horns midway between the base and summit. Connecting crest low and inconspicuous. Nasals broad, well rounded in front, and but slightly arched beneath. Zygomata expanded and deep, with a well-rounded outer face. Dentition: Superior incisors represented by the deep and well-defined median alveoli and by the lateral teeth, which remain in place and which have hemispherical crowns which show little sign of wear. The canines are lanceolate, with a well-developed postero-internal cingulum. There is a short diastema in front of, and a longer one behind, the canine. Premolars with a smooth internal cingulum, less pronounced in the middle of the tooth, and with no external cingulum. The deuterocone is well developed, while the tetartocone, especially of premolar 4, is inconspicuous.
>
> The jaw is deep and robust, with the alveoli of two incisors, probably of the second and third, deep and distinct. There is no space between the lateral incisors and the canine, though between the two median alveoli a considerable gap occurs. There seems to have been a small diastema behind the lower canines, which are lanceolate, though with a less prominent cingulum, and not so strongly recurved as the upper ones.

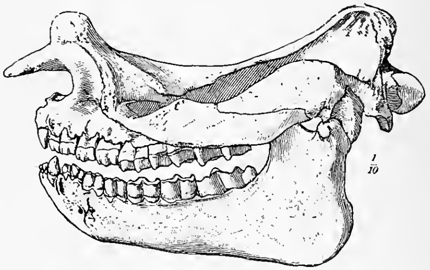

FIGURE 197.—Type skull of *Megacerops marshi*

After Osborn, 1902. Am. Mus. 501. One-tenth natural size. The lower jaw (Am. Mus. 516) figured with this skull does not belong with it. It is probably referable to *Brontotherium leidyi*.

Etymology.—Named in honor of Prof. John M. Tyler, of Amherst College, "a teacher of men, who, by his earnest efforts, as well as by his own generosity, was mainly instrumental in making possible the expedition which secured the specimen" (Lull).

Present determination.—This species is probably valid. It is discussed on page 502 of this monograph.

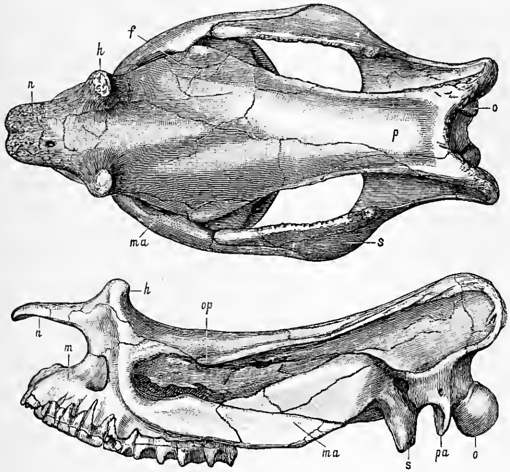

FIGURE 198.—Type (holotype) skull of *Brontotherium leidyi*

After Osborn, 1902. Nat. Mus. 4249. One-eighth natural size. The side view of this skull was figured by Marsh (Am. Jour. Sci., October, 1887) as *Menops varians.*

SPECIES DESCRIBED BY OSBORN IN 1908

Brontotherium hatcheri Osborn, 1908

Cf. *Brontotherium hatcheri*, this monograph, page 563

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 24, pp. 615–616, fig. 20, 1908 (Osborn, 1908.318).

Type locality and geologic horizon.—South Dakota; Chadron formation, middle *Titanotherium* zone (Chadron B), lower levels. J. B. Hatcher, collector.

Type.—A nearly complete skull (Nat. Mus. 1216, skull a) lacking the premaxillaries and anterior portion of the maxillaries. (See fig. 202.)

Specific characters.—Osborn writes:

> $I\frac{2}{2}$, $P\frac{4}{4}$. Nasals moderately long (97 mm.), thin at the edges. Horns 250+ millimeters, two-thirds the length of *B. gigas* horns. Skull length (pmx-condyles), 710 (estimated), width across zygomata, 530 (estimated). This species appears to represent an early phase of evolution of *B. gigas*. The horns are very round or convex in section and have a well-defined malar ridge on the lower outer portion. The connecting crest is relatively shallow, and the nasals are thin. The premolars are well advanced, the tetartocone of p^4 being well rounded and quite distinct.

Etymology.—Named "in honor of the late J. B. Hatcher, who discovered many of Professor Marsh's titanothere types, brought together the great collection of titanotheres in the National and Yale Museums, and placed the stratigraphic succession of the species upon a secure basis." (Osborn.)

Present determination.—The species is probably valid.

Symborodon copei Osborn, 1908

Cf. *Megacerops copei* Osborn, this monograph, page 548

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 24, pp. 616, 617, fig. 21, 1908 (Osborn, 1908.318).

Type locality and geologic horizon.—South Dakota, Big Badlands, Indian Draw; Chadron formation, level probably middle *Titanotherium* zone (Chadron B). J. B. Hatcher, collector.

Type.—A complete skull (Nat. Mus. 4711, skull V′), collected by J. B. Hatcher, 1888. (See fig. 203.)

Specific and generic characters.—Osborn writes:

> Incisors (type) persistent but greatly reduced; canines very small, reduced (28 mm.); premolars with cingula reduced or absent; tetartocones connected with deuterocones by a longitudinal ridge. Skull: nasals thin, short and broad in proportion, 80 by 125 millimeters; horns, ♂, 300, no connecting crest, transverse oval near summit; buccal processes of zygomata ♂ stout and convex; malar in front of buccal process very deep, beneath postorbital process stout, convex; occipital pillars not greatly expanded at the summits.

Etymology.—Named in honor of the late Prof. E. D. Cope, prolific author of "The Vertebrata of the Tertiary formations of the West," original describer of *Symborodon*, founder of the "Cope collection," now in the American Museum of Natural History.

Present determination.—The species is probably valid.

CANADIAN SPECIES DESCRIBED BY LAMBE IN 1908

Megacerops primitivus Lambe, 1908

Cf. *Teleodus primitivus*, this monograph, page 482

Original reference.—Contr. Canadian Paleontology, vol. 3, pt. 4, pp. 49–51, pl. 6, figs. 4, 5, 1908 (Lambe, 1908.1).

FIGURE 199.—Upper premolars of type skull of *Brontotherium leidyi*

After Osborn, 1902. Nat. Mus. 4249. One-half natural size.

Type locality and geologic horizon.—"Oligocene deposits of the Cypress Hills," Saskatchewan. Collector, L. M. Lambe, 1904.

Type.—Both halves of the lower jaw, with the dentition of the left side complete. Ottawa Museum. (See fig. 204.)

Specific characters.—Lambe writes:

> Incisors, in three pairs, with a space between the inner pair; canines, of small diameter, apparently short; a diastema

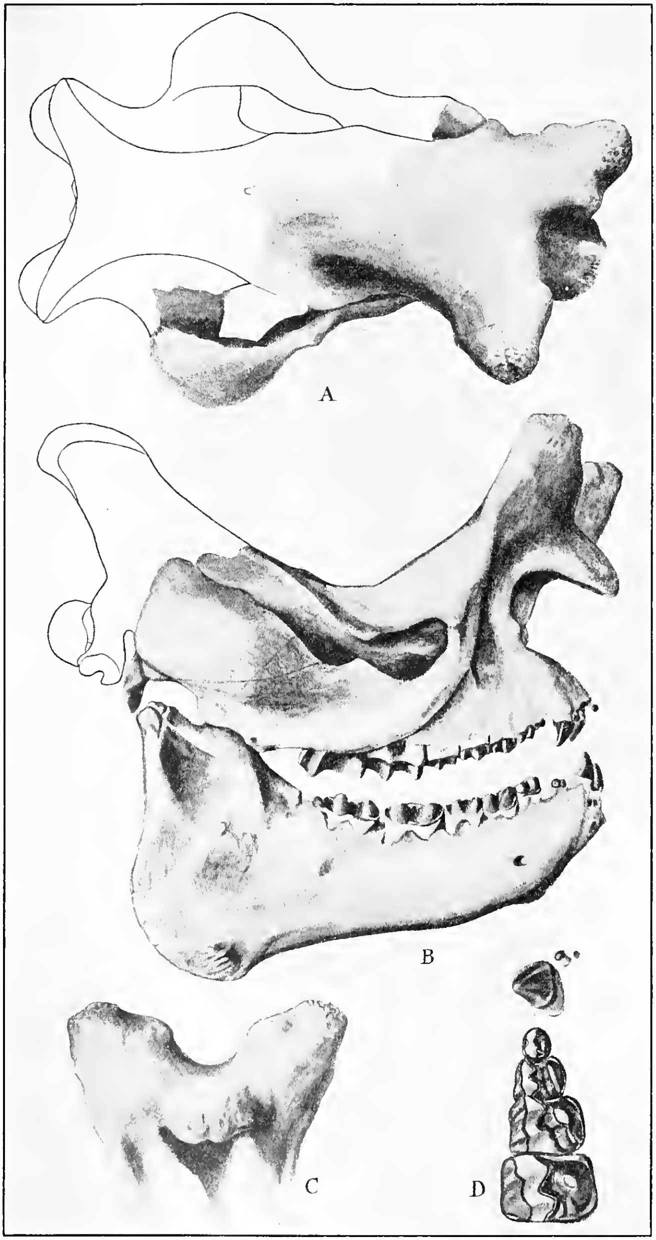

FIGURE 200.—Type (holotype) skull of *Megacerops tyleri*

After Lull. Amherst Mus. 327. A, Dorsal aspect of skull; B, lateral aspect of skull and jaw; C, anterior aspect of horns and nasals; all about one-eighth natural size. D, Upper dentition (incisor, canine, and premolar series), one-fourth natural size.

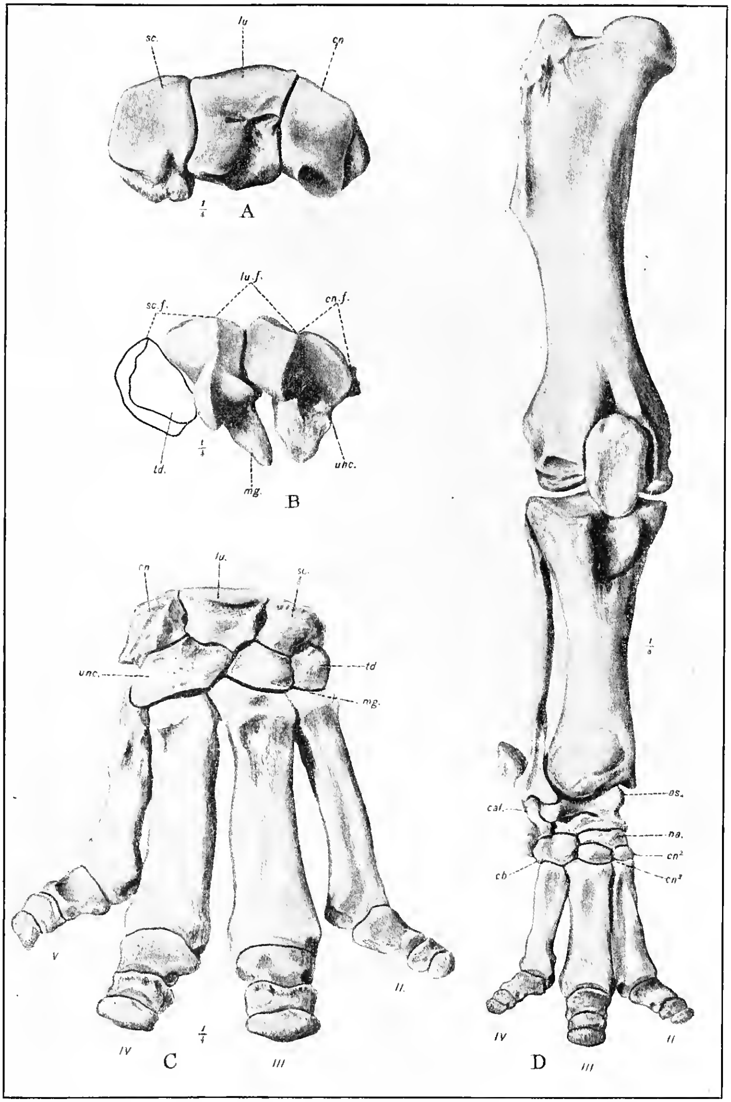

FIGURE 201.—Right manus and right hind limb of the type of *Megacerops tyleri*

After Lull, 1905. Amherst Mus. 327. A, Proximal row of carpals, proximal aspect; B, distal row of carpals, proximal aspect (*sc. f.*, scaphoid facet, *lu. f.*, lunar facet, *cn. f.*, cuneiform facet); C, right manus; all one-fourth natural size. D, Right hind limb, one-eighth natural size.

between the canine and the first premolar; first premolar small; third premolar becoming molariform; fourth premolar molariform; symphysis long; symphyseal surface between canines narrow; jaw contracted at the diastema; external cingula moderately developed; internal cingula wanting; mental foramen beneath the second premolar; coronoid process short.

Megacerops avus (Marsh), from the Oligocene of South Dakota, has three pairs of inferior incisors but only three premolars below on each side, and there is a short diastema behind the lower canine. Its dimensions are greater than those of *M. primitivus.* These two species are apparently the only ones of the Oligocene titanotheres in which there are three pairs of incisors in the lower jaw.

FIGURE 202.—Type (holotype) skull of *Brontotherium hatcheri*

Top view. Nat. Mus. 1216. After Osborn, 1908. One-tenth natural size.

In the Cypress Hills specimen the crowns of the incisors are of a depressed spherical shape, with a tendency to come to a rounded central point above. The second incisor is the largest, and the first is slightly smaller than the third, which is the most upright. The first is more procumbent than the second. Between the inner pair is a very decided interval, leaving a space of 6.5 millimeters between the crowns of the two teeth. The crowns of the canines are broken off (that of the right tooth being restored in fig. 5 of pl. 6) and the right first premolar is lost from its alveolus. * * *

Keeping in mind the differences due to sex in titanotheres generally and the apparent variability, both specific and individual, of certain dental characters, such as the degree of development of the cingula, the presence or absence of the first premolar, the size of the canines, and the number of the incisors, *M. primitivus* is apparently a well-marked species, characterized principally, so far as known at present, by the breadth of the mandible anteriorly (as compared with *M. angustigenis*) and the presence of the full number of teeth, with a comparatively long diastema behind the canines.

This species, for which the name *primitivus* is used, is regarded as representing a rather early stage in the development of the titanotheres. The general character of the dentition suggests the appropriateness of referring the species to the genus *Megacerops.*

Measurements

	Millimeters
Length of ramus	475
Depth of same at posterior end of fourth premolar	74
Depth of same at posterior end of second molar	81
Depth of same from tip of coronoid process to lower border	247
Maximum thickness of same beneath third molar	46
Length of symphysis	144
Distance apart of inside surface of base of canines[17]	31
Length of premolar series	103
Length of molar series	183
Diameter of canines at base:	
Anteroposterior	18
Transverse	16
Diameter of second premolar:	
Anteroposterior	26
Transverse	18
Diameter of third premolar:	
Anteroposterior	32
Transverse	23
Diameter of fourth[18] premolar:	
Anteroposterior	35
Transverse	27

Etymology.—primitivus, primitive; in reference to the presence of three lower incisors.

Present determination.—The species is probably valid. It is probably referable to *Teleodus.*

Megacerops assiniboiensis nom. prov., Lambe, 1908

Cf. *Brontotherium curtum,* this monograph, page 574

Original reference.—Contr. Canadian Paleontology, vol. 3, pt. 4, pp. 51–53, pl. 5, fig. 6, 1908 (Lambe, 1908.1).

FIGURE 203.—Type (holotype) skull of *Symborodon copei*

After Osborn, 1908. Nat. Mus. 4711. One-tenth-natural size.

Type locality and geologic horizon.—Oligocene deposits of the Cypress Hills, Saskatchewan. Collection of 1904.

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[17] In the mandible of *M. angustigenis* (No. 11) figured by Cope, op. cit. [1891.2] this measurement is about 18 millimeters, and in the symphysis of the jaw (No. I, also figured) a like measurement given, by the same authority, as 27 millimeters, should be 22 millimeters.

[18] First premolar in Cope's description of *M. angustigenis.*

Type.—"A robust, short left mandibular ramus," lacking the posterior end. The three molars and the fourth premolar are preserved, as well as part of the symphyseal region. Ottawa Museum. (See fig. 205.)

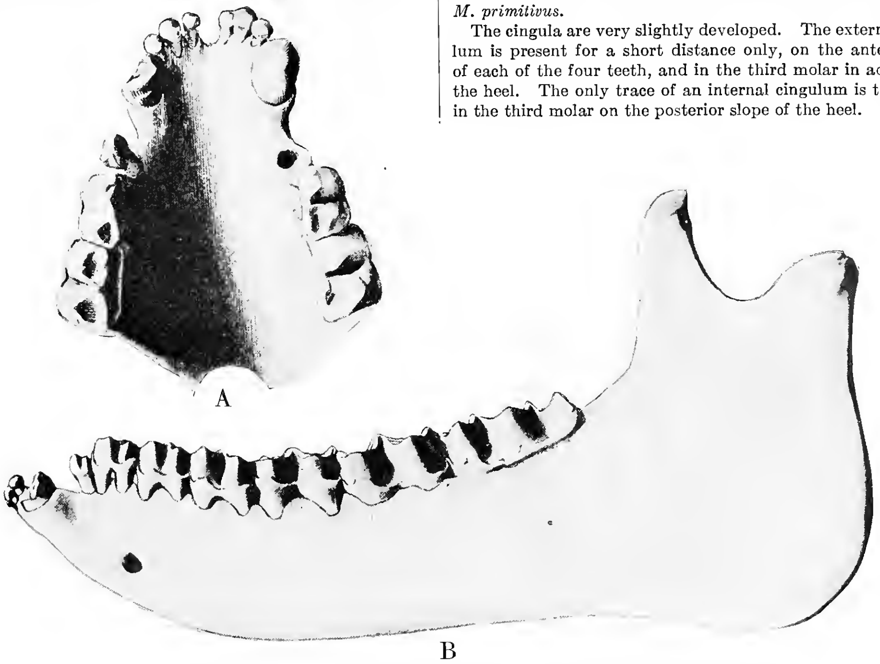

FIGURE 204.—Type (holotype) jaw of *Megacerops primitivus*

In the collection of the Ottawa Museum. After Lambe, 1908. A, Superior aspect, one-half natural size; B, lateral aspect, one-third natural size.

FIGURE 205.—Type (holotype) jaw of *Megacerops assiniboiensis*

In the collection of the Ottawa Museum. After Lambe, 1908. One-third natural size.

Characters.—Lambe writes:

> The jaw is much deeper, thicker, and relatively shorter than in *angustigenis* and *primitivus*, and the teeth are much larger than in these species. It is narrow anteriorly, and the symphysis extends back to a point in line with the division between the fourth premolar and the first molar. The bone is massive and heavy throughout. The mental foramen is placed beneath the posterior root of the third premolar, farther back than in *M. primitivus*.
>
> The cingula are very slightly developed. The external cingulum is present for a short distance only, on the anterior face of each of the four teeth, and in the third molar in advance of the heel. The only trace of an internal cingulum is to be seen in the third molar on the posterior slope of the heel.
>
> The fourth premolar is fully molariform. The teeth are stout and of about the size of the corresponding ones in *M. marshi* Osborn, but the jaw is relatively shorter than in this species.
>
> From the material available, the species, for which the provisional name *assiniboiensis* is proposed, can not be definitely characterized.

Measurements of ramus (type)

	Millimeters
Depth of ramus at posterior end of fourth premolar	80
Depth of ramus at posterior end of third molar	156
Thickness of ramus above lower border beneath posterior end of first molar	55
Vertical thickness of symphysis a little in advance of its posterior termination	53
Vertical thickness of symphysis in line with front root of third premolar	31
Space occupied by fourth premolar and the molars	260
Diameter of fourth premolar:	
Anteroposterior	41
Transverse	31
Diameter of first molar:	
Anteroposterior	55
Transverse	36
Diameter of second molar:	
Anteroposterior	71
Transverse	41
Diameter of third molar:	
Anteroposterior	99
Transverse	43
Space occupied by roots of third premolar (anteroposterior)	34
Space between fourth premolars (twice the distance of fourth premolar from vertical plane through symphysis)	60

Etymology.—*assiniboiensis*, in allusion to the geographic occurrence of the type.

Present determination.—This species apparently belongs in the Brontotheriinae. It is smaller than *Brontotherium hatcheri*. The nasals doubtfully referred by Lambe to this species suggest those of *Brontotherium curtum*.

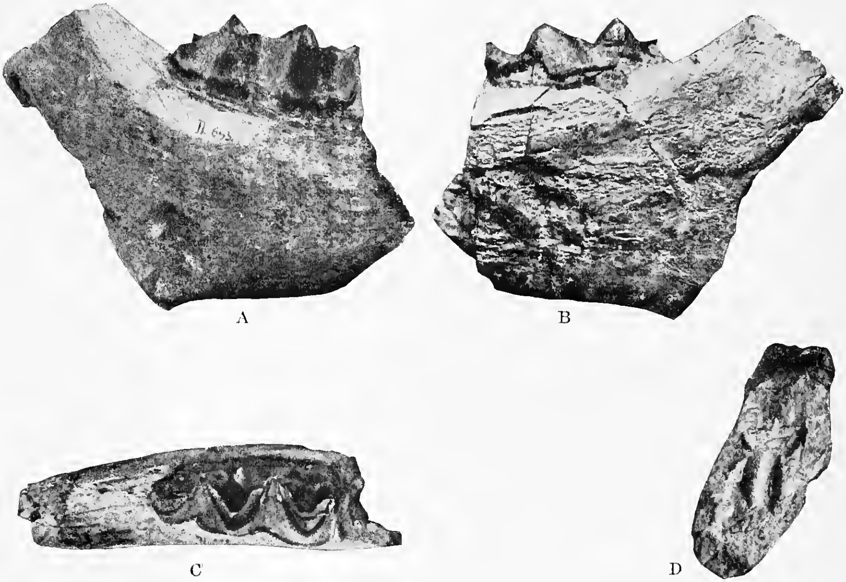

Figure 206.—Type of *Titanotherium bohemicum* Kiernik

Fragment of a lower jaw with third right lower molar. After Kiernik. A, Outer side view; B, inner side view; C, top view, showing the grinding surface of m_3; D, front view, showing the exposed posterior roots of m_2. About one-fourth natural size.

SECOND EUROPEAN OLIGOCENE SPECIES, DESCRIBED BY KIERNIK, 1913

Titanotherium bohemicum Kiernik, 1913

Cf. *Menodus giganteus*, this monograph, page 530

Original reference.—Acad. sci. Cracovie Bull., ser. B, vol. 10B, pp. 1211–1225, pl. 63, 1913 (Kiernik, 1913.1).

Type locality.—Uncertain. The specimen, a fragment of the lower jaw containing the third right lower molar, was received with a lot of fossils from the diluvium near Prague. It was supposed to have come from the lime pits of Podbaba, near Prague, and to have been sold by one of the workers in the lime pits to Herr Baumeister Kuchta (died 1910). He gave it, along with other prehistoric specimens, to Herr Rožanek, who in turn gave it to Herr Jira, who presented it to the Institute for Comparative Anatomy at Prague. After carefully considering the possibility that the specimen might have been of American provenience the author, Herr Kiernik, inclines rather to the view that it really came from Bohemia, although not from Přodbaba, but from the fresh-water Tertiary deposits of Tuchořitz (northwestern Bohemia). The well-known fauna of Tuchořitz is, however, of lower Miocene facies.

Type.—A lower jaw fragment containing the third right lower molar. (See fig. 206.)

Characters.—Kiernik carefully compares the fragment with the types of *Brachydiastematherium transilvanicum* Böckh and Maty, *Menodus rumelicus* Toula, and *Titanotherium proutii* Leidy. He shows that the third lower molar is much larger than that of either *Brachydiastematherium* or *Menodus rumelicus,* but that it is nearer in its measurements to the type of *Titanotherium proutii,* as indicated in the following table:

Measurements of Titanotherium bohemicum, T. proutii, and Menodus rumelicus, in millimeters

	T. bohemicum	M. rumelicus	T. proutii
Total length of the wearing surface	108	93	93
Breadth of the first section (lobe) of the tooth	48	43	40
Breadth of the second section (lobe) of the tooth	27	27	28

The author concludes that this species is widely distinct from the known European forms but that possibly it may eventually prove to be identical with either *Titanotherium proutii* or another species of the same genus. This, however, he considers unlikely, in view of its [supposed] European origin, so that he thinks he is quite justified in retaining the name *Titanotherium bohemicum.*

Etymology.—*bohemicum,* in allusion to the country where the specimen was supposedly found.

Present determination.—According to Dr. W. K. Gregory, who has compared a cast of the type of *Titanotherium bohemicum* with various American titanotheres, the type specimen is closely similar to one in the American Museum of Natural History referred to *Menodus giganteus* (Am. Mus. 1007). It differs chiefly in the greater width of the anterior lobe of m_3. It appears indeed to be specifically referable to *Menodus giganteus,* and it seems possible that it is in reality an American specimen which became mixed with the collection of fossils from Podbaba, near Prague. (Cf. pp. 230, 560, 941.)

Measurements of Menodus bohemicus and M. giganteus, in millimeters

	M. bohemicus (type)	M. giganteus (trigonoceras), Am. Mus. 1007
M_3, total length (estimated)	108	109
M_3, breadth of first lobe at base	52	47
M_3, breadth of second lobe	47	47
M_3, breadth of third lobe	33	----------
Center of protoconid to center of hypoconid	39	39
Center of metaconid to center of entoconid	39+	39+
Depth of jaw below front edge of m_3	111	111
Depth of jaw just behind m_3	152	143

FINAL OLIGOCENE SPECIES DESCRIBED BY OSBORN IN 1916–1919

Allops walcotti Osborn, 1916

See page 509

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 35, pp. 721, 722, fig. 1, 1916 (Osborn, 1916.433).

Type locality and geologic horizon.—"Big Badlands," S. Dak., probably Corral Draw; Chadron formation (*Titanotherium* zone), lower levels (Chadron A).

Type.—A nearly complete skull in the National Museum (No. 4260, skull Q). (See fig. 207.)

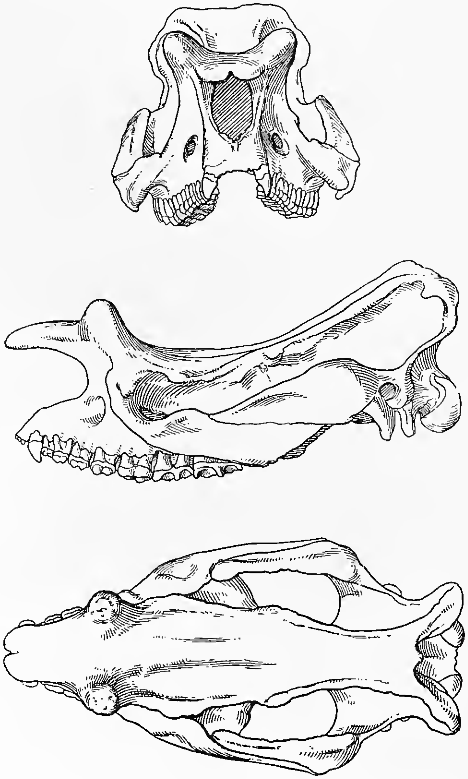

FIGURE 207.—Type (holotype) skull of *Allops walcotti*

Nat. Mus. 4260. After Osborn, 1916. One-eighth natural size.

Specific characters.—Osborn writes:

> Premolars with small tetartocones; p^1–m^3 285 millimeters. Incisors $\frac{2}{6}$. Horns elongate oval, no connecting crest. Mesaticephalic. Nasals elongate, broad. Face relatively elongate.

The type skull of this species (U. S. Nat. Mus. 4260) from level A is narrow and elongate, partly owing to lateral crushing. This feature conceals its resemblance to *Allops marshi,* which is apparent in other features—namely, (1) primitive, long nasals, (2) horns primitively short and obliquely oval, (3) large lateral incisor (i_2) and small first (i_1) or median incisor, (4) premolars accelerated, tetartocones more advanced than in *Brontops robustus* of level C.

Observations on the measurements of Allops walcotti.—The type and only known specimen of this species exhibits the following comparison in measurements with skulls of *B. brachycephalus* and *Menodus heloceras*, which show that the type of *Allops walcotti* has relatively large premolars and small molars.

Measurements of Allops walcotti, Menodus heloceras, and Brontops brachycephalus, in millimeters

	A. walcotti, Nat. Mus. 4260 (type)	M. heloceras, Am. Mus. 14576	B. brachycephalus	
			Nat. Mus. 4940	Nat. Mus. 4261
P^1–m^3	285	265	265	280
P^1–p^4	112	--------	101	[a] 104
M^1–m^3	169	170	160	178
Pmx–condyles	640	603	--------	580
Nasal length	105	132	--------	--------
Horn length	100	70	102	85
P^4, ap. by tr	35×51	--------	32×51	33×53
M^3, ap. by tr	60×61	--------	62×70	68×73

[a] Estimated.

Etymology.—"The species is named in honor of the Secretary of the Smithsonian Institution, Charles D. Walcott." (Osborn.)

Present determination.—The skull is crushed laterally but probably had a low zygomatic index—that is, it was mesaticephalic. While its reference to *Allops* requires confirmation, its nearer affinities appear to be with this genus rather than with *Brontops* or *Menodus*. The external cingula of the premolars are not as sharply defined as in other primitive members of the menodontine group.

Megacerops riggsi Osborn, 1916

See page 550

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 35, p. 723, fig. 2, 1916 (Osborn, 1916.433).

Type locality and geologic horizon.—Northeastern Colorado, Horsetail Creek; Chadron formation (*Titanotherium* zone), upper (?) levels.

Type.—A nearly complete lower jaw in the American Museum (No. 6364). E. D. Cope, collector. (See fig. 208.)

Specific characters (Osborn).—Of small size, smaller than any known individual of *Megacerops* or *Brontotherium*. Very massive jaw with a small coronoid process and a very short symphysis. Premolar series greatly abbreviated (85 mm.). Premolars and molars with reduced external cingula.

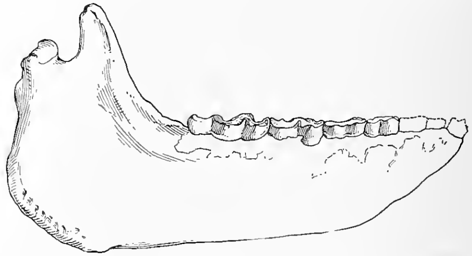

FIGURE 208.—Type (holotype) jaw of *Megacerops riggsi*

Am. Mus. 6364. After Osborn, 1916. One-sixth natural size.

Measurements of type

	Millimeters
Symphysis to condyle (estimated)	465
Premolar-molar series (p_1–m_3)	282
Premolar series (p_1–p_4)	85
Molar series (m_1–m_3)	194

Etymology.—Named "in honor of Mr. E. S. Riggs, of the Field Museum of Natural History, in recognition of his discoveries of Eocene titanotheres." (Osborn.)

Present determination.—The type of this species is a jaw in the Cope collection (Am. Mus. 4636), which was wrongly referred by Cope to his species "*Symborodon*" *acer*. It represents a highly specialized and small form of *Megacerops*.

NOTE.—For descriptions of upper Eocene and lower Oligocene titanotheres from Mongolia described by Osborn in 1923 see appendix; also the final opinion regarding the titanotheres of eastern Europe, page 941.

CHAPTER IV

SYSTEMATIC CLASSIFICATION OF THE TITANOTHERES

SECTION I. PHYLETIC VERSUS LINNAEAN SYSTEM OF CLASSIFICATION

NEO-LINNAEAN SYSTEMATIC DIVISIONS (ZOOLOGIC) AND EVOLUTIONARY PHYLA (PALEONTOLOGIC)

As explained in the introduction, the Linnaean system was based on the theory of the special creation of all systematic divisions coinciding in geographic space, so that its application to our modern paleontologic phyla, which succeed one another over long periods of geologic time, is beset with great difficulties and has led to different uses of systematic terms by different authors. The present monograph employs a phyletic system which has been used by the author since 1892 in the classification of the Perissodactyla (Osborn, 1892.67, pp. 90–94).

The taxonomic principle is that ancestral affinity is stronger than contemporary resemblance. Thus an animal that is directly ancestral to the titanotheres is placed in the family Brontotheriidae; an animal that is directly ancestral to *Brontotherium* is placed in the subfamily Brontotheriinae; a series of ascending species in the same line are placed in the genus *Brontotherium;* a series of "ascending mutations" may be placed within the single species *Brontotherium gigas*.

Such a vertical or phyletic application of the Linnaean system involves, it is true, a departure from the traditional Linnaean methods, but in the author's opinion it is far preferable to the introduction of a new systematic terminology. If necessary the author's system may be distinguished as neo-Linnaean. It is an adaptation of the Linnaean system to phylogeny as revealed by paleontology.

The degrees or steps in the evolution of neomorphic and heteromorphic characters, or rectigradations and allometrons, afford the real basis of our division of the great family tree of the titanotheres into branches and subbranches as follows:

Family, a branch of the Perissodactyla having a large number of similar characters and similar tendencies of evolution.

Subfamily, a branch of the main family embracing one or more genera retaining certain similar characters and developing certain peculiar evolutionary tendencies.

Genus, a branch of a subfamily or a stage of a subfamily distinguished by the prominent position of certain distinctive characters, which may be in widely different stages of development—for example, *Brontotherium leidyi, B. platyceras.*

Species and *subspecies,* divisions distinguished by certain gradations in the development of characters common to the genus, also by certain rectigradations and allometrons.

Ascending mutations, divisions distinguished by various intermediate stages of development of rectigradations and allometrons.

These principles of phyletic classification as developed and adopted in this monograph are also fully explained in Chapter I.

Classification is simply a convenient and condensed expression of our knowledge of hereditary lines of descent. It is constantly shifting and changing with discovery. The final classification can be attained only after we have worked out all the lines of descent of this great family. In the meantime we may review the history of the successive attempts at classification made up to the present time.

SUPERFAMILY NAMES PROPOSED BY OSBORN (1898) AND HAY (1902)

Superfamily Titanotherioidea Osborn, 1898

Original reference.—Am. Mus. Nat. Hist. Mem., vol. 1, pt. 3, p. 79, 1898 (Osborn, 1898.143).

Osborn divided the Perissodactyla into five superfamilies:

I. Titanotherioidea ("including the single family Titanotheriidae"), understood by Osborn to include both Eocene and Oligocene titanotheres.

II. Hippoidea, including Equidae and Palaeotheriidae.

III. Tapiroidea, including Tapiridae and Lophiodontidae.

IV. Rhinocerotoidea, including Hyracodontidae, Amynodontidae, Rhinocerotidae.

V. Chalicotherioidea, Chalicotheriidae.

Present determination.—Superfamily names are formed by adding *oidea* to the stem of the family name, and as Brontotheriidae is now regarded as valid, it appeared necessary to Doctor Hay to substitute for Osborn's term Titanotherioidea the term Brontotherioidea, first used by Hay in 1902.

Superfamily Brontotherioidea Hay, 1902

Original reference.—U. S. Geol. Survey Bull. 179, p. 629, 1902 (Hay, 1902.1).

The content of this term is as follows:

Brontotherioidea:
  Brontotheriidae:
    Lambdotheriinae (Eocene titanotheres).
    Brontotheriinae (Oligocene titanotheres).

The content of the term Brontotherioidea Hay, 1902, is thus the same as that of Titanotherioidea Osborn, 1898.

FAMILY NAMES PROPOSED OR ADOPTED BY MARSH (1873), FLOWER (1875), COPE (1879-1889), AND OSBORN (1889)

Family Brontotheridae Marsh, 1873

Original reference.—Am. Jour. Sci., 3d ser., vol. 5, p. 486, 1873 (Marsh, 1873.1).

Included genera.—*Titanotherium* Leidy and *Brontotherium* Marsh.

Family characters.—Not distinguished, but statement is made that *Brontotherium* was a "true perissodactyl with limb bones resembling those of *Rhinoceros.*" Marsh gave the family characters fully in a paper entitled "On the structure and affinities of the Brontotheridae." He writes (Marsh, 1874.1, p. 82):

> Among the more marked characters of the Brontotheridae, which readily distinguished them from the Rhinocerotidae, apparently their near allies, may be mentioned the following: There are four short and thick toes in the manus, and three in the pes. The skull supports a pair of large horn cores, placed transversely, as in modern artiodactyls.[19] There are well-developed canine teeth in both jaws. The molar teeth, above and below, are not of the *Rhinoceros* type but resemble those of *Chalicotherium.*

Present determination.—As long as *Brontotherium* was regarded as a synonym of *Titanotherium* the term Brontotheriidae had no standing, but since *Brontotherium* has been shown to be a good genus the term Brontotheriidae must be held valid.

Family Limnohyidae Marsh, 1875

Cf. Palaeosyopinae, this monograph, page 298

Original reference.—Am. Jour. Sci., 3d ser., vol. 9, p. 246, 1875 (Marsh, 1875.1).

Present determination.—In defining the genus *Diplacodon*, Marsh says: "From the Eocene Limnohyidae, already described, this genus is sharply distinguished." The name Limnohyidae does not occur in Marsh's previous descriptions, and so far as one can judge the family had not been defined. As *Limnohyus* is a synonym of *Palaeosyops* the family name is invalid.

Family Titanotheriidae Flower, 1876

Cf. Brontotheriidae Marsh, this monograph, page 279

Original reference.—Nature, vol. 13, p. 328, 1876 (Flower, 1876.1).

Present determination.—Flower regarded *Brontotherium* as synonymous with *Titanotherium* and so naturally called the family Titanotheriidae; but since *Brontotherium* is now regarded as valid, Flower's term becomes a synonym of Brontotheriidae Marsh.

Family Chalicotheriidae Cope, 1879

Original reference.—U. S. Geol. and Geog. Survey Terr. Bull., vol. 5, p. 228, 1879 (Cope, 1879.1).

Included genera.—"*Limnohyus* Leidy [=*Limnohyops* Marsh], *Palaeosyops* Leidy, '*Leurocephalus* S., O. & S.' [=*Telmatherium cultridens*], *Menodus* Pomel, *Symborodon* Cope, *Daeodon* Cope, *Chalicotherium* Kaup, *Nestoritherium* Kaup."

Present determination.—The titanotheres should never have been included in the same family with *Chalicotherium.*

Menodontidae Cope, 1881

Cf. Brontotheriidae Marsh

Original reference.—Am. Philos. Soc. Proc., vol. 19, pp. 378, 379, 397, 1881 (Cope, 1881.1).

Present determination.—The name Menodontidae as applied to the Oligocene titanotheres is invalid because antedated by Brontotheriidae Marsh.

Family Lambdotheriidae Cope, 1889

Cf. Lambdotheriinae, this monograph, page 279

Original reference.—Am. Naturalist, March, 1889 p. 153 (Cope, 1889.1).

Included genera.—From Cope's description it is plain that he intended to refer to the Lambdotheriidae not only the type genus *Lambdotherium* but all titanotheres with "but a single internal cusp on the first (posterior) superior premolar." He thus contrasts the Lambdotheriidae with the Menodontidae (=Brontotheriidae). Cope then also referred to the family Lambdotheriidae an Oligocene genus "*Haplacodon*" (=*Megacerops angustigenis*).

Synonymy.—The term Lambdotheriidae as used by Nicholson and Lydekker (1889.1, vol. 2, p. 1371) had the same connotation. It was apparently first limited to the genera *Lambdotherium*, *Palaeosyops*, and "*Limnosyops*" (=*Limnohyops*) by Flower and Lydekker (1891.1, p. 413) in 1891. Later authors, as Earle in 1892 (1892.1) and Zittel in 1893 (1893.1, p. 300), used the term Palaeosyopidae or Palaeosyopinae to include the same genera.

Present determination.—In this monograph the group under consideration is treated as a subfamily Lambdotheriinae of the Brontotheriidae.

Family Titanotheriidae Osborn, 1889 (1890?)

Cf. Brontotheriidae Marsh, this monograph, page 279

Original reference.—Am. Philos. Soc. Trans., new ser., vol. 16, p. 514, 1889 (1890) (Scott and Osborn, 1890.1).

Included genera.—Osborn writes:

> *Palaeosyops* has hitherto been referred to the Chalicotheriidae, but the discovery of the footbones of *Chalicotherium* by Filhol shows that the genera are widely separated. The discovery of the skeleton of *Diplacodon*, however, links *Palaeosyops* very closely to *Titanotherium.* * * * It seems best to group the three genera [*Palaeosyops*, *Diplacodon*, and *Titanotherium*] in the single family Titanotheriidae.

Present determination.—This was the first description which included the true titanotheres of the Eocene and Oligocene without extraneous elements (*Chalicotherium*). The term is nevertheless preoccupied by Titanotheriidae Flower, 1876, which is in turn a synonym of Brontotheriidae Marsh, 1873.

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[19] *Rhinoceros pleuroceros* Duv., from the Miocene of France, has a transverse pair of small horn cores on the nasals, not unlike those in *Dinoceras*. *R. minutus* Cuv. has somewhat similar processes.

SUBFAMILY NAMES AND PHYLA PROPOSED BY STEINMANN AND DÖDERLEIN (1890), EARLE (1892), AND RIGGS (1912)

Subfamily Palaeosyopinae Steinmann and Döderlein, 1890

Original reference.—Elemente der Paläontologie, p. 777, 1890 (Steinmann and Döderlein, 1890.1).

Included genera.—The authors divide the Chalicotheriidae into three subfamilies—Palaeosyopinae, Brontotheriinae, Chalicotheriinae. The Palaeosyopinae include the genera *Palaeosyops*, *"Limnohyus"* (*Limnohyops*), *Diplacodon.*

Present determination.—Palaeosyopinae Steinmann and Döderlein, 1890, thus has priority over Palaeosyopinae Earle, 1892.

Subfamily Palaeosyopinae Earle, 1892

Cf. Palaeosyopinae Steinmann and Döderlein

Original type reference.—Acad. Nat. Sci. Philadelphia Jour., 2d ser., vol. 9, pp. 272 et seq., 1892 (Earle, 1892.1).

Included genera.—*Lambdotherium*, *Limnohyops*, *Palaeosyops*, *Telmatherium*, *Haplacodon* [*Megacerops angustigenis*].

Present determination.—Earle gives a detailed and accurate description of the subfamily characters (pp. 274–276). The term is preoccupied by Palaeosyopinae Steinmann and Döderlein, 1890, and in its content is preoccupied by Lambdotheriidae Cope, 1889.

Subfamily Dolichorhinae Riggs, 1912

Cf. Dolichorhininae

Original reference.—Field Mus. Nat. Hist. Pub. 159, Geol. ser., vol. 4, No. 2, p. 25, June, 1912 (Riggs, 1912.1).

Included genera.—Middle Eocene titanotheres having nasals elongate and deeply recessed laterally, face shorter than cranium, an infraorbital process more or less developed, and molars only moderately expanded.

This group is proposed in order to designate those long-nosed titanotheres which evidently sprang from a common stock and form a natural and homogeneous group. It includes the genera *Mesatirhinus*, *Metarhinus*, *Dolichorhinus*, and *Rhadinorhinus*.

DIVISION OF THE OLIGOCENE TITANOTHERES INTO FOUR CONTEMPORARY PHYLA, OSBORN (1902)

Original reference.—Am. Mus. Nat. Hist. Bull., vol. 16, pp. 91–109, February 18, 1902 (Osborn, 1902.208).

Included genera.—Osborn writes:

> The Oligocene titanotheres consisted of at least four contemporary phyla, to which the prior generic names *Titanotherium*, *Megacerops*, *Symborodon*, and *Brontotherium* may be applied.
>
> They represent an adaptive radiation for different local habitat, different modes of feeding, fighting, locomotion, etc., which took origin, in part at least, in the middle or upper Eocene. Europe and Asia also may have shared in this radiation, since titanotheres are now definitely known in the Balkan region.
>
> The main phyletic characters are analogous to those recently (Osborn, 1900, p. 231) determined among rhinoceroses; the great antiquity of the lines leading to the existing species of rhinoceroses necessitated the revival of a number of discarded generic names to distinguish them. Similarly the separateness of four of the titanothere phyla, throughout the Oligocene and possibly from the Eocene, renders it desirable to revive certain generic names which in my first review I considered undefinable.
>
> Radiation involved three main sets of characters, two of which were correlated:
>
> First, dolichocephaly and brachycephaly, associated with numerous changes in the skull and teeth and, in at least two phyla, with longer and shorter limbs.
>
> Second, four distinct types in the shape and position of the horns, correlated with the structures of the nasals and frontals and indicative of different modes of combat among the males. (See fig. 209.)
>
> Third, canines of different form; and, finally, the presence of one or two pairs of functional incisor teeth, or the total degeneration of these teeth.
>
> *Titanotherium* Leidy applies to long-limbed animals with long skulls, persistently long and broad nasals, short triangular horns placed slightly in front of the eyes, vestigial incisors, $\frac{2-0}{2-0}$, large canine teeth. Known from the base to the summit of the Oligocene.

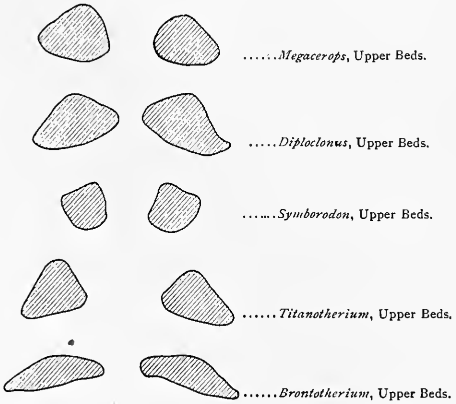

FIGURE 209.—Characteristic basal sections of horns of Oligocene titanotheres

> *Megacerops* Leidy applies to titanotheres with broad skulls, nasals progressively shortening, short horns rounded or oval in section, shifting anteriorly, one or two pairs of incisor teeth, $\frac{2-1}{2-1}$, medium-sized canine teeth. Known from the base to the summit of the Oligocene.
>
> Probably related to this are the subgenera of the types named *Allops* and *Diploclonus* by Marsh, differing from the above in horn characters. Known chiefly from the upper beds.
>
> *Symborodon* Cope includes titanotheres with skulls of varying proportion, nasals slender and progressively shortening, horns elongate and peculiar in being placed above the eye instead of shifting forward, incisors vestigial, $\frac{2-0}{2-0}$, canines small, approximated. Known only from the middle and upper beds.
>
> *Brontotherium* Marsh embraces the largest titanotheres, with very broad zygomatic arches, nasals shortening while horns elongate and shift forward; incisors persistent, $\frac{2}{2}$ in the males, canines stout and obtuse.
>
> Representatives of *Titanotherium* and *Megacerops* can now be continuously traced from the base to the summit of the Oligocene. Primitive species of *Brontotherium* also appear at

the base, although the phyletic sequence through the middle to the upper beds is not so clear. *Symborodon* suddenly appears in the middle beds.

The names of three of the genera thus recognized were subsequently changed, for the reasons given, as follows: For "*Titanotherium* Leidy" was substituted *Menodus* Pomel; for "*Megacerops* Leidy" was substituted *Brontops* Marsh; for "*Symborodon* Cope" was substituted *Megacerops* Leidy; "*Brontotherium* Marsh" was permanently accepted. The phyla subsequently were called subfamilies. (See below.)

RECLASSIFICATION OF THE EOCENE AND OLIGOCENE SUBFAMILIES BY OSBORN (1914)

Original reference.—Geol. Soc. America Bull., vol. 25, pp. 403–405, Sept. 15, 1914 (Osborn, 1914.409).

Reasons for reclassification.—Osborn makes the following statement:

> Recent discoveries have modified the author's earlier opinions as to the lines of descent of the titanotheres, and still further changes are anticipated with increase of knowledge of the connections between upper Eocene, or Uinta, titanotheres and those of the lower Oligocene, or White River.
>
> The main lines of division are indicated in the proportions of the limbs, whether cursorial, mediportal, or graviportal; the proportions of the skull, whether mesaticephalic, brachycephalic, or dolichocephalic; the development of frontonasal horns, whether accelerated or retarded; the molarization of the premolar teeth, whether accelerated or retarded; the presence or absence of incisor teeth; the abbreviate or elongate, the triangular or oval form of the frontonasal horns as developed in Oligocene times.

The new arrangement.—With these criteria the various phyla were distinguished in 1914 as follows:

A. Wind River titanotheres, face longer than cranium:
  I. Lambdotheriinae, light-limbed, cursorial:
    Lambdotherium.
  II. Eotitanopinae, medium-limbed, mediportal:
    Eotitanops.
B. Bridger and succeeding titanotheres, cranium longer than face:
  III. Palaeosyopinae, short-limbed, brachycephalic:
    Palaeosyops, Limnohyops.
  IV. Telmatheriinae, mesaticephalic to dolichocephalic:
    Telmatherium, Sthenodectes.
  V. Diplacodontinae, dolichocepahlic, with accelerated molarization of the premolars, imperfectly known:
    Diplacodon.
  VI. Manteoceratinae, mesaticephalic to brachycephalic, accelerated development of the horns, mediportal:
    Manteoceras, Protitanotherium.
  VII. Dolichorhinae, mesaticephalic to dolichocephalic, limbs, so far as known, abbreviate:
    Dolichorhinus, Mesatirhinus, Sphenocoelus, Metarhinus, Rhadinorhinus.
  VIII. Menodontinae, mesaticephalic to dolichocephalic, with abbreviate, triangular horns, with incisor teeth reduced or wanting, feet and limbs elongate:
    Menodus (=*Titanotherium*), *Allops.*
  IX. Brontopinae, brachycephalic, horns abbreviated, rounded, or oval, incisors persistent:
    Brontops (=*Megaceratops*[20]), *Diploclonus.*
B. Bridger and succeeding titanotheres—Continued.
  X. Megaceropinae, mesaticephalic to extreme brachycephalic, horns elongate, vertically placed, no incisor teeth:
    Megacerops (=*Symborodon*).
  XI. Brontotheriinae, mesaticephalic to brachycephalic, horns elongate, transversely flattened and divergent:
    Brontotherium.

The free use of subfamily divisions to express the distinct phyletic series is similar to that which the author adopted in the phylogeny of the rhinoceroses. More conservative usage would have divided the titanotheres into four subfamilies only. Of these names of phyla those assigned to Nos. II, IV, V, VI, VIII, IX, X, and XI had apparently not hitherto been published, and those assigned to Nos. I, III, and VII, although they had been used in previous publications, mostly by other authors, were now used in a more restricted sense.

Other subfamilies awaited further study and the discovery of connecting forms, namely:

Diplacodontinae = ancestors of Menodontinae or Brontotheriinae.
Eotitanopinae = ancestors of Palaeosyopinae.
Rhadinorhininae = ancestors of Megaceropinae.

Each subfamily name is carried back as far as possible—that is, to the point, even very remote, where the subfamily characters and tendencies of evolution are first clearly and unmistakably manifested.

SPECIES WRONGLY REFERRED TO THE TITANOTHERES

Palaeosyops minor Marsh, 1871 (=Anchippodus minor)

Original reference.—Am. Jour. Sci., 3d ser., vol. 2, p. 36, 1871 (Marsh, 1871.1).

Type.—"A molar tooth, from the right lower jaw, and probably by some other less characteristic remains" from Grizzly Buttes, Bridger Basin, Wyo.

Present determination.—This specimen was wrongly referred to *Palaeosyops*, as was recognized by Marsh, Cope, and others. The specimen pertains to the order Tillodontia.

Helotherium procyoninum Cope, 1872

Original reference.—Pal. Bull. No. 2, p. 466, 1872 (Cope, 1872.2).

Synonymy.—*Lambdotherium procyoninum* Cope, Tertiary Vertebrata, pp. 631, 711, pl. 24, fig. 22, 1884 [1885] (Cope, 1885.1).

"Syn.? of *Orohippus pumilis*," Hay (1902.1, p. 612).

Hyracotherium procyoninum Matthew, Am. Mus. Nat. Hist. Bull., vol. 12, p. 45, 1899 (Matthew, 1899.1).

Orohippus sp. Granger, Am. Mus. Nat. Hist. Bull., vol. 24, p. 227, 1908 (Granger, 1908.1).

Daeodon shoshonensis Cope, 1878

Original reference.—Pal. Bull. No. 30, "December 3, 1878" (Cope, 1878.1).

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[20] Error; should have been *Megacerops*.

Type and geologic horizon.—"The terminal portion of the lower jaw of a huge mammal" (Am. Mus. 7387), from the Miocene of Oregon.

Present determination.—The genus and species belong in the family Entelodontidae (Peterson, 1909.1, p. 63).

SECTION 2. CLASSIFICATION OF THE TITANOTHERES ADOPTED IN THIS MONOGRAPH

SYNOPSIS OF THE CLASSIFICATION

The natural classification or ancestral tree of the titanotheres is based on the characters of the skull and teeth, as set forth in Chapters V and VI, combined with those of the limbs and feet, as set forth in Chapter VII. The full definitions of the family and of the 12 subfamilies into which the titanotheres are now divided are presented in Chapters V and VI, of which the following classification is a synopsis. It should be compared with the phylogenetic tree given in Chapter X (p. 769). Each of the chief phyla has a subfamily name.

A. Wind River titanotheres, face longer than cranium:
   I. Lambdotheriinae, light-limbed, cursorial:
      Lambdotherium.
   II. Eotitanopinae (=?Palaeosyopinae), medium-limbed, mediportal:
      Eotitanops.

B. Bridger and succeeding titanotheres, cranium longer than face:
   III. Palaeosyopinae (=?Eotitanopinae), short-limbed, brachycephalic:
      Palaeosyops, Limnohyops.
   IV. Telmatheriinae, mesaticephalic to dolichocephalic:
      Telmatherium, Sthenodectes.
   V. Manteoceratinae (=Brontopinae), mesaticephalic to brachycephalic, accelerated development of the horns, mediportal:
      Manteoceras, Protitanotherium, Brachydiastematherium.
   VI. Dolichorhininae, mesaticephalic to dolichocephalic; limbs, so far as known, abbreviate; facial region downturned:
      Eometarhinus, Dolichorhinus, Mesatirhinus, Sphenocoelus, Metarhinus.
   VII. Rhadinorhininae (=?Megaceropinae), mesaticephalic, facial region cyptocephalic, upturned:
      Rhadinorhinus.
   VIII. Diplacodontinae (=?Menodontinae, =?Brontotheriinae), dolichocephalic, with accelerated molarization of the premolars, imperfectly known:
      Diplacodon, Eotitanotherium.
   IX. Brontopinae (=Manteoceratinae), brachycephalic, horns abbreviated, rounded or oval, incisors persistent; premolars retarded:
      Teleodus, Brontops (=Megacerops), Diploclonus.
   X. Menodontinae (=?Diplacodontinae), mesaticephalic to dolichocephalic, with abbreviate, triangular horns, with incisor teeth reduced or wanting, feet and limbs elongate, premolars accelerated:
      Menodus (=Titanotherium), Allops.

B. Bridger and succeeding titanotheres—Continued.
   XI. Megaceropinae (=?Rhadinorhininae), mesaticephalic to extreme brachycephalic, horns elongate, vertically placed, no incisor teeth:
      Megacerops (=Symborodon).
   XII. Brontotheriinae (=?Diplacodontinae), mesaticephalic to brachycephalic, horns elongate, transversely flattened and divergent, premolars accelerated:
      Brontotherium.

Suggestions as to resemblance or the affinity between subfamilies are given above in parentheses, and the families are arranged according to the general geologic sequence. One of these suggestions of ancestral affinity is now apparently well established, namely, that the Manteoceratinae are ancestors of the Brontopinae.

I. TITANOTHERES OF LOWER EOCENE TIME

(Face elongate)

Group I. Hornless:

1. Subfamily Lambdotheriinae Osborn. "Lambdotheres." (Lower Eocene titanotheres. Long-headed, very small; body and limbs slender and cursorial; face longer than cranium, slender.)

	Pages
Genus *Lambdotherium* Cope	168, 279, 590
Species *priscum* Osborn	194, 286, 590
primaevum Loomis	178, 283, 590
popoagicum Cope	168, 281, 590
progressum Osborn	194, 286, 590
magnum Osborn	199, 288, 590

2. Subfamily Eotitanopinae (=?Palaeosyopinae) Osborn. "Eotitanopines." (Lower Eocene titanotheres of intermediate size. Head of medium length; body and limbs less slender and cursorial than in the lambdotheres; gait submediportal; face longer than cranium.)

Genus *Eotitanops* Osborn	179, 289, 591
Species *gregoryi* Osborn	192, 291, 593
brownianus (Cope)	169, 292
borealis (Cope)	168, 292, 593
princeps Osborn	193, 295, 593
major Osborn	193, 296, 597
minimus Osborn	199, 296

II. TITANOTHERES OF MIDDLE AND UPPER EOCENE TIME

(Face abbreviate)

Group II. Retarded horn rudiments:

3. Subfamily Palaeosyopinae (=? Eotitanopinae) Steinmann and Döderlein. "Palaeosyopines." (Titanotheres larger than tapirs. Broad-headed, skull and limb proportions becoming stout; skull broad; zygomata progressively brachycephalic; grinders small; nasals tapering distally; face shorter than cranium; feet abbreviate, brachypodal; gait graviportal.)

	Pages
Genus *Limnohyops* Marsh (mesaticephalic to brachycephalic)	170, 303, 612
Species *priscus* Osborn	180, 306
laevidens (Cope)	163, 305
matthewi Osborn	180, 308
monoconus Osborn	180, 309, 614
laticeps Marsh	160, 311, 618

Group II. Retarded horn rudiments—Continued.

3. Subfamily Palaeosyopinae—Continued. Pages

Genus *Palaeosyops* Leidy (brachycephalic, hyperbrachycephalic) — 157, 312, 619
- Species *?fontinalis* Cope — 165, 317
- *longirostris* Earle — 172, 319
- *paludosus* Leidy — 157, 319
- *major* Leidy — 158, 321, 620
- *grangeri* Osborn — 181, 335
- *leidyi* Osborn — 181, 323, 620
- *robustus* (Marsh) — 161, 331, 626
- *copei* Osborn — 181, 336, 629

4. Subfamily Telmatheriinae Osborn. "Telmatheres." (Middle and upper Eocene titanotheres of larger size. Heads of medium length, with large cingulate incisors and heavy, sublanceolate canines; grinders large; mesaticephalic (*Telmatherium*) or subbrachycephalic (*Sthenodectes*); of mediportal gait.)

Genus *Telmatherium* Marsh (mesaticephalic, narrow sagittal crest) — 160, 340
- Species *cultridens* (Osborn, Scott, and Speir) — 168, 341
- *validum* Marsh — 160, 344
- *altidens* Osborn — 184, 351
- *ultimum* Osborn — 184, 345

Genus *Sthenodectes* Gregory (mesaticephalic to subbrachycephalic) — 190, 353
- Species *incisivus* (Douglass) — 185, 354

Group III. Accelerated horn rudiments:

5. Subfamily Manteoceratinae (Brontopinae) Osborn. "Manteoceratines" (prophet-horn), "brontopines." (Precociously horned titanotheres, of the same stock as the Dolichorhininae. Skull mesaticephalic, face abbreviate; feet abbreviate, brachypodal, gait graviportal; premolars retarded, incisors rounded; ancestral or related to the *Brontops* phylum of the Oligocene.)

Genus *Manteoceras* Hatcher (horns rudimentary) — 177, 362, 631
- Species *manteoceras* Hay — 177, 365, 631
- *washakiensis* Osborn — 182, 371
- *uintensis* Douglass — 186, 372

Genus *Protitanotherium* Hatcher (horns elongate, oval, more prominent than in *Manteoceras*) — 176, 375
- Species *emarginatum* Hatcher — 177, 377
- *superbum* Osborn — 185, 379

Genus *Brachydiastematherium* Böckh and Maty (large size; upper Eocene of Transylvania) — 166, 382
- Species *transilvanicum* Böckh and Maty — 166, 382

6. Subfamily Dolichorhininae Riggs. "Dolichorhines" (long-snouted). (Middle and upper Eocene titanotheres. Typically dolichocephalic and dolichopic; nasals typically long and expanding distally; precocious horn rudiments; infraorbital shelf usually conspicuous.)

Genus *Eometarhinus* Osborn (ancestral to *Metarhinus*, primitive, mesaticephalic) — 200, 419
- Species *huerfanensis* Osborn — 200, 420

Group III. Accelerated horn rudiments—Continued.

6. Subfamily Dolichorhininae—Continued. Pages

Genus *Mesatirhinus* Osborn (ancestral to *Dolichorhinus;* subdolichocephalic) — 182, 387, 636
- Species *junius* (Leidy) — 159, 388
- *megarhinus* (Earle) — 170, 388
- *petersoni* Osborn — 182, 389, 641

Genus *Dolichorhinus* Hatcher (extremely dolichocephalic, cyptocephalic; becoming extinct) — 177, 396, 645
- Species *superior* (Riggs) — 190, 395, 405
- *longiceps* Douglass — 188, 406, 651
- *vallidens* (Cope) — 162, 401
- *heterodon* Douglass — 187, 416
- *intermedius* Osborn — 184, 405
- *hyognathus* (Osborn) — 169, 173, 409, 646
- *fluminalis* Riggs — 191, 417

Genus *Metarhinus* Osborn (dwarfed, aberrant, mesaticephalic) — 183, 420, 648
- Species *earlei* Osborn — 183, 420
- *fluviatilis* Osborn — 183, 421
- *cristatus* Riggs — 191, 429
- *riparius* Riggs — 191, 429

Genus *Sphenocoelus* Osborn (little known; (?) branch of *Mesatirhinus*) — 174, 417
- Species *uintensis* Osborn — 175, 419

7. Subfamily Rhadinorhininae (=?Megaceropinae) Osborn. "Rhadinorhines" (slender-nosed). (Middle Eocene titanotheres. Mesaticephalic, cyptocephalic; infraorbital shelf reduced.)

Genus *Rhadinorhinus* Riggs (nasals short, pointed; possibly ancestral to the Oligocene *Megacerops;* cyptocephalic) — 192, 430
- Species *abbotti* Riggs — 192, 430
- *diploconus* (Osborn) — 173, 431

Group IV. Short-horned:

8. Subfamily Diplacodontinae (=?Menodontinae, Brontotheriinae) Osborn. "Diplacodonts." (Upper Eocene ancestors of the Oligocene subfamily Menodontinae. Heads probably mesaticephalic; grinding teeth foreshadowing the menodont type.)

Genus *Diplacodon* Marsh (horns well developed) — 166, 439
- Species *elatus* Marsh — 166, 439

Genus *Eotitanotherium* Peterson (horns well developed) — 196, 435, 656
- Species *osborni* Peterson — 195, 435, 656

III. TITANOTHERES OF LOWER OLIGOCENE TIME

(Face extremely abbreviate)

Group I. Short-horned:

9. Subfamily Brontopinae (Manteoceratinae) Osborn. "Brontopines." (Lower Oligocene and possibly middle to upper Eocene titanotheres. Progressively brachycephalic, with short-crowned teeth and moderately short feet; horns short, suboval; incisor teeth persistent, rounded crowns, one or two pair; premolars with retarded tetartocones.) Pages

Genus *Teleodus* Marsh (with three lower incisors; basal Oligocene) — 227, 481
- Species *avus* Marsh — 228, 481
- *primitivus* (Lambe) — 235, 482

	Pages
Group I. Short-horned—Continued.	
9. Subfamily Brontopinae—Continued.	
Genus *Brontops* Marsh (with two or one lower incisors; lower Oligocene)	222, 482, 664–676
Species *brachycephalus* (Osborn)	231, 483, 675, 676
dispar Marsh	223, 488, 664
robustus Marsh	222, 492, 666
?angustigenis (Cope)	219, 482
Genus *Diploclonus* Marsh (with internal branching horns; lower Oligocene)	227, 499, 675–678
Species *?tyleri* (Lull)	234, 502, 675
?bicornutus (Osborn)	231, 501
amplus Marsh	227, 504
selwynianus (Cope)	225, 502
10. Subfamily Menodontinae (=?Diplacodontinae) Osborn. "Menodonts." (Lower Oligocene and possibly upper Eocene titanotheres. Heads of medium width, progressively elongating (*Menodus*) or broadening (*Allops*); horns short, trihedral in section; incisor teeth vestigial; grinding teeth long-crowned with prominent cingula; premolars with accelerated tetartocones.)	
Genus *Menodus* Pomel (=*Titanotherium* Leidy)	204, 522, 681
Species *heloceras* (Cope)	212, 524, 681
torvus (Cope)	210, 525
proutii (Owen, Norwood, and Evans)	205, 526
trigonoceras (Cope)	213, 528, 683
varians (Marsh)	223, 535
giganteus Pomel	204, 530, 687
Genus *Allops* Marsh	224, 506, 678
Species *walcotti* Osborn	241, 509
marshi (Osborn)	233, 511, 678
serotinus Marsh	225, 515
crassicornis Marsh	228, 517, 679

	Pages
Group II. Long-horned:	
11. Subfamily Megaceropinae (=?Rhadinorhininae) Osborn. "Megaceropines," "symborodonts." (Relatively small, long-horned titanotheres, possibly descended from *Rhadinorhinus*. Of lower Oligocene age. Horns precociously evolved, with little or no connecting crest; head mesaticephalic to brachycephalic, cyptocephalic; narrow-lipped; premolars with precocious tetartocones; grinding teeth without cingulum; vestigial incisor teeth.)	
Genus *Megacerops* Leidy (=*Symborodon* Cope) (horns rounded, erect)	208, 541, 691
Species *riggsi* Osborn	242, 550
assiniboiensis Lambe	239, 549
copei (Osborn)	235, 548
acer Cope	211, 545
bucco (Cope)	212, 544
coloradensis Leidy	208, 544
?syceras (Cope)	226, 549
12. Subfamily Brontotheriinae (=?Diplacodontinae) Osborn. "Brontotheres." (Lower Oligocene titanotheres. Primitively dolichocephalic, progressively mesaticephalic and brachycephalic, slightly cyptocephalic; broad-lipped; very precocious development of the horns; accelerated development of internal cones of superior premolars; prominent cingulate incisor teeth in males.)	
Genus *Brontotherium* Marsh (horns progressively elongate, nasals abbreviate; lower Oligocene)	209, 555, 690
Species *leidyi* Osborn	234, 558, 690
hypoceras (Cope)	216, 562
hatcheri Osborn	235, 563, 695
tichoceras (Scott and Osborn)	219, 565
gigas Marsh	209, 567
dolichoceras (Scott and Osborn)	220, 572
medium (Marsh)	228, 576
curtum (Marsh)	224, 574
ramosum (Osborn)	231, 577
platyceras (Scott and Osborn)	221, 578
?rumelicum (Toula)	230, 560

Note.—Additional species are described and classified in the appendix, including Mongolian, east European, and Burmese titanotheres.

CHAPTER V

EVOLUTION OF THE SKULL AND TEETH OF EOCENE TITANOTHERES

SECTION 1. GENERAL PRINCIPLES OF THE STUDY OF THE CHARACTERS OF THE SKULL AND TEETH

PROPORTION CHARACTERS AND TENDENCIES OF EVOLUTION DISTINGUISHED BY ANALYSIS AND SYNTHESIS

The key to the evolution of the titanotheres is afforded by the analysis and synthesis of the separate characters of which the individuals in each line of ascent are composed—characters large or small, single or multiple—in correlation with one another and in correlation with the individual as a whole; characters progressing or retrogressing in successive generations; characters evolving rapidly or evolving slowly: such is the composition of each individual titanothere, as well as of each phylum.

Out of an almost infinite number of characters that are independently evolving we select a few that are visible and measurable. In a few individuals we observe the origin of new characters, but generally we observe the changes of form and of proportion in existing characters, which make up the greater part of the transformation of the individuals composing the family. In heredity each character is a separate unit, completely separable from all others; in adaptation it is correlated with other characters of the individual, as is fully explained in Chapter IX.

DISTINCTIONS BETWEEN PROPORTION CHARACTERS AND NEW RECTIGRADATION CHARACTERS

Methods employed.—The present chapter explains how the characters of titanotheres have been observed, examined, and measured, partly by new methods, largely devised especially to solve the problems that have arisen in the task of working out the genealogy of this family, and partly by old methods, which have been in use by paleontologists and systematists. To distinguish the characters of the teeth, skull, and limbs, which are generally but fragments, necessitates very refined and precise systems of measurement and comparison, because the individual members of different lines of descent may be very close to each other in certain characters yet readily separable in others. Animals that the zoologist would readily distinguish as species and subspecies by their external coloring, bodily form, or habits of life may be extremely similar in skeletal characters, yet the close methods of measurement and analysis that we have been compelled to adopt prove that every character has distinctions that may be revealed by minute and precise observation.

Researches on proportion characters.—The chief papers on the principles of evolution of the mammalian skull and teeth which the author has published in the investigation of the titanotheres are the following:

1896.110. The cranial evolution of *Titanotherium:* Am. Mus. Nat. Hist. Bull., vol. 8, art. 9, pp. 157–197, July 31, 1896.

1902.207. Dolichocephaly and brachycephaly in the lower mammals: Am. Mus. Nat. Hist. Bull., vol. 16, art. 7, pp. 77–89, Feb. 3, 1902.

1902.208. The four phyla of Oligocene titanotheres: Am. Mus. Nat. Hist. Bull., vol. 16, art. 8, pp. 91–109, Feb. 18, 1902.

1907.301. Evolution of mammalian molar teeth to and from the triangular type, 250 pp., New York and London, Macmillan Co., September, 1907.

1912.368. Skull measurements in man and the hoofed mammals: Science, new ser., vol. 35, No. 902, p. 596, Apr. 12, 1912.

1912.372. The continuous origin of certain unit characters as observed by a paleontologist (Harvey lecture): Am. Naturalist, vol. 46, No. 544, pp. 185–206, April, 1912; No. 545, pp. 249–278, May, 1912; Harvey Soc. Volume, 7th ser., pp. 153–204, November, 1912.

1912.382. Craniometry of the Equidae: Am. Mus. Nat. Hist. Mem., new ser., vol. 1, pt. 3, pp. 57–100, figs. 1–17, June, 1912.

1915.416. Origin of single characters as observed in fossil and living animals and plants (Presidential address before the Paleontological Society of America, Dec. 31, 1914): Am. Naturalist, vol. 49, No. 580, pp. 193–239, April, 1915.

Proportion characters defined by indices and ratios.—Many specific, generic, and subfamily characters of animals can be best expressed in mathematical ratios and indices, for these figures record most precisely the movements or tendencies of development that lead from species to species. In all ascending series of titanotheres every measurable character is in a state of movement either progressively or retrogressively.

Significance of tendencies in proportion.—A tendency or trend to evolve in a certain proportional direction is found to be a phyletic distinction of prime importance, which leads us through all the stages of mutative, specific, generic, and subfamily characteristics. For example, certain titanotheres become more and more broad-headed from lower to higher geologic levels; progressive brachycephaly thus becomes a phyletic character of taxonomic value. One genus may be defined as "progressively brachycephalic," whereas a related genus, in which the tendency to become long-headed prevails, may be defined as "progressively dolichocephalic."

Taxonomic value of proportion tendencies.—Thus the true relations of most of the lines of descent among the Eocene and Oligocene titanotheres have been gradually discovered, partly by the old methods of descriptive anatomy, used by Leidy, Marsh, and Cope, and partly by the new methods which have been developed since 1900 in the preparation of this monograph. It has been found that the changing proportions of the various parts of the skull, of the individual grinding teeth, of every part of the skeleton, especially the limbs, are highly distinctive systematic and phyletic characters.

Five distinctions of phyla.—Each line of descent is distinguished by five different methods: First, by the presence or absence of certain characters; second, by the new proportions of certain characters; third, by the tendencies or directions in which proportions are being changed; fourth, by the rates of change in proportion characters, whether retarded or accelerated; fifth, by the appearance of new rectigradation characters.

Numerous extinct branches or phyla.—The distinctions in characters multiply with the multiplication of the phyla. In 1914 no less than 20 branches of the titanothere family were known, and probably many more existed that had not yet been discovered. Throughout Eocene time titanotheres continued to migrate into the mountain region of the Bridger and Washakie Basins of Wyoming. Allowing for certain branches that drop out, we find that the number of their known branches constantly increases from lower to higher levels, as shown below.

Oligocene: White River group	7–8
Summit of upper Eocene: Lower part of Uinta C (true Uinta formation), Uinta Basin, Utah	4
Upper Eocene: Uinta B 2 of Uinta Basin, Utah; Washakie B 2 of Washakie Basin, Wyo	6
Upper Eocene: Washakie B 1 of Washakie Basin, Wyo.; and Uinta B 1 of Uinta Basin, Utah	8
Middle Eocene: Bridger C and D of Bridger Basin, Wyo.; Washakie A of Washakie Basin, Wyo	5
Middle Eocene: Bridger A and B of Bridger Basin, Wyo.; Huerfano B, Huerfano Park, Colo	2
Lower Eocene: Wind River formation, Wind River Basin, Wyo.; Huerfano A, Huerfano Park, Colo	2

Universal change of form.—No characters in any genus or phylum are stationary. During the long intervals of geologic time the members of each of these branches were constantly diverging in some characters and converging in others and becoming more and more unlike one another both as a whole and, so far as we can observe, in each one of their single characters.

Allometrons and rectigradations.—The term allometrons (Osborn, 1912.372, pp. 249–278) designates characters that arise through continuous changes of size or proportion in old features—that is, purely quantitative changes—such as may be expressed in differences of measurement as well as in indices and ratios. Rectigradations are new characters that tend to evolve in a definite direction—the earliest "rudiments" or discernible stages of absolutely new forms. In 1889 Osborn called such characters "definite variations" (Osborn, 1907.301, p. 239).

Six points in the distinction between allometrons and rectigradations may be readily grasped: (1) When the shadowy beginning of a new cusp on the grinding teeth or the rudiment of a horn is first discernible as a new character it appears as a "rectigradation"; (2) when this same rudiment of a cusp or horn takes on a new shape the change of form appears as an "allometron"; (3) in the hard parts of a titanothere, as of any other mammal, the rectigradations—the numerically new characters of any kind—are comparatively few and uncommon, but the allometrons—the transformations of existing characters—comprise the larger number of changes; (4) both allometrons and rectigradations are distinctly heritable characters; (5) in the genesis of rudiments (rectigradations) of new cusps or of horns all the branches or phyla of titanotheres sooner or later tend to resemble one another—that is, to develop the same cusps and the same horn swellings—and thus to become convergent; (6) on the other hand, in changes in the proportions (allometrons) of the skull, the different phyla may differ widely from one another and through dissimilar allometrons may become divergent. (See fig. 210.)

STEPS IN TRANSFORMATION OF CHARACTERS

So far as we have observed, all absolutely new characters that we have traced to their very beginnings in titanotheres arise gradually and continuously; there is no evidence of sudden leaps from mutation to mutation or from species to species. This continuous mode of evolution is more fully considered in Chapter IX.

The addition (rectigradation) or the modification (allometron) of a single character is theoretically the first step in transformation, but as a matter of fact all characters are being simultaneously more or less modified, and in the individual as a whole new characters are constantly being added. Only when fully developed after the lapse of many generations does a rectigradation or an allometron become of sufficient systematic value to define the mutation or the species. None the less each of these changes forms one in a series of steps in the transformation of species.

One by one the characters, either rectigradations or allometrons, in many parts of the titanothere are independently changed until the changes build up what paleontologists call an "ascending mutation" in the sense in which the German invertebrate paleontologist Waagen defined this term in 1869. An ascending mutation is a stage in a continuous evolutional ascent in one or more characters from one species to another; there is no evidence that it is a saltation or "mutation" in the sense of that word as used by De Vries.

Finally these rectigradations and allometrons attain by accumulation sufficient importance to enable us to call a stage a "species" in the Linnaean sense or a "subspecies" in the modern sense.

The divergence between the several branches of the titanothere family therefore actually consists of the sum total of changes in an almost infinite number of single characters, only a few of which are measurable. These changes are of the following principal kinds:

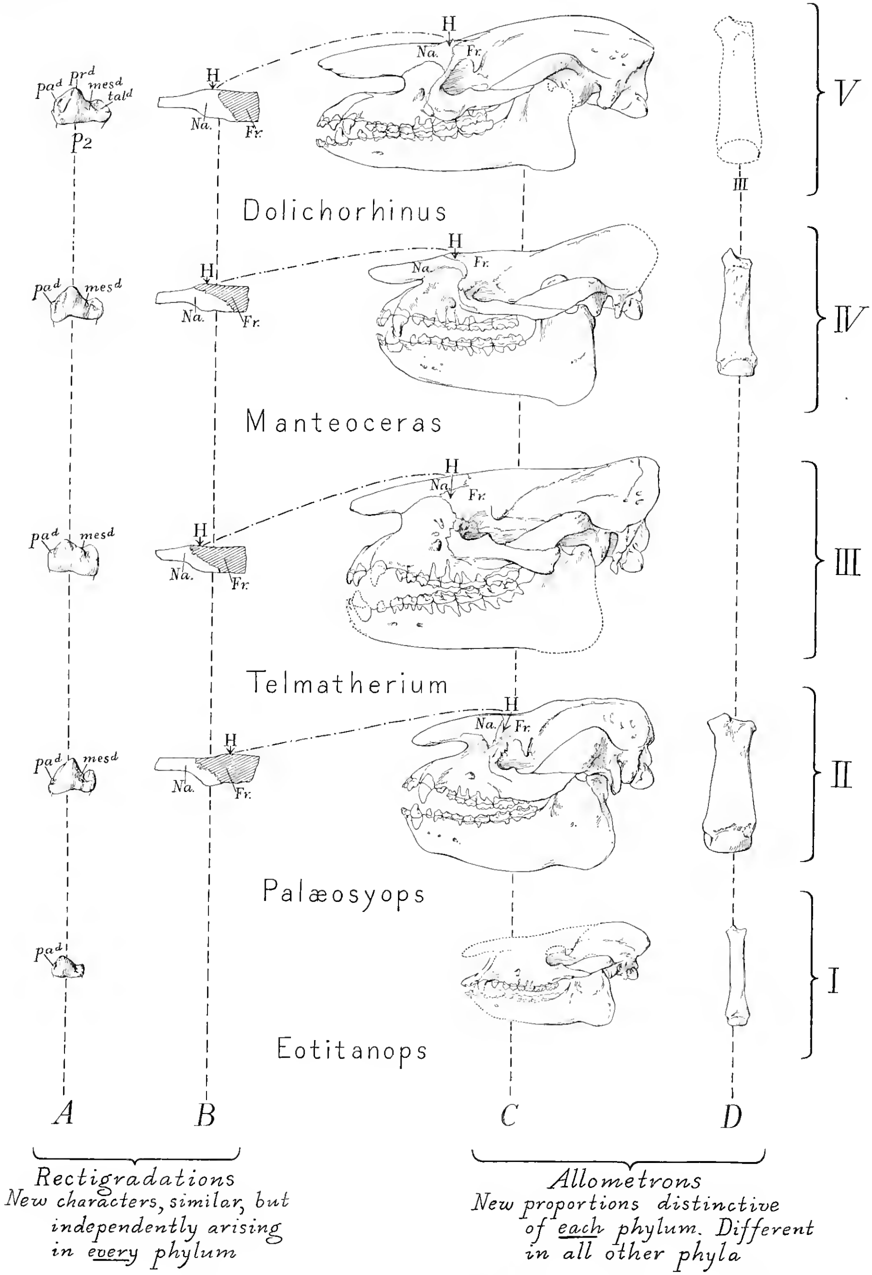

FIGURE 210.—Skulls showing different numerical and proportional characters in five separate phyla of titanotheres

Similar numerical characters (rectigradations, *A, B*) and dissimilar proportional characters (allometrons, *C, D*), all arising independently in descendants of the same ancestors. Each of the five phyla (I–V) exhibits similar rectigradations of the premolar teeth and in the osseous horn rudiments (H) but dissimilar allometrons of the skull (*C*) and of the foot bones (*D*). pa^d, mes^d, New cuspules on the teeth; H, rudiments of the newly arising horns. I, *Eotitanops*, a dolichocephalic ancestral form; II, *Palaeosyops*, brachycephalic; III, *Telmatherium*, mesaticephalic; IV, *Manteoceras*, mesaticephalic; V, *Dolichorhinus*, dolichocephalic.

1. Loss of old characters (paleomorphs): Absolute loss of character is rare in the titanotheres. The trapezium is the only bone known to be lost during the recorded history of the family, whereas in the horses many bones disappear. The incisor teeth disappear in several phyla. The grinding teeth lose certain cusps.

2. Appearance of new characters (neomorphs), including rectigradations: A large number of new cusps appear on the premolar grinding teeth, and a few new features appear on the molar grinding teeth. A pair of new hornlets appear on the frontonasal region of the skull.

3. Increase or diminution of size as a whole (heteromorphs): Increase of size is the prevailing tendency among the titanotheres, but in some phyla size is persistent or is even arrested, as in the dwarf *Metarhinus;* or it is reduced, as in the species *Palaeosyops copei.*

4. Change in proportions of different regions of the skeleton (heteromorphs, including allometrons): Such changes are expressed in ratios—for example,

$$\frac{\text{length of tibia}}{\text{length of femur}}$$

These ratios are extremely significant. Thus one phylum may become short limbed or brachymelic, another long limbed or dolichomelic; one short footed or brachypodal, another long footed or dolichopodal; one phylum may become large headed or macrocephalic, another small headed or microcephalic.

5. Change in proportions of single parts of the cranial skeleton (allometrons): Such changes are best expressed in indices, such as

$$\frac{\text{width of skull}}{\text{length of skull}}$$

Some series become long headed or dolichocephalic, others broad headed or brachycephalic; some become long faced or dolichopic, others become short faced or brachyopic.

The manner in which these changes of proportion (allometrons) and the successive addition of rectigradations serve to distinguish the genera of Eocene titanotheres from one another is clearly shown in the following descriptive characterizations of ten Eocene genera:

Lambdotherium: Small, long headed, long limbed, without horns.

Eotitanops: Larger, long faced, limbs somewhat heavier, hornless.

Limnohyops: Still larger, broad headed, short faced, light limbed, broad footed, hornless.

Palaeosyops: Massive, broad headed, short faced, heavy limbed, short footed, rudiments of horns (rectigradations).

Telmatherium: Large, long headed, short faced, light limbed, rudiments of horns (rectigradations).

Manteoceras: Large, medium headed, short faced, medium limbed, short footed, small, distinct horns (rectigradations).

Mesatirhinus: Of medium size, narrow headed, short faced, light limbed, long footed, small horns quite distinct.

Metarhinus: Very small, medium headed, short faced, light limbed, horns not very distinct.

Dolichorhinus: Large, extremely long headed, short limbed, short footed, horn rudiments very prominent.

Rhadinorhinus: Medium size, medium headed, light limbed, horn rudiments indistinct.

The degrees of change among the "species" constituting each of these "genera" are exemplified in the "standard measurement tables" that accompany the description of every genus in Chapters V and VI. In these tables it is demonstrated, first, that the Linnaean lines of division between species do not exist; second, that occasionally the type and paratype specimens of a single species selected by the pioneer paleontologists belong to separate stages because they were found at different geologic levels. Some of these ancient specific names have historic value and are retained for convenience, although some that were applied to forms on the border line between two specific stages are very inconvenient.

PROPORTIONS AND FLEXURES OF THE SKULL

The skull is the chief center of evolution movement in the titanotheres, both in the transformation of its proportions and in the development of horns, and with the teeth it furnishes a complete key to the evolution, relationship, and ascent of these mammals, although the proportions of the skeleton and the feet also furnish valuable indications. The forms of the feet, which are evolving so rapidly and are so significant in the horses, are relatively stationary in the titanotheres.

The chief principles in the transformation of the skull through changes of proportion are the following:

1. Elongation and narrowing of the skull as a whole—that is, dolichocephaly.
2. Abbreviation of the cranium and elongation of the face—that is, proopic dolichocephaly or dolichopy, as in *Equus.*
3. Abbreviation of the face and elongation of the cranium—that is, postopic dolichocephaly or brachyopy, as in all Oligocene titanotheres.
4. Abbreviation and broadening of the skull as a whole—that is, brachycephaly.
5. Flexure of the facial upon the cranial region—that is, cyptocephaly.

The principal measurements of the skull in the titanotheres differ somewhat from those employed in the craniometry of the Equidae. (Osborn, 1912.382.) They are listed below and are illustrated in Figure 211.

Direct measurements of skull

1. Cephalic or basilar length from incisive border to occipital condyles, inclusive.
2. Facial length from postorbital process to incisive border, inclusive (projected on the basilar line).
3. Cranial length from postorbital processes to occipital condyles, inclusive (projected on the basilar line).
4. Facial breadth, or frontal width, as measured in the horses across the postorbital processes to establish the cephalic index. This measurement is not practicable in titanotheres.
5. Zygomatic breadth across the widest part of the zygomatic arches.
6. Premolar-molar length, or superior grinding series (p^1 to m^3 if the first premolar is retained, otherwise p^2 to m^3).
7. Molar length, anteroposterior measurement along middle of crowns (m^1 to m^3).

8. Molar length and width, anteroposterior measurement of first superior molar (m^1) and transverse measurement of the same (least width, near center of crown).

Indices of skull (expressed as per cent)

9. Zygomatic-cephalic index $=\dfrac{\text{breadth across zygomata}}{\text{basilar or cephalic length}}$

10. Premolar-molar cephalic index $=\dfrac{\text{length of six superior grinding teeth, } p^2\text{–}m^3}{\text{cephalic length}}$

11. Molar-cephalic index $=\dfrac{\text{length of upper true grinders, } m^{1-3}}{\text{cephalic length}}$

12. Molar index $=\dfrac{\text{breadth of a molar, } m^1 \text{ or } m^2}{\text{length of a molar}}$

13. Faciocephalic index $=\dfrac{\text{length of face [21]}}{\text{cephalic length}}$

14. Craniocephalic index $=\dfrac{\text{length of cranium [21]}}{\text{cephalic length}}$

Flexures of skull

15. Palatocranial flexure = angle that the palate, from the posterior to the incisive border, makes with the basal line of the cranium. (Not used in the study of titanotheres.)

16. Faciocranial flexure = angle that the preorbital part of the skull, determined from the optic foramen (see figs. 213, 214) to the incisive alveolus, makes with the line from the optic foramen to the middle of the occipital condyle.

SUMMARY AS TO CRANIOMETRY

1. *Direct measurement.*—Since the fossil skulls and dental series are rarely complete or perfect, the paleontologist requires an additional series of direct detailed measurements of parts of the skull and teeth that are not needed by the zoologist.

2. *Significance.*—Every one of these direct measurements, indices, and angles is significant, because all skulls are in a continuous process of movement, or evolution. The indices are even more significant than the direct measurements, because every genus and probably every species has its distinctive indices in adult specimens, and the direct measurements vary greatly with the age, sex, and individual variation of the specimen.

3. *Imperfection.*—In fossil skulls the indices are often difficult to determine; a slight crushing or distortion seriously disturbs the index, for a skull that is crushed on its side is narrowed and lengthened at the same time. Nevertheless, the indices and ratios should be used wherever obtainable.

4. *Age.*—The proportions between the several parts are largely altered with the age of the animal; this statement is especially true of progressive allometrons, such as the proportion between the face and the cranium. Thus the faciocephalic or craniocephalic index may alter rapidly as the titanothere advances from youth to maturity; similarly the flexure (cyptocephaly) becomes extreme only in mature skulls. The age of the animal measured is thus to be considered in all the indices and ratios of the skull, teeth, and skeleton.

5. *Sexual correlations.*—Certain proportions and indices are correlated sexual characters—that is, in brachycephalic phyla the males have relatively broader heads than the females. For example, we observe in the genus *Brontops* the following proportions:

Males of *Brontops validus* (brachycephalic), indices 73–87.
Females of *Brontops validus* (mesaticephalic), indices 60–70.

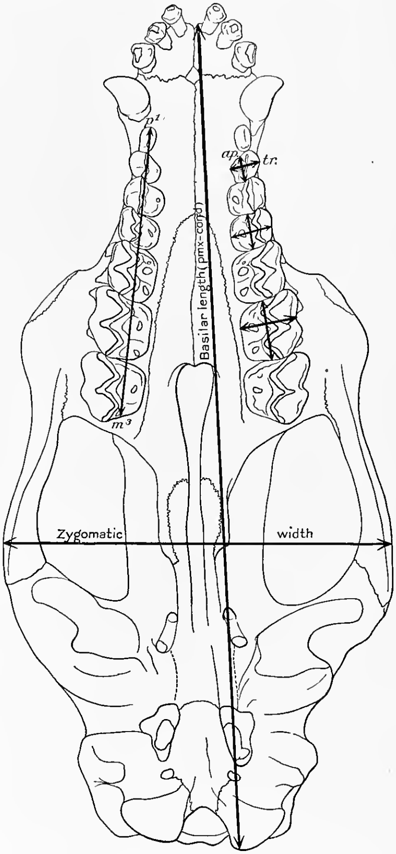

FIGURE 211.—Standard measurements of Eocene titanothere skulls

Palatal view of a skull of a middle Eocene titanothere, *Mesatirhinus petersoni*, showing (by arrows) how the basilar or cephalic length, the zygomatic width, and the length and width of the upper premolars and molars are measured.

6. *Effects of crushing.*—The indices of fossil skulls are profoundly modified by vertical or lateral crushing: vertical crushing tends to give brachycephalic indices; lateral crushing tends to give dolichocephalic indices. To these facts are due in part the wide variations in the tables of indices, especially in the chapter on the Oligocene titanotheres.

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[21] As projected on basilar line.

CHANGING PROPORTIONS OF THE CRANIUM AND FACE

The back of the eye socket, or orbit, is the dividing line between the face, which lies in front of it, and the cranium, which lies behind it, as indicated by the shaded and unshaded parts of the skulls in Figure 212, which shows that in the oldest true titanothere (*Eotitanops*) of lower Eocene time, as in the oldest true horse (*Eohippus*) of the same period, the face (shaded) and the cranium (outline) are equally long—in fact, in *Eotitanops* the face is a little longer than the cranium. The universal allometric character of titanotheres is abbreviation of the face (proopic region) and elongation of the cranium (postopic region)—that is, brachyopy and dolichocrany. Thus in all middle and upper Eocene titanotheres the cranium is longer than the face. This disparity keeps increasing until in the Oligocene titanotheres, such as *Brontotherium* (fig. 212), the face is greatly abbreviated and the cranium greatly elongated. In the horses (*Equus*) this allometry is just reversed: the face becomes very long (fig. 212), but the cranium remains very short (dolichopy and brachycrany). These differences are expressed in the so-called faciocephalic index, which is obtained as follows:

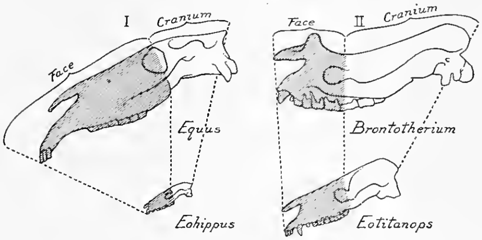

FIGURE 212.—Unequal elongation of face and cranium in titanotheres and horses

Eotitanops and *Eohippus*, primitive perissodactyl type; face and cranium subequal in length. *Brontotherium*, titanothere type; face abbreviated, cranium elongated. *Equus*, Equidae type; face elongated, cranium abbreviated.

$$\frac{\text{length of face including orbits} \times 100}{\text{basilar length of skull}}$$

The relative faciocephalic indices in titanotheres and horses are as follows:

Titanotheres:	Horses:
Brontotherium, 33.	Equus, 70.
Eotitanops, 56.	Eohippus, 53.

In the titanotheres the universal tendency of facial abbreviation and cranial elongation distinguishes all the branches alike, but since the allometric movement takes place at unequal rates each genus or phylum has its distinctive faciocephalic index.

CYPTOCEPHALY, OR FACIOCRANIAL FLEXURE

The upward or downward flexure of the facial and palatal parts of the skull upon the basicranial axis was first erroneously termed "cytocephaly" by the author (Osborn, 1912.382); the term "cyptocephaly" is correct.

In primitive ungulate skulls and in the fetal skull the anteroposterior planes of the face and palate and of the basicranial axis are more nearly in parallel lines—that is, the skulls are "orthocephalic."

In certain specialized ungulates there is either an upward or a downward deflection of the face on the cranium, which appear respectively to be adapted to different forms of feeding, as follows: (1) Horizontal and upward flexure of the face is characteristic of certain browsing types, such as *Alces* and *Rangifer;* (2) downward flexure of the face and palate on the basicranial axis is characteristic of certain grazing types, such as the hartebeest (*Bubalis*) and other grazing antelopes (see fig. 213); (3) in the young of certain species of Equidae, Bovidae, and Cervidae the palatal line makes an angle of 19° to 25° with the basicranial line, which may increase to 53° in the adults of extremely deflected types.

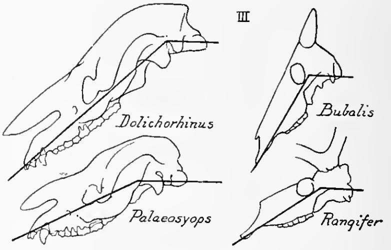

FIGURE 213.—Faciocranial flexure, or cyptocephaly

In the reindeer (*Rangifer*) the face is much less bent upon the cranium than in the hartebeest (*Bubalis*). A similar but less pronounced contrast is seen in the Eocene titanotheres *Palaeosyops* and *Dolichorhinus*.

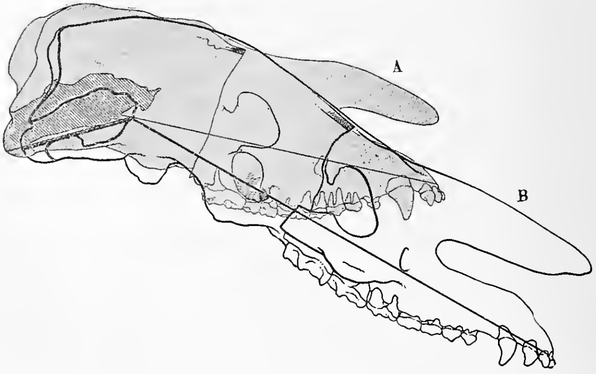

FIGURE 214.—Faciocranial flexure in *Palaeosyops* (A), orthocephalic, and *Dolichorhinus* (B), cyptocephalic

Among the many authors who have more or less directly contributed to this subject are Rütimeyer

(Cervidae, 1882.1), Flower (1885.1, pp. 185–201), Lankester (Giraffidae, 1902.1), Ewart (Equidae, 1907.1). Rütimeyer pointed out that the Cervidae, as browsing animals, have an extremely horizontal axis of the skull, in contrast with that of the Bovinae, grazing animals, in which the face is strongly deflected. Lankester pointed out that in the hornless *Okapia*, a forest animal that browses on the leaves of trees, the facial and cranial regions are orthocephalic, or nearly in the same horizontal plane; in the related *Giraffa*, however, which also browses on high trees but possesses horns, the face is deflected on the cranium almost as much as in the grazing sheep (*Ovis*), which feeds upon the ground. Lankester consequently attributed the deflection of the face to the possession of horns. Ewart applied cyptocephaly as a means of distinguishing the various phyla of horses and, like Rütimeyer, explained the flexures as adaptations to a prevailing browsing or grazing habit, respectively. He pointed out that *Alces* and *Ovis* illustrate the two extreme types of skull: (1) the elk (*Alces*) is a short-necked, forest form adapted to feeding on shrubs and trees—that is, to holding the head in a nearly horizontal position, (2) whereas the sheep (*Ovis*) grazes or browses on the ground and is adapted to holding the head when feeding in a nearly vertical position.

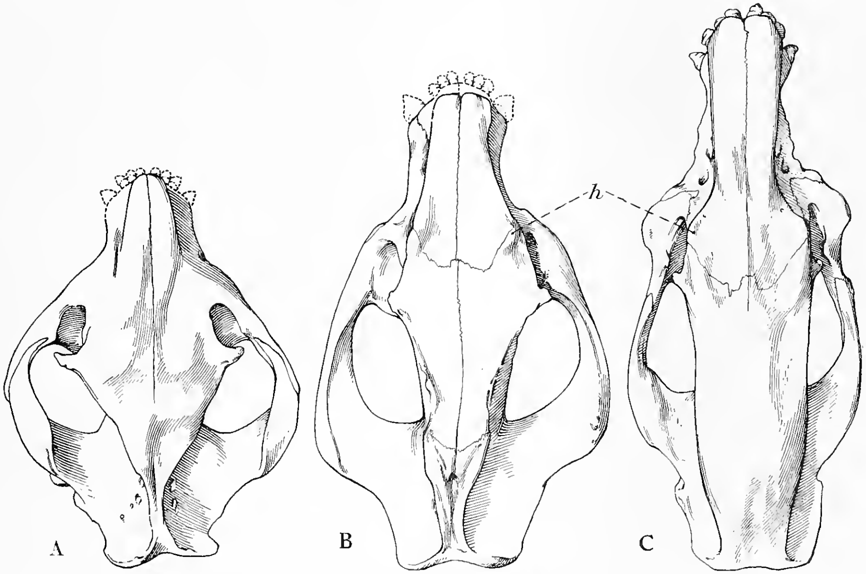

FIGURE 215.—Cranial proportions of Eocene titanotheres—*Palaeosyops*, *Manteoceras*, and *Dolichorhinus*

A, Brachycephalic (*Palaeosyops major*), zygomatic-cephalic index 77. B, Mesaticephalic (*Manteoceras manteoceras*), zygomatic-cephalic index 63–68. C, Dolichocephalic (*Dolichorhinus hyognathus*), zygomatic-cephalic index 43–46. *h*, Rudiments (rectigradations) of the horns.

There are excellent reasons for believing that a bent skull facilitates grazing on short herbage.

Osborn's examination of the horses (1912.382, p. 96) shows that in the adult domesticated horse the palatocranial angle ranges from 10° to 17°; in the Burchell zebra the palatocranial angle increases with age from 19° at three years to 25° at six years. In the domesticated horses it varies from 20° to 23°. In the Burchell zebras it increases from 15° at birth to 25° at the fourth year. Since the asses are more given to browsing than the horses or zebras the slight difference in flexure may be attributed to the prevailing browsing habit. (See p. 259.)

In titanotheres the faciocranial angle is measured as shown in Figure 214. In a comparison of the brachycephalic *Palaeosyops*, presumably a browsing type with short-crowned teeth, the lines of the face and the cranium are more nearly parallel, the angle being 154°. In the extremely dolichocephalic *Dolichorhinus*, which has more hypsodont teeth and presumably subgrazing habits, the face is sharply bent down on the cranium, forming an angle of 135°. (See fig. 214.)

Cyptocephaly, whatever its adaptive significance, is certainly one of the important progressive characters in the transformation of the ungulate skull and is decidedly marked in certain titanotheres.

DOLICHOCEPHALY, BRACHYCEPHALY, AND CORRELATION

In 1902, when the measurements of Oligocene titanotheres were brought together, the conclusion was again reached that dolichocephaly and brachycephaly are among the dominating tendencies affecting the skull and grinding teeth of titanotheres, but that they are not invariably correlated with similar abbreviation or elongation in the trunk and limbs.

The principle of correlation, however, was found to explain a vast number of dry detailed facts concerning all parts of the skulls of titanotheres, including the teeth, which had been recorded by Cope, Marsh, Earle, Osborn, and others without any appreciation of their morphologic significance.

In brief, the progressive dolichocephaly or brachycephaly of the skull is found to dominate the shape of every bone in the skull but more particularly that of the nasals, horns, zygomatic arches, and palate, as well as the confluence or separation of the foramina in the base and sides of the skull, the form of the occiput and of the mastoid, and the relations of other bones around the auditory meatus, the shape of the premaxillary and mandibular symphyses, the diastemata between and behind the teeth, the number and shape of the teeth, the shape, number, and relations of the cusps of the teeth, and even, it would appear, the cingulum around the grinding teeth.

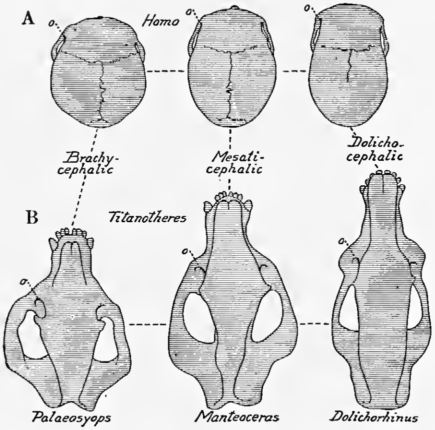

FIGURE 216.—Cranial proportions in man (A) and in the titanotheres (B)

Viewed from above. Used in reference to man the words brachycephalic, mesaticephalic, and dolichocephalic denote, respectively, brachycranial, mesaticranial, and dolichocranial. In other words, they describe the proportions of the cranial cavity. Used in reference to the titanotheres the same words describe the relative length and breadth of the entire skull.

The three skulls of middle and upper Eocene titanotheres shown in Figure 216 also illustrate admirably the extremes of brachycephaly and dolichocephaly and the intermediate condition of mesaticephaly.

The skulls are those of the species *Palaeosyops major*, with its extremely broad head, of the moderately broad-headed *Manteoceras manteoceras*, and of the extremely long and narrow-headed *Dolichorhinus hyognathus*.

The cranium of these titanotheres varies in width like the skulls of man (fig. 216) and the rhinoceros, and the excessive width is contributed chiefly by the great expansion of the zygomata. The skull of *Dolichorhinus* as a whole, however, is far more elongate than that of *Palaeosyops*. We find also very pronounced differences of proportion in every bone and every tooth when we compare *Palaeosyops* and *Dolichorhinus* minutely. The table on page 259 presents some of the extremes of structure observed especially in the titanotheres, in which the most careful comparison of dolichocephalic and brachycephalic skulls has been made.

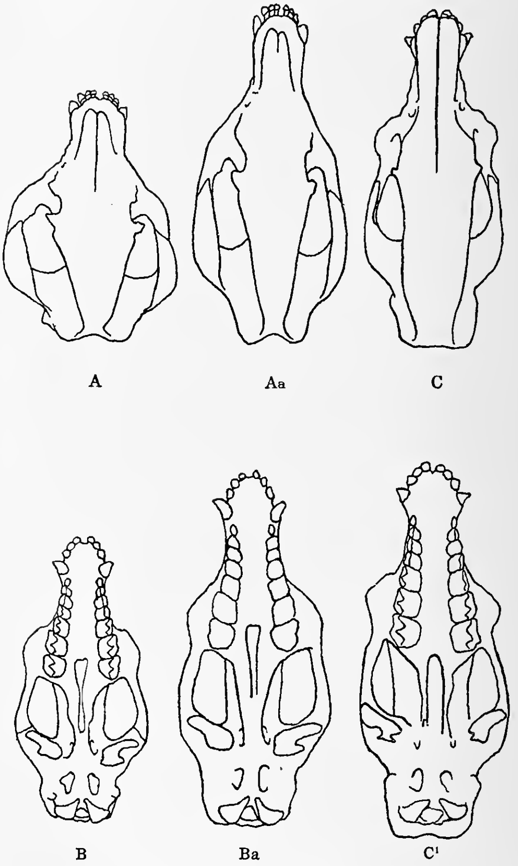

FIGURE 217.—Natural and artificial brachycephaly and dolichocephaly. After Osborn, Science, 1908, pp. 750, 751

A, *Palaeosyops*, extreme brachycephalic type, superior view; Aa, *Palaeosyops*, artificial dolichocephaly produced by stretching A to length of C; B, *Mesatirhinus*, primitive dolichocephaly, palatal view; Ba, *Mesatirhinus*, artificial dolichocephaly, palatal view, produced by stretching B to length of C^1; C, *Dolichorhinus*, progressive dolichocephaly, superior view; C^1, *Dolichorhinus*, progressive dolichocephaly, palatal view.

When we compare a long-skulled with a short-skulled titanothere the skull at first appears to be compressed laterally or stretched out longitudinally as if composed of india rubber, all parts being elongated alike. (See fig. 217.) This appearance is entirely deceptive, because every bony element of the skull has a different rate of elongation. As above noted, although the face of the titanothere is abbreviated (brachyopic), the cranium is elongated (dolichocranic), and it is chiefly the midregion of the cranium that is notably elongated—that is, the region between the orbits and the postglenoid processes. There is no predetermined innate or invariable correlation of brachycephaly or dolichocephaly in all parts of the skull, nor is there any fixed correlation between elongation or abbreviation of the skull and of the limbs respectively. (See law of correlation, Chap. XI.)

ZYGOMATIC-CEPHALIC INDICES IN THE TITANOTHERES AND OTHER PERISSODACTYLS

RELATIVE VALUE OF INDICES

The proportions and indices applied to different groups of mammals are largely relative. The terms applied to the human cranium and the indices are as follows:

Brachycephalic = brachycranial, 80.1–100
Mesaticephalic = mesaticranial, 75.1–80
Dolichocephalic = dolichocranial 60–75

Among the perissodactyl ungulates that have ordinal relationships to the titanotheres some of the indices of total length and width of skull are shown in the accompanying table.

Indices of length of skull of perissodactyl ungulates related to the titanotheres

	Basilar length, premaxillaries to condyles (millimeters)	Transverse width across zygomatic arches (millimeters)	Index
Sumatran rhinoceros (Rhinoceros (Dicerorhinus) sumatrensis)	580	345	59
Black African rhinoceros (R. (Opsiceros) bicornis)	568	320	56
South American tapir (Tapirus terrestris)	355	178	50
White African rhinoceros (R. (Ceratotherium) simum)			43–50
Indian tapir (Tapirus indicus)	387	183	47
Domestic horse (Equus caballus)	513	202	39
Domestic horse (Equus caballus)			40. 4–44. 1
Domestic ass (Equus asinus)			46. 9–49. 9

Most of the skulls of the above-named species are dolichocephalic in comparison with the skulls of titanotheres. A standard of skull proportions among the perissodactyl ungulates, including the rhinoceroses, tapirs, horses, and titanotheres, may be established as shown in the table below.

Summary of the zygomacephalic indices of the perissodactyls

Form of skull	Index	Perissodactyl ungulates
Dolichocephalic:		
Hyperdolichocephalic	39. 0–50	Horse, tapir (Indian), white rhinoceros, Dolichorhinus, tapir (South American), Eotitanops.
Dolichocephalic	50. 1–55	Mesatirhinus petersoni, Rhadinorhinus.
Subdolichocephalic	55. 1–60	Black rhinoceros, Sumatran rhinoceros, Mesatirhinus megarhinus.
Mesaticephalic	60. 1–70	Telmatherium ultimum, Metarhinus earlei, Manteoceras, Menodus sp., Allops marshi, Menodus giganteus.
Brachycephalic:		
Subbrachycephalic	70. 1–75	Limnohyops laticeps, Allops serotinus, Brontotherium curtum.
Brachycephalic	75. 1–85	Palaeosyops leidyi, Brontotherium platyceras.
Hyperbrachycephalic	85. 1–91+	Brontops robustus, Diploclonus amplus.

INDICES OF SKULLS OF EOCENE AND OLIGOCENE TITANOTHERES

The study of these proportions and indices of the titanotheres demonstrates that the skull in this family presents an ascending scale from primitive dolichocephalic ancestors like *Lambdotherium* and *Eotitanops*, which, on the one hand, evolved into extremely broad-headed forms like *Palaeosyops* and *Megacerops*, and, on the other, into extremely long-headed forms like *Mesatirhinus* and *Dolichorhinus*, as shown in the following table:

Zygomatic-cephalic indices in the titanotheres

[Arranged in chronologic and taxonomic order]

	Index
Lower Eocene:	
Eotitanops borealis (dolichocephalic)	50
Lambdotherium popoagicum (dolichocephalic)	(?)
Middle Eocene:	
Limnohyops monoconus (brachycephalic)	72
Limnohyops laticeps (brachycephalic)	75
Palaeosyops leidyi (brachycephalic)	74–75
Upper Eocene:	
Telmatherium ultimum (crushed) (mesaticephalic)	61
Sthenodectes incisivus (mesaticephalic)	63–65
Manteoceras manteoceras (mesaticephalic)	63–68
Mesatirhinus megarhinus (dolichocephalic)	56–59
Mesatirhinus petersoni (dolichocephalic)	49–52
Dolichorhinus superior (dolichocephalic)	49
Dolichorhinus hyognathus (dolichocephalic)	46
Metarhinus fluviatilis (dolichocephalic)	58
Metarhinus earlei (dolichocephalic)	59–63
Rhadinorhinus abbotti (dolichocephalic)	51–52
Lower Oligocene:	
Brontops brachycephalus, ♀ (mesaticephalic)	64
Brontops brachycephalus, ♂ (brachycephalic)	72
Brontops validus (brachycephalic)	85
Brontops robustus (brachycephalic)	76–83
Allops marshi (mesaticephalic)	64–69
Allops serotinus (brachycephalic)	72–78
Diploclonus amplus (brachycephalic)	91
Diploclonus tyleri (brachycephalic)	85
Menodus giganteus (mesaticephalic)	62–70
Menodus varians (brachycephalic)	73
Menodus heloceras (brachycephalic)	79(?)
Megacerops coloradensis (brachycephalic)	76
Megacerops acer (brachycephalic)	84
Brontotherium leidyi (brachycephalic)	66
Brontotherium gigas (brachycephalic)	84
Brontotherium sp. div. (brachycephalic)	74–80

Generic tendencies.—Certain generic ascending series are progressively brachycephalic—for example, *Brontops* and *Megacerops;* others are progressively dolichocephalic—for example, *Menodus.*

Zygomatic-cephalic indices of the titanotheres and other perissodactyls

[Arranged in ascending numerical order]

	Index
Dolichocephalic:	
Hyperdolichocephalic—	
Domestic horse (Equus caballus)	39, 40. 4–44. 1
Dolichorhinus hyognathus (Eocene)	43–49
White African rhinoceros (Ceratotherium simum)	43–50
Domestic ass (Equus asinus)	46. 9–49. 9
Indian tapir (Tapirus indicus)	47
Mesatirhinus petersoni (Eocene)	49
Dolichorhinus superior (Eocene)	49
Eotitanops princeps (Eocene)	50
Dolichocephalic—	
Mesatirhinus petersoni (Eocene)	51, 52
Rhadinorhinus abbotti (Eocene)	51–52, 53, 54, 54. 9
Subdolichocephalic—	
Black African rhinoceros (Opsiceros bicornis)	56
Mesatirhinus megarhinus (Eocene)	56–57
Metarhinus fluviatilis (Eocene)	58
Metarhinus earlei (Eocene)	59
Sumatran rhinoceros (Rhinoceros sumatrensis)	59
Mesaticephalic:	
Telmatherium ultimum (Eocene)	61
Metarhinus earlei (Eocene)	60. 1–61, 62–63
Menodus giganteus (Oligocene)	62–70
Sthenodectes incisivus (Eocene)	63–65
Manteoceras manteoceras (Eocene)	63–68
Allops marshi (Oligocene)	64–69
Brontops brachycephalus, ♀ (Oligocene)	64
Brontotherium leidyi (Oligocene)	66
Menodus giganteus (Oligocene)	69. 9, 70
Brachycephalic:	
Subbrachycephalic—	
Allops serotinus (Oligocene)	72
Brontops brachycephalus, ♂ (Oligocene)	72
Menops varians (Oligocene)	73
Brontotherium curtum (Oligocene)	74
Palaeosyops leidyi (Eocene)	74–77
Limnohyops laticeps (Eocene)	75
Brachycephalic—	
Megacerops? coloradensis (Oligocene)	76
Brontotherium curtum (Oligocene)	78
Allops crassicornis (Oligocene)	76
Palaeosyops major (Eocene)	77
Allops serotinus (Oligocene)	78
Brontops dispar (Oligocene)	78–79
Brontotherium platyceras (Oligocene)	80
Brontotherium peltoceras (Oligocene)	80
Brontotherium curtum, ♀ (Oligocene)	80
Brontotherium gigas (Oligocene)	82, 84
Brontops validus (Oligocene)	83
Megacerops acer (Oligocene)	84
Diploclonus tyleri (Oligocene)	85
Hyperbrachycephalic—	
Brontotherium gigas (Oligocene)	87?
Brontops dispar (Oligocene)	87
Brontops robustus (Oligocene)	87?
Diploclonus amplus (Oligocene)	91?

DIFFERENCES IN TERMINOLOGY OF SKULL PROPORTIONS IN TITANOTHERES AND MAN

In the Oligocene genus *Menodus* the zygomatic-cephalic index rises above 60, and the skull is therefore "mesaticephalic," as defined above, rather than "dolichocephalic," as described in the author's earlier papers. The term "stenocephalic," meaning narrow headed, may therefore be used to describe the narrow cranium and dentition of *Menodus,* in contrast with the wide and truly brachycephalic cranium and dentition of *Brontops, Megacerops,* and *Brontotherium.*

According to the indices adopted for all perissodactyls, no Oligocene titanotheres are truly dolichocephalic; all are mesaticephalic or brachycephalic as compared with many Eocene titanotheres. The term dolichocephalic, as used in the section on the Oligocene, may be considered equivalent to "stenocephalic" (see Chap. V) as applied to Oligocene titanotheres having relatively narrow face and teeth but a zygomatic index of 64–70.

The terms given above are not used in the same sense as in anthropology. The anthropologists for cranial form should have introduced the terms "dolichocranial" and "brachycranial," but as a matter of fact they used "brachycephalic" and "dolichocephalic." There is no other word left for craniometry, because there is no other Greek word descriptive of the head as a whole. We can not use "dolichocranial," because our indices measure the whole skull, not the calvarium alone.

The standard zygomatic-cephalic indices adopted in this monograph are as follows:

Dolichocephalic	39–60
Mesaticephalic	60. 1–70
Brachycephalic	70. 1–91+

It is true that in the top view of *Brontotherium platyceras* the skull top itself is long, but the indices show that the head as a whole is extremely brachycephalic. In uncrushed skulls of *Brontotherium gigas* the index is 82–87, which is doubtfully exceeded only by *B. robustus* and *Diploclonus amplus.*

CONTRAST IN FEATURES OF BRACHYCEPHALIC AND DOLICHOCEPHALIC SKULLS AND TEETH

The later brontotheres are excessively brachyopic, not only in measurements but in all the characters of the teeth, including molars and premolars. This brachyopy, no doubt, supervened upon an earlier stage in which the middle portion of the cranium was elongate, and it is the elongation of the middle part of the cranium that gives a dolichocephalic tendency. Far from being elongate as viewed from below, the palatal and basicranial regions of brontotheres are excessively wide and short, as well as the zygomata and the face, and thus contrast very strongly with the narrow face and unexpanded zygomata of *Menodus.* Hence there is no available substitute for the term brachycephaly for the brontotheres.

Contrasts in features of brachycephalic and dolichocephalic teeth and skulls

Features	Brachycephalic type	Dolichocephalic type
Teeth:		
Grinding series	Abbreviated	Elongated.
Diastema between cutting and grinding series.	Closed	Open.
Anterior premolars, p $\frac{1}{1}$	Suppressed, or one fang suppressed	Persistent and spaced.
Intermediate tubercles or conules of molars.	Persistent	Reduced or aborted.
Opposite cutting and grinding series	Converging or arched	Parallel or elongated.
Incisor series	Placed transversely	Convergent anteriorly.
Canine teeth	Rounded or broadened	Elongated or compressed.
Grinding teeth, or molars	Shortened and widened	Lengthened and narrowed.
Cingulum between molar teeth	Suppressed	Persistent.
Skull:		
Entire skull	Shortened and broadened	Lengthened and narrowed.
Most of the constituent bones	do	Do.
Palate	Broadened and flattened	Narrowed and transversely arched.
Nasals	Shortened and spreading	Elongated with curved and straight borders.
Bridge over infraorbital foramen	Narrowed	Broadened.
Infraorbital foramen	Not seen on side of face	Conspicuous on side of face.
Lacrimal bone	Crowded toward orbit	Exposed on side of face.
Lacrimal foramen	Crowded into orbit	Seen on edge of orbit.
Zygomatic arches	Broadened, especially in the buccal plates; in section broad rather than deep.	Elongated and vertically deepened; in section deep rather than broad.
Areas of insertion of masseteric and temporal muscles.	Increased in thickness	Elongated horizontally.
Mastoid portion of periotic	Exposure abbreviated or covered	Expanded and exposed.
Exoccipital, postglenoid and post-tympanic processes.	Broadened	Deepened and narrowed.
Postglenoid and post-tympanic processes	Approximated, especially below, inclosing the external auditory meatus inferiorly.	External auditory meatus not closed inferiorly.
Tympanic bulla	Thrust inward	Exposed laterally.
Foramen ovale and foramen lacerum medius.	Approximated	Separated by a bridge of bone.
Alisphenoid canal	Abbreviated	Elongated.
Presphenoid	do	Do.
Vomer	Thrust backward	Not thrust backward.
Premaxillary symphysis	Abbreviated and massive	Elongated.
Frontonasal horns	Transversely expanded	Less expanded transversely.
Jaw:		
Ramus of jaw	Shortened, thickened, deepened	Elongated with straight lower borders and backward produced angle.
Area of insertion of temporal muscle	Reduced	Balance maintained.
Coronoid process	do	Lengthened anteroposteriorly.
Mandibular symphysis	Abbreviated and massive	Elongated.

Comparison of the auditory region in the skull of these seven divergent Eocene species shows that the auditory meatus tends to close in the brachycephalic types, is moderately open in the mesaticephalic types, and is widely open in the dolichocephalic types of titanotheres, and thus parallels the auditory region of some modern perissodactyls, as shown in Figure 379.

The chief allometric characters that distinguish the Eocene titanotheres are the following:

1. Abbreviation of the face (brachyopy) and elongation of the cranium (dolichocrany), combined with general brachycephaly or with general dolichocephaly.
2. Flexure of the face upon the cranium (=cyptocephaly, upward or downward bending).
3. Broadening and elongating of the nasals or narrowing and recession of the anterior narial openings.
4. Pneumaticity, development of great pneumatic cavities in the upper part of the face and cranium.

We observe a long series of modifications of all the great adaptive functions in the evolution of the mammalian skull—namely, (1) prehension of food, (2) mastication of food, (3) passage of food to the fauces, (4) channels of respiration, (5) lodgment of sense organs, (6) lodgment of the brain, (7) offensive use of the canine teeth, (8) offensive use of the horns. It would appear that the two functions last indicated (7, 8) exert little influence in the middle Eocene titanotheres. In wide contrast are the latest Eocene and the Oligocene titanotheres, in which the horns predominate. The canines vary greatly in size and in the telmatheres become effective offensive weapons. The prehensile functions of the lips and anterior teeth vary with the development of a broad muzzle, the firmly united premaxillae, the greater or less recession of the nasal bones; but there is little evidence of strong development of prehensile powers in the upper lip such as is seen in the skull of the tapirs.

LIST OF ABBREVIATIONS USED IN ILLUSTRATIONS OF SKULLS

The following abbreviations are used in this monograph in the illustrations of skulls. Names of complete bones are begun with capital letters; names of parts of bones with small letters.

As. Alisphenoideum.
Bo. Basioccipitale.
Bs. Basisphenoideum.
c. As (car. ex. mx.). canalis alisphenoideus, carotis externa, ramus maxillaris.
c. i. o. (V_2 car. ex.). canalis infraorbitalis, nervus maxillaris, carotis externa.
cond. ac. condylus occipitalis accessorius.
cond. condylus occipitalis.
cr. lamb. crista lambdoidea.
cr. sag. crista sagittalis.
cr. tem. crista temporalis.
dct. la. ductus nasolacrymalis.
em. ar. eminentia articularis.
em. Fr. eminentia frontalis.
Ex. o. Os exoccipitale.
f. c. (XII). foramen condylare, nervus XII.
f. la. foramen lacrimale.
f. l. a. (III, IV, V, VI). foramen lacerum anterius, nervi III, IV, V, VI.
f. l. m. (car. in.). foramen lacerum medium, carotis interna.
f. l. p. (IX, X, XI). foramen lacerum posterius, nervi IX, X, XI.
f. mg. foramen magnum.
f. mn. (V_3). foramen mentale, nervus V_3.
f. ms. (jug.). foramen mastoideum.
f. op. (II). foramen opticum, nervus II.
f. ov. (V_3). foramen ovale, nervus V_3.
f. pl. a. (N. nas. pl.). foramen palatinum anterius, nervus nasopalatinus.
f. p. gl. foramen postglenoideum.
f. pl. p. (N. pl. post.). foramen palatinum posterius, nervus palatinus posterior.
f. r. (V_2). foramen rotundum, nervus V_2.
f. sph. pl. (V_2). foramen sphenopalatinum.
f. stm. (VII). foramen stylomastoideum, nervus VII.
f. su. or. foramen supraorbitale.
f. ven. foramen venosum.
fis. nar. ant. fissura narialis anterior.
fos. gl. fossa glenoidea.
fos. interpa. fossa interparietale.
fos. men. in. fossa menisci interna.
fos. nar. ant. fossa narialis anterior.
fos. nar. post. fossa narialis posterior.
fos. st. hy. fossa ossis stylohyoidei.
Fr. Os frontale.
H. Umbo cornu ("horn").
I. P. Os interparietale.
La. Os lacrimale.
lig. nu. ligamentum nuchae.
m. a. e. meatus acusticus externus.
m. obl. cap. sup. musculus obliquus capitis superior.
m. rect. cap. lat. musculus rectus capitis lateralis. (attachments).
m. rect. cap. post. musculus rectus capitis posticus.
Ms. mastoideum.
ms. Per. pars mastoidea, ossis periotici.
Mx. maxilla.
Mx. (alv.) maxilla (processus alveolaris).
Mx. tb. maxilloturbinale.
Na. Os nasalis.
nar. post. naris posterior.
obl. cap. sup. musculus obliquus capitis superior.
Orb. Orbis.
Pa. Os parietale.
petr. pars petrosa ossis periotici.
p. gl. Sq. Processus postglenoideus ossis squamosi.
Pl. Os palatinum.
Pmx. Premaxilla.
p. o. Ex. Processus paroccipitalis ossis exoccipitalis.
p. o. Fr. Processus postorbitalis ossis frontalis.
p. o. Mal. Processus postorbitalis ossis malaris.
pr. cor. processus coronoideus.
pr. i. o. Mal. processus infraorbitalis ossis malaris.
pr. p. o. processus postorbitalis.
Psph. Os presphenoideum.
Pt. Os pterygoideum.
pt. As. Processus pterygoideum ossis alisphenoidei.
p. ty. Sq. processus post-tympanicus ossis squamosi.
rect. cap. musculus rectus capitis (antice).
rect. cap. post. musculus rectus capitis posticus.
sin. lat. eth. sinus lateralis ethmoidalis.
So. Os supraoccipitale.
Sq. Os squamosum.

t. la. tuberculum ossis lacrimalis.
XII. foramen condylare (nervus XII).
z. Sq. processus zygomaticus ossis squamosi.
z. Mx. processus zygomaticus maxillae.

TERMINOLOGY OF THE UPPER MOLAR TEETH

The accompanying table shows the terms used to designate the upper molar teeth of ungulates:

Comparative terminology of the superior molar teeth

All ungulates: Terminology based upon evolution from a tritubercular, bunodont ancestral molar type. Osborn (1888, 1892)	Titanotheres: Leidy (1873), Cope (1883), Marsh (1877)	Horses: Huxley (1876) and Lydekker (1886, p. 67)	Rhinoceroses: Cuvier (1836), De Blainville (1846), Gaudry (1878), Pavlow (1892)	Rhinoceroses, English authors: Boyd-Dawkins (1867), Busk (1877) and Lydekker (1882), Foote (1874)	Rhinoceroses and ungulates, German and Russian authors: Rütimeyer (1863) and Kowalevsky (1873)
Primary molar cones:					
Protocone		Anterior pillar	Denticule interne du premier lobe.		Innenpfeiler des Vorjochs.
Paracone	Antero-external lobe.	Anterior crescent	Denticule externe du premier lobe.	Second costa	
Metacone	Postero-external lobe.	Posterior crescent	Denticule externe du second lobe.	Costae (in part)	
Hypocone	Postero-internal lobe.	Posterior pillar	Denticule interne du second lobe.		Innenpfeiler des Nachjochs.
Intermediate molar cones:					
Protoconule	"Tubercles"				
Metaconule					
Premolar cones[a]:					
Protocone	Antero-internal be.				
Deuterocone					
Tritocone					
Tetartocone					
Secondary pillars or styles:					
Parastyle	Buttress	Anterior ridge		First costa (buttress)	Pericones, Randgipfeln.
Mesostyle	Median fold	Middle ridge			
Metastyle		Posterior ridge			
Hypostyle		Posterior prominence.		Posterior collis (in part).	
Secondary crests:					
Ectoloph			Crête externe	External lamina (dorsum).	Aussenwand.
Protoloph			Colline seconde = crête ou lobe antérieur.	Anterior collis	Vorjoch.
Metaloph			La troisième colline = crête ou lobe postérieur.	Median collis	Nachjoch.
Valleys:					
Medisinus			Vallon oblique	Anterior valley	
Postsinus			Fossette postérieure	Posterior valley	
Secondary folds:					
Crochet			Crochet	Posterior combing plate (uncus, crochet).	
Antecrochet			Crochet antérieur	Antecrochet	
Crista			Antecrochet	Anterior combing plate = crista.	
Secondary pits:					
Pre-, medi-, and postfossettes.			Fossette postérieure = fossettes.		
Cingulum	Basal ridge		Bourrelet	Posterior collis (in part) = cingulum, guard.	Wulst.

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[a] Premolar cusp; term proposed by W. B. Scott (1891).

SECTION 2. INTRODUCTION TO THE ANATOMY OF THE SKULL AND TEETH OF THE EOCENE TITANOTHERES

TYPES OF SKULL OF EOCENE TITANOTHERES

For reasons that are fully set forth in Chapter VIII, on the origin and descent of the titanotheres, we regard the skull of *Eotitanops borealis* (figs. 250, 251), from the lower Eocene, as the ancestral type from which all the highly modified Eocene skulls were derived.

The structure of the middle Eocene skulls is correlated with certain feeding habits and exhibits a marked contrast to that of the Oligocene skulls. In middle Eocene time the horns had not yet become weapons of offense and defense.

The forms of the skulls of the following Eocene titanotheres are noteworthy:

1. *Limnohyops priscus*, a primitive hornless titanothere, had a moderately brachycephalic skull and primitive low-crowned grinding teeth.

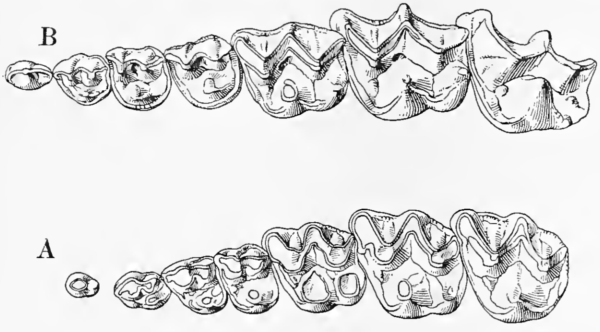


FIGURE 218.—Contrasting forms of upper teeth in Eocene titanotheres

Brachycephalic (A) and dolichocephalic (B) types of upper premolar-molar series. One-half natural size. A, *Palaeosyops leidyi*, Am. Mus. 1544 (type); B, *Dolichorhinus hyognathus*, Am. Mus. 1851.

2. *Palaeosyops leidyi* (figs. 275–278) was entirely hornless and represents the extreme brachycephalic and brachyodont type.

3. The skull of *Telmatherium ultimum* (figs. 294–296) may be regarded as an elongated or mesaticephalic modification of the primitive *Limnohyops* type. The horn rudiments are retarded, and the crowns of the teeth are more elongated than in *Palaeosyops*. In many respects this skull resembles that of the succeeding type, *Manteoceras*.

4. The skull of *Manteoceras manteoceras* (figs. 303–308) differs from that of *Telmatherium ultimum* in the vigorous development of the very precocious horn rudiments, which are seen in profile above and in front of the eyes. It is also mesaticephalic, and the molars are more brachyodont than those of *Telmatherium*.

5. The skull of *Mesatirhinus petersoni* has passed from mesaticephaly into dolichocephaly. It resembles an elongated skull of *Manteoceras* in having similar rudiments of horns above the eyes, and the conformation of the zygomatic arch is similar to that of *Manteoceras* and very distinct from that of *Palaeosyops* and *Telmatherium*.

6. The skull of *Dolichorhinus hyognathus* (figs. 347–349) is a decidedly long-headed derivative of *Mesatirhinus petersoni* (figs. 327–329). The horn rudiments are much more prominent and show some progressive characters, such as the flattening of the top of the cranium, which is analogous even to the cranium of the Oligocene titanotheres. It is also decidedly cyptocephalic, the face being strongly bent down on the cranium. This is perhaps a river-loving type.

7. The skull of *Metarhinus earlei* (fig. 361) presents a striking contrast to that of *Mesatirhinus petersoni*. It is less dolichocephalic and shows a marked recession of the narial openings and very prominent orbits, indicative, perhaps, of semiaquatic habits.

FEEDING HABITS OF BROAD-HEADED AND LONG-HEADED TITANOTHERES

Peculiar forms of the teeth.—The mode of feeding and the food of the titanotheres can not be inferred with certainty, because their dentition differs considerably from that of any modern mammal. In middle Eocene titanotheres the grinding teeth were perfectly adapted to a combination of cutting and crushing the food, as noted below. This adaptation implies a choice of succulent food consisting of relatively coarse leaves, grasses, buds, twigs, roots, and tubers such as would be found in forest and stream habitats. In later Eocene and Oligocene titanotheres the shearing action of the teeth was more perfect and the food may have included smaller objects of tougher fiber.

Although the structure of the grinding teeth of the titanotheres is very different from that of the grinding teeth of members of related families—the tapirs, rhinoceroses, and horses—the titanotheres nevertheless present certain analogies in the form of the head, from which we may infer that analogies existed also in the feeding habits.

Again, a survey of the feeding habits of the existing Perissodactyla reveals a certain family likeness running throughout the families of this order, which was probably manifest also among the extinct Perissodactyla.

Primitive types.—The primitive form of head and tooth of *Eotitanops* is analogous to that of the primitive paleotheres and horses, in which the proportions of the cranium and face and the structure of the grinding teeth are again similar. We may infer that all these animals had a marked similarity of diet, from which the Eocene titanotheres diverged in two directions, developing into the extremely brachycephalic *Palaeosyops* and into the extremely dolichocephalic *Dolichorhinus*.

Brachycephalic types.—In the short-skulled *Palaeosyops* we observe heavy canine tusks, large caniniform outer incisor teeth, deep and heavy zygomatic arches and lower jaw, high and relatively thin sagittal crest, and large areas of attachment for the temporal and masseter muscles. This indicates a notably vertical movement of the jaw and great power in crushing the food. Such an animal would seem well fitted for plucking and tearing up succulent bulbs, tubers, and roots from the ground as well as for browsing on twigs and leaves, a diet much in favor with the American tapir. But it differed from the tapir in that the nasals are not retracted, and there is no evidence that the upper lip had exceptional prehensile power. (See fig. 220.) This titanothere presented the extreme of the browsing type. It had a lumbering gait and

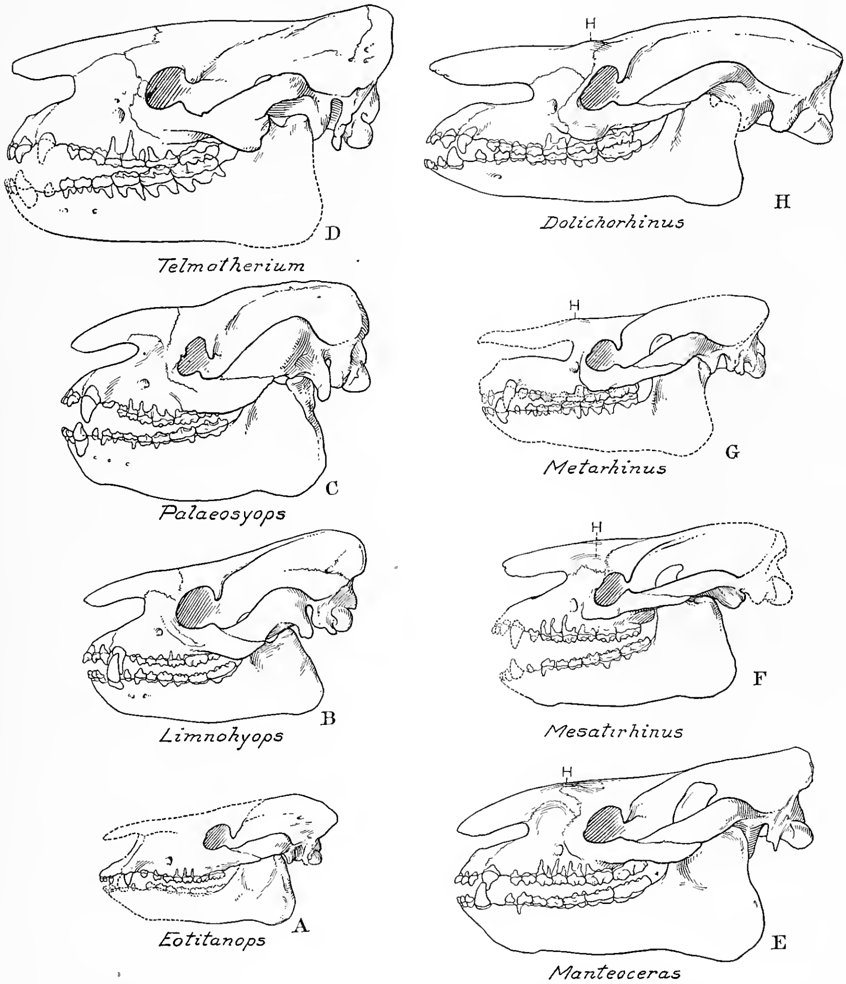


FIGURE 219.—Skulls of Eocene titanotheres of the principal genera

Side views. One-eighth natural size. A, *Eotitanops borealis*, lower Eocene, Wind River formation; B, *Limnohyops priscus*, middle Eocene, Bridger formation, horizon Bridger B; C, *Palaeosyops leidyi*, middle Eocene, Bridger formation, horizon Bridger D; D, *Telmatherium ultimum*, upper Eocene, Uinta formation (Uinta C); E, *Manteoceras manteoceras*, middle Eocene, Bridger formation, horizon Bridger D; F, *Mesotirhinus petersoni*, middle Eocene, Bridger formation, horizon Bridger D; G, *Metarhinus earlei*, upper Eocene of Uinta Basin, level Uinta B 1; H, *Dolichorhinus hyognathus*, upper Eocene of Uinta Basin, level Uinta B 2. H, Horn.

spreading feet, and to judge from the associated fauna in comparison with that of the living tapirs it inhabited semitropical forests, especially those near streams.

Dolichocephalic types.—The other extreme of structure among Eocene titanotheres is the long-skulled *Dolichorhinus*, which succeeds *Palaeosyops* in geologic time, belonging more to the upper Eocene. The muzzle of this animal (fig. 219) was rather expanded or truncate. The incisors were arranged in a semicircle and made some approach to the cropping incisors of a ruminant, being also partly cupped as in Oligocene species of the horse. The space behind the canine tusk was longer, as in typical herbivorous forms. The canines were recurved, compressed, or sharp-edged and may have been used in fighting, as in the camels. The offensive power of the front teeth was, however, much less than in *Palaeosyops*. The cheek teeth were relatively long-crowned with pointed cusps and constituted a relatively elaborate cutting and triturating apparatus, as compared with the very short-crowned grinders of *Palaeosyops*. The excursion of the more slender mandible was partly vertical, partly oblique. The oblique position of the grinding teeth produced an oblique shearing action. Conditioning these changes the length and proportions of the masticating muscles and their angles of action were also changed. (See Chaps. V, VIII for details.

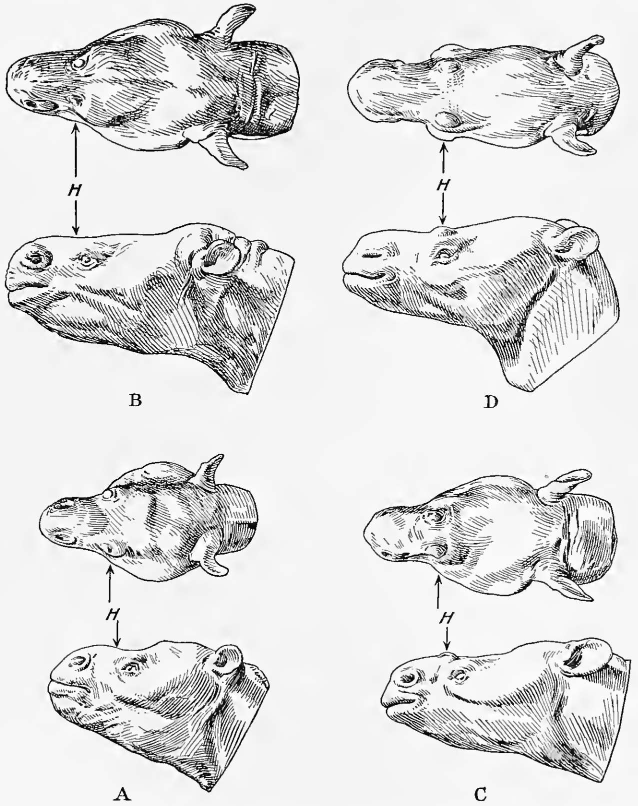


Figure 220.—Heads of Eocene titanotheres of four phyla

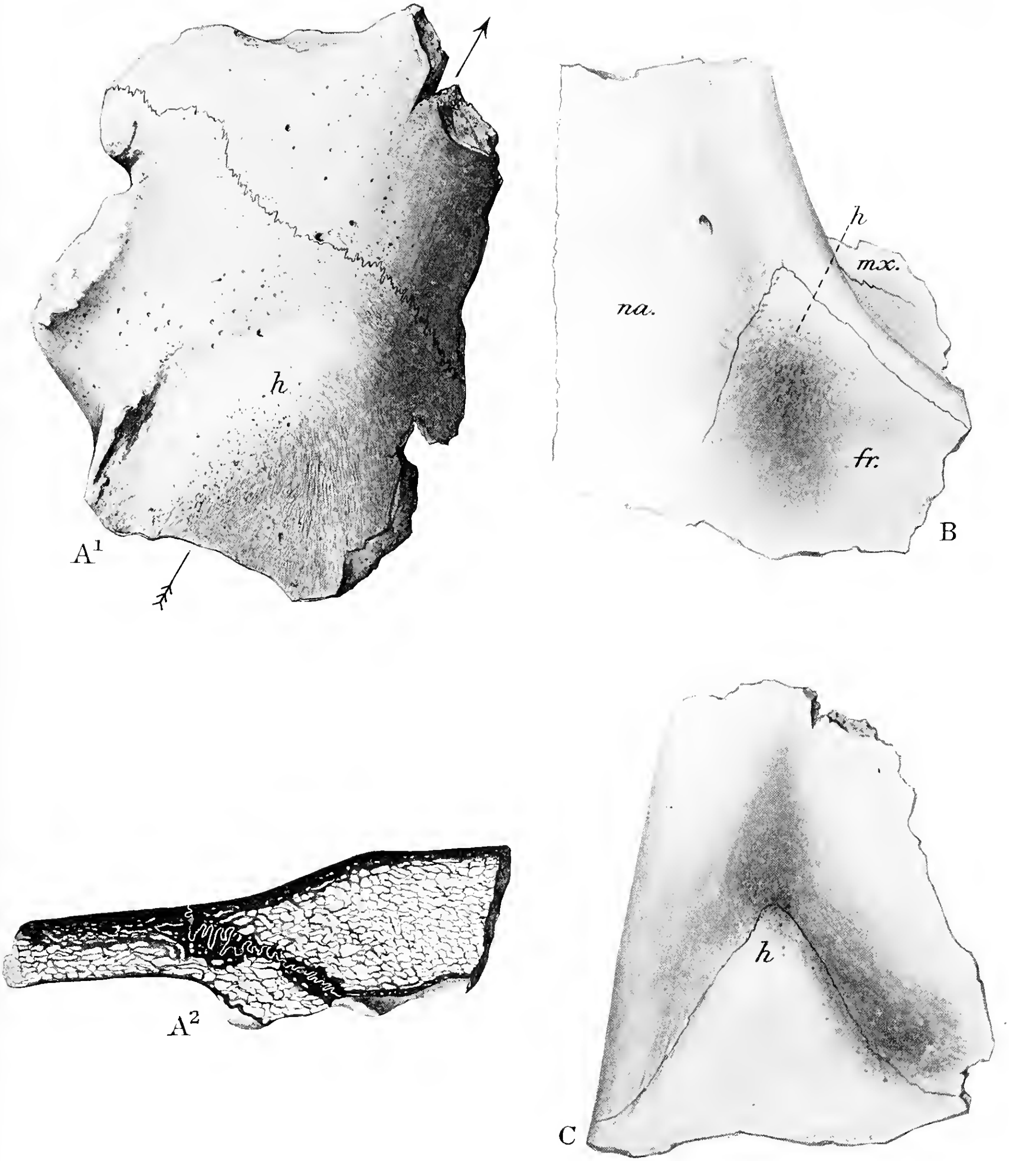
Modeled by Charles R. Knight. A, *Palaeosyops*, brachycephalic; B, *Telmatherium*, mesaticephalic; C, *Manteoceras*, mesaticephalic; D, *Dolichorhinus*, dolichocephalic. The nostrils were actually more nearly terminal than those shown in the models, and the upper lip may have been more markedly pointed or prehensile. H, Horn rudiments.

These features of the head of *Dolichorhinus* indicate that the food of this animal required finer cutting and better trituration than that of *Palaeosyops*. Although in no sense a grazing animal as compared with the grazing Equidae and Bovinae, *Dolichorhinus* was better adapted to grazing than *Palaeosyops*. Its remains are very frequently found in coarse sandstones laid down by rapid streams, and it may well have lived partly in the rivers and along their banks.

Intermediate types.—The other Eocene titanotheres, such as *Manteoceras* (fig. 220, C) and *Telmatherium* (fig. 220, B) are more or less intermediate between these extremes in the form of the head. Thus *Manteoceras* has very heavy, almost boarlike tusks and large, blunt incisor teeth, together with cheek teeth that are more elongate than those of *Palaeosyops*. *Telmatherium* had much more trenchant canine tusks, pointed incisor teeth, and somewhat elongated grinding teeth.

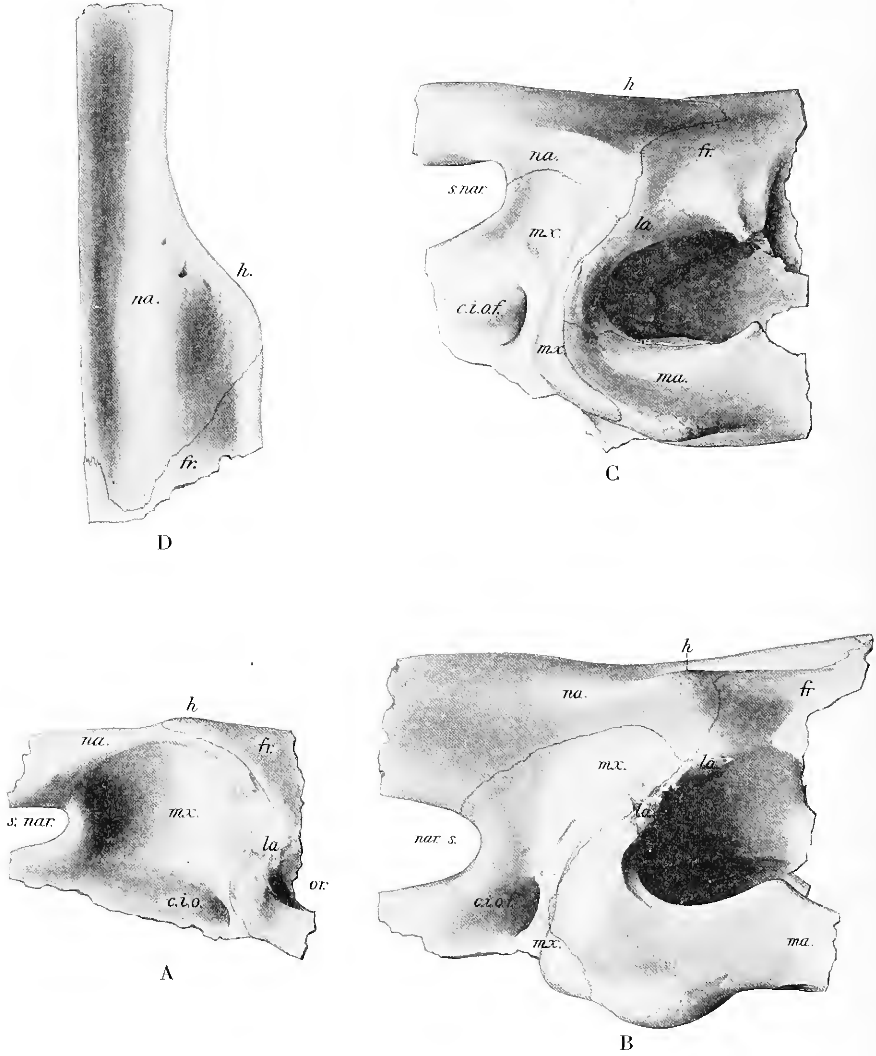
ORIGIN AND STRUCTURE OF THE "HORNS" IN TITANOTHERES

The so-called horns of titanotheres arise as rectigradations; they consist of osseous protuberances of the skull above the eyes, where the frontals overlap the nasal bones. In life they were probably covered with tough skin, rather than with horn. In the earliest titanotheres, of lower Eocene age (*Lambdotherium*, *Eotitanops*), the frontonasal junction shows no beginning of the horns. In the genera *Palaeosyops* and *Limnohyops* (middle Eocene) most of the skulls were equally hornless, but some very old males of *Palaeosyops* show an incipient nasofrontal protuberance and roughening of the outer tabula of the bone. (See Pl. XVI.) In the middle Eocene contemporary



THE REGION OF THE HORN SWELLING IN PALAEOSYOPS, MANTEOCERAS, AND TELMATHERIUM

A^1, *Palaeosyops robuſtus* (Am. Mus. 1554), superior view; A^2, the same, vertical longitudinal section. B, *Manteoceras manteoceras* (Am. Mus. 1569). C, *Telmatherium ultimum* (Am. Mus. 2004). *fr*, Frontals; *h*, rudimentary horn; *mx*, maxillary; *na*, nasal. All natural size



THE REGION OF THE HORN SWELLING IN MANTEOCERAS, MESATIRHINUS, AND DOLICHORHINUS

A, *Manteoceras manteoceras* (Am. Mus. 2353), lateral view, left side (right side reversed). B, *Dolichorhinus hyognathus* (Am. Mus. 1851), lateral view, left side (right side reversed). C, *Mesatirhinus petersoni* (Am. Mus. 1556), lateral view, left side. D, *Dolichorhinus hyognathus* (Am. Mus. 1851), superior view. *c. i. o. f.*, *c. i. o.*, Infraorbital foramen; *fr*, frontal; *h*, rudimentary horn; *la*, lacrimal; *mo*, molar; *mx*, maxillary; *na*, nasal; *or*, orbit; *s. nar.*, external narial aperture

Telmatherium cultridens there appears to have been a distinct nasofrontal protuberance, but in the geologically later *Telmatherium ultimum* only the faintest indication of its presence is found; it is possible that the horn retrogressed in this phylum. In *Manteoceras manteoceras* of the upper part of the Bridger formation (middle Eocene) the protuberance, although small, is perfectly distinct and fully characteristic in form. In *Protitanotherium* of the upper Eocene the horns (figs. 317–319) consist of oval protuberances about 20 millimeters high and 90 millimeters long. In nearly all the lower Oligocene titanotheres the horns are of large size and finally become the dominant feature of the whole skull, affording generic and specific characters.

The horns are believed to have evolved concomitantly with the fighting habits of these animals and with the general increase in size and body. The conditions of the horns in the titanotheres may be summarized as follows:

Summary of character or condition of the horns in Eocene and Oligocene titanotheres

Subfamily or genus	Horizon	Character or condition of horns
Lambdotheriinae	Lambdotherium zone (Wind River B)	Hornless.
Eotitanopinae	do	Do.
Palaeosyopinae	Lower horizons of Bridger Basin to lower horizons of Washakie Basin, inclusive.	Hornless, or nasofrontal horn swelling barely perceptible.
Telmatheriinae	Upper horizon of Bridger Basin to Uinta C, inclusive.	Do.
Sthenodectes	Uinta B 1 only	Horn swelling small.
Manteoceratinae	Upper horizons of Bridger Basin to Uinta C	Horn swelling small but distinct.
Dolichorhininae:		
Mesatirhinus-Dolichorhinus	Upper horizons of Bridger Basin to Uinta B 2.	Horn swelling more pronounced; on nasals only.
Metarhinus	Lower horizons of Washakie Basin to Uinta B 1, inclusive.	Horn swelling small; chiefly on nasals.
Rhadinorhininae:		
Rhadinorhinus	Uinta B 1 only	Horn swelling small.
Manteoceratinae:		
Protitanotherium	Uinta C only	Nasofrontal horn swelling pronounced and progressive.
Eotitanotherium	Uinta B 2	Do.
Brontopinae	Chadron A to C, inclusive	Nasofrontal horn swelling at first small, slowly becoming progressively larger.
Menodontinae	do	Do.
Megaceropinae	do	Nasofrontal horn swelling of medium to large size.
Brontotheriinae	do	Nasofrontal horn swelling at first small, rapidly becoming progressively larger.

PROPORTION AND RECTIGRADATION IN THE GRINDING TEETH OF EOCENE TITANOTHERES

The chief characters of the grinding teeth in the Eocene titanotheres were evolved from the bunoselenodont pattern (see fig. 221) and were modified by changes of proportion and rectigradation, under eight principles, as follows:

1. The primitive grinders seen in *Lambdotherium* and *Eotitanops* are extremely low crowned, or brachyodont. The numerous phyla can be distinguished chiefly by the different degrees and rates of elongation of the crown, which shows progressive hypsodontism.

2. The six main grinding teeth in the upper and lower jaws, p^2–m^3, p_2–m_3, are closely crowded together, and this crowding causes the crowns of the grinders to be closely proportioned to the brachycephaly or dolichocephaly of the skull. In brachycephalic titanotheres the transverse diameters of the grinding teeth generally exceed the anteroposterior diameters, whereas in dolichocephalic skulls the reverse is true. Thus we shall speak of the grinders as of the "brachycephalic" or of the "dolichocephalic" type.

3. The general tendency of the grinders in titanotheres is to become macrodont, because the pattern of the grinding teeth is mechanically imperfect, and the grinders compensate in size, in some degree, for what they lack in mechanical perfection.

4. The transformation of the "cone and crescent" or bunoselenodont pattern of the upper and lower grinding teeth in the titanotheres can be best understood by comparing that pattern with that seen in the other bunoselenodonts—the primitive chalicotheres, horses, and paleotheres—a pattern similarly derived from the same primitive type of upper and lower grinding teeth (fig. 222), which presents four main cones above and four main cones below, known as the "primary molar cones."

5. The secondary accessory folds, known as "styles," or pillars, and "lophs," or crests, as well as the "fossettes," or pits, may also be homologized by comparing the superior and inferior molars of the titanothere (*Telmatherium*) and of equine forms (*Anchitherium*) with those of the rhinoceros.

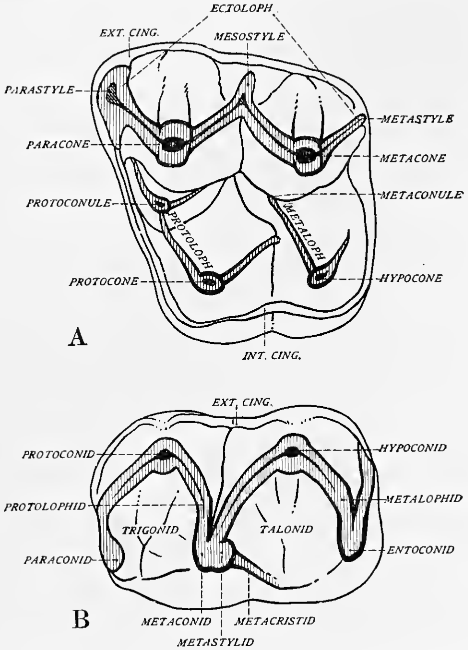


FIGURE 221.—Upper (A) and lower (B) molars of bunoselenodont pattern

Molars of *Lambdotherium*, a lower Eocene titanothere. Enlarged. The worn enamel surface is cross hatched; the exposed dentine is shown in dense black.

6. Arrested or retrogressive development is the chief characteristic of the titanothere molar evolution—that is, parts are arrested or vestigial in titanotheres that evolve rapidly and strongly in paleotheres, chalicotheres, and equines. Thus the titanothere molar begins its evolution in the form of the *Lambdotherium* molar (figs. 221, 235) or of the *Eotitanops* molar (figs. 229, 249), in which 32 primary and secondary elements may be more or less clearly distinguished in the typical upper and lower grinders. In the course of evolution these grinders, through arrested development, lose six or more of these elements. Thus the grinding teeth are impoverished as compared with those of the other bunoselenodonts (fig. 223).

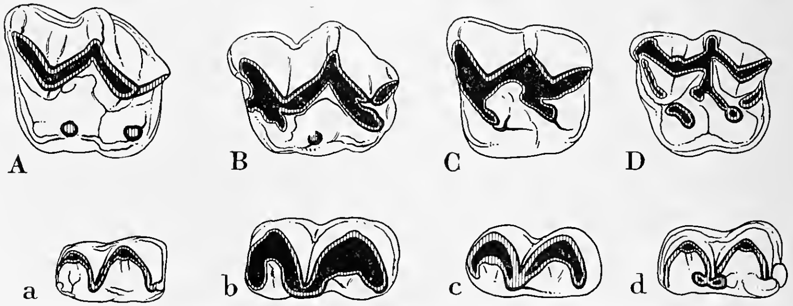


FIGURE 223.—Bunoselenodont patterns of upper and lower molars in Tertiary perissodactyls

A, *Telmatherium ultimum*, an upper Eocene titanothere, upper molar; a, *Telmatherium cultridens*, a middle Eocene titanothere, lower molar; B, b, *Moropus* sp., a Miocene chalicothere; C, c, *Palaeotherium* sp., an Eocene paleothere; D, d, *Anchitherium* sp., a Miocene hippoid.

The parts that gradually become vestigial or disappear in titanotheres are the following:

Protoconule, anterior intermediate cusp of superior molars; degenerates.

Metaconule, posterior intermediate cusp of superior molars; degenerates.

Protoloph, anterior transverse crest of superior molars, formed of protocone, protoconule, paracone (inner base); disappears.

Metaloph, posterior transverse crest of superior molars, formed of hypocone, metaconule, metacone (inner base); disappears.

Paraconid, antero-internal cusp of inferior molars, reduced or vestigial in all Perissodactyla; disappears.

Hypoconulid, posteromedian cusp of inferior molars; abortive except in third inferior molar.

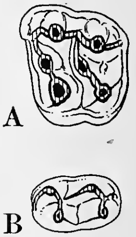


FIGURE 222.—Upper (A) and lower (B) molar patterns of *Hyracotherium*, a primitive Eocene equine perissodactyl (ancestor of the horse)

Enlarged.

7. All stages in the reduction and disappearance of these six or more elements in the upper and lower grinding teeth are observed among the Eocene titanotheres (Pls. LIV–LXV), whereas the lower Oligocene titanotheres exhibit grinding teeth (fig. 381) in which all these parts have totally disappeared and certain new secondary rectigradations, such as the "fossette" and crochet, have appeared.

8. The appearance or disappearance of these single elements is generally gradual or continuous; yet it is much more rapid in certain phyla than in others. The variation in the rate of degeneration distinguishes the phyla from one another and thus becomes a character of generic value. The numerical gain or loss of one of these elements is of specific value and marks off the subspecific stages or mutations.

MECHANISM OF THE TITANOTHERE GRINDING TEETH

The pattern of the upper and lower grinding teeth of the titanotheres is one that has entirely disappeared among the existing mammals. It has no counterpart among any living ungulates, but it is closely analogous to that of many Eocene and Oligocene mammals, both artiodactyls and perissodactyls. There is no perfected grinding function, such as that between the upper and lower molars of the horse, nor could such a grinding function evolve out of the titanothere molar tooth.

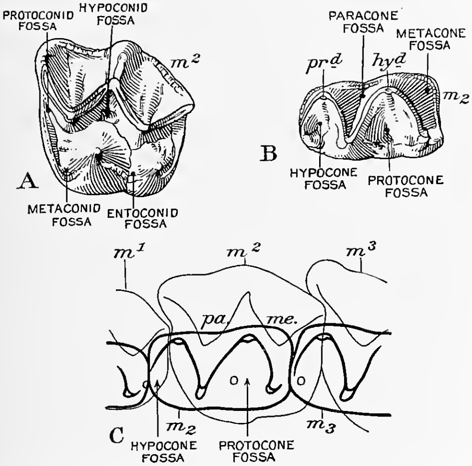


FIGURE 224.—Relations of upper and lower molars in an Eocene titanothere, *Telmatherium cultridens*

Princeton Mus. 10027 (type). Two-thirds natural size. A, Second upper molar showing the crushing parts and the cutting parts, also the pits or fossae for the reception of the projections on the lower teeth; B, second lower molar, showing the fossae for the parts of the upper teeth; C, diagram showing how each lower molar articulates with two upper molars, the trigonid of m_3 wedging between m^1 and m^2, and the talonid of m_3 receiving the protocone of m^2.

The dental mechanism is a combination of two functions which may be described as crushing and cutting, the crushing being effected by a double pestle and mortar or peg in socket mechanism, and the cutting by a mechanism of double shears or reversed double-bladed crescents.

In the accompanying diagram (fig. 224) the manner in which this double function is subserved in the upper and lower grinders is clearly shown.

(1) The superior molars consist of a double-cutting shear **W**, composed of the paracone and metacone crescents, which oppose the reversed double shear **M**, composed of the crescents developed from the protoconid and hypoconid. (2) The chief crushing action is performed by the superior cones, the protocone and hypocone, which fit into the protocone and hypocone fossae of the inferior molars. (3) The apex (**O**) of each of the four primary superior cones (protocone, paracone, metacone, hypocone) has its contact or abrasion point (oblique shading in figure), or fossa, in the inferior molars. (4) Similarly the apex of each of the four inferior primary cones (protoconid, metaconid, entoconid, hypoconid) has its contact or abrasion point (oblique shading), or fossa, in the superior molars.

This double cutting and crushing function is mechanically imperfect in the short-crowned molars of *Lambdotherium* and *Eotitanops* (figs. 229, 235, 242, 253). It becomes more efficient as the crowns become higher and the cones and crescents are vertically elongated in *Telmatherium* (fig. 225). The evolution of the titanothere grinders is directed to overcome the deficiency of this cone and crescent mechanism, which proves to be inherently defective in design.

The crushing function of the grinders is best observed in the internal view (fig. 226) of the upper and lower grinders of a telmathere, in which the pestles (p–h) are sinking into the mortars (m–e) in exactly the same manner as in the primitive insectivores. This closely correlated mechanism of the upper and lower grinding teeth, which was first studied by Cope (1889.3) and more fully by Gregory (1916.1), indicates that every new character (rectigradation, allometron) added to the upper grinders must be correlated with a new and mechanically adaptive character (rectigradation, allometron) in the lower grinders. The cutting function performed by the **W** of the upper ectoloph and the **M** of the lower ectoloph is illustrated (figs. 224, 225) and displays the close mechanical relation of the alternating crests as well as the simultaneous development of the new cusps (rectigradations) of the premolar teeth.

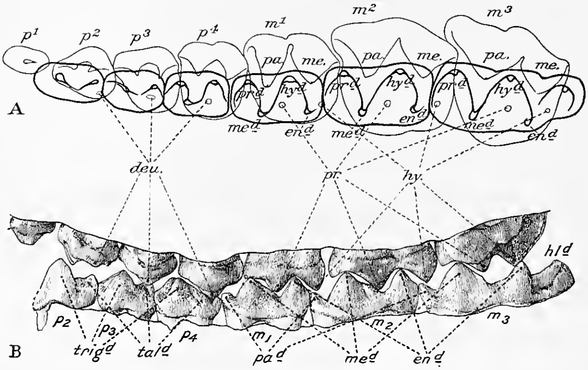


FIGURE 225.—Dental mechanism of titanotheres

Interlocking relations of upper and lower premolar-molar series. One-half natural size. A, *Telmatherium cultridens*, Princeton Mus. 10027 (type); upper teeth (light line), with pattern of lower teeth (heavy line) projected upon them. Crown view. B, Internal view of the same teeth, showing the crushing action of the cones and conids.

The partial transformation in the titanotheres of a more vertical chopping, crushing, and cutting motion of the jaw into a more oblique sweeping or true grinding action of the molars finally results in the entire loss of the conules and transverse crests (protoloph, metaloph), in the partial molarization of the premolars, and in the development of two gigantic internal crushing cones (protocone, hypocone) and of a very powerful external cutting crest (ectoloph).

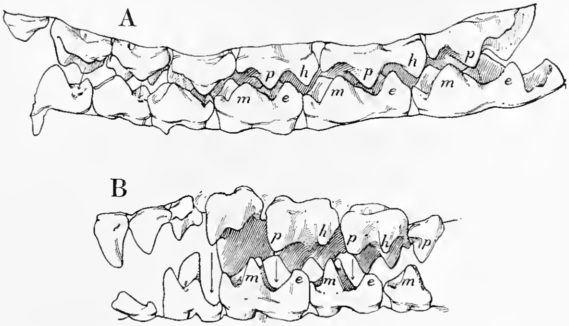


Figure 226.—Dental mechanism: Grinding teeth of a titanothere (A) and an insectivore (B)

After W. K. Gregory. Internal view of the opposed upper and lower grinding teeth of *Telmatherium cultridens* (A), natural size, and *Erinaceus* (B), much enlarged. The protocones (*p*) fit into the talonid basins (fossae) between the metaconids (*m*) and entoconids (*e*). The hypocones (*h*) fit into the trigonid basins (fossae) between the entoconids (*e*) and metaconids (*m*). Similar relations are found in all primitive mammals.

Three other interesting features in the evolution of the dental mechanism of the titanotheres are the following:

1. The marked protrusion of the roots on the outer sides of the upper molars in old Oligocene titanotheres is a result of the bunoselenodont pattern of the molars and of the vertical-oblique pressure of the lower teeth. As the outer side of the molar crowns becomes more hypsodont, in passing from lower Eocene to Oligocene titanotheres, so the external roots protrude more prominently.

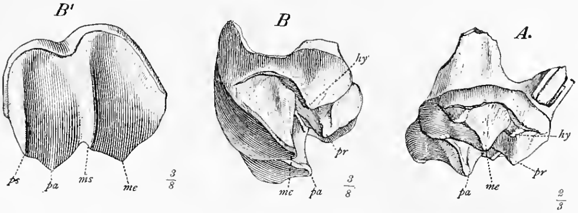


Figure 227.—Contrast of molars of a brachyodont Eocene titanothere (A) and a semihypsodont Oligocene titanothere (B, B¹)

A, Third left upper molar of *Palaeosyops leidyi*, seen from the rear. The internal and external cones are subequal in height. B, Third left upper molar (unworn) of *Menodus giganteus*, seen from the rear. The internal cones are low; the external cones have greatly increased in height and have grown inward at the tip. B¹, The same seen from the outer side, showing the much deepened ectoloph.

2. The excursion of the mandible was made from the outer side upward and inward, as in rhinoceroses and horses, in contrast with the opposite motion in ruminants.

3. In Eocene titanotheres the lack of a tetartocone in the upper premolars and of an entoconid in the lower premolars leaves an open space when the jaws are shut. This open space is filled in the Oligocene titanotheres by the opposing tetartocone and entoconid.

MOLARIZATION OF THE PREMOLARS

The titanotheres resemble all the other families of Perissodactyla in the gradual molarization of the premolar teeth—that is, in the transformation of the premolars into the molar pattern. The mechanical inferiority of the teeth of the titanotheres lies in the fact that this transformation is never perfected; it is very slow or retarded, and the premolars never completely acquire the molar pattern, as they do in the Equidae, for example, in which the premolars become actually superior to the molars both in pattern and in mechanical perfection. The arrested transformation of the premolars in the titanotheres is undoubtedly a defect that is correlated with the abbreviation of the facial region and with the great increase in the relative size of the molars.

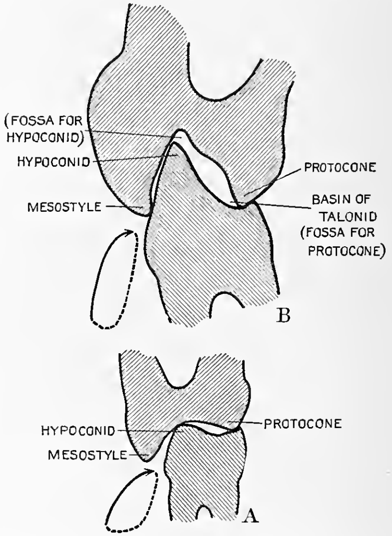


Figure 228.—Cross sections through second upper and lower molars of *Lambdotherium* and *Menodus*

A, A brachyodont lower Eocene titanothere, *Lambdotherium popoagicum*, three-halves natural size; B, a semihypsodont lower Oligocene titanothere, *Menodus giganteus*, one-half natural size. In A the excursion of the mandible was more transverse in direction than it was in B, where, in correlation with the deepening of the ectoloph, the movement of the mandible was more vertical.

The primitive superior premolars of *Eotitanops* (fig. 229, A) when contrasted with those of *Brontotherium* (fig. 229, B) are seen to be triangular in outline and surmounted with three more or less perfectly developed cusps. The transition between these primitive and specialized extremes, by the addition of neomorphs or rectigradations, furnishes a whole series of specific characters and mutations in the ascending phyla of titanotheres.

All the phyla exhibit a similar orthogenic tendency to molarization, but in some phyla this tendency is rapid and in others it is slow. Thus the different rates of molarization are of taxonomic value: they furnish distinctions between different generic or phyletic series. (See Velocity of movement, Chap. XI, pp. 810–812.)

A careful review of the premolars in lower and middle Eocene titanotheres shows that the order of appearance of the premolar cusps is as follows:

Lower premolars	Upper premolars
1. Protoconid.	1. Protocone.
2. Hypoconid.	2. Deuterocone.
3. Paraconid.	3. Tritocone.
4. Metacristid.	4. Parastyle.
5. Metaconid.	5. Tetartocone.
6. Entoconid.	6. Mesostyle.

In the above terminology of the upper premolar cusps the names are those proposed by Scott in 1892 in his paper on the evolution of the premolar teeth in the mammals (1892.1), but they are used throughout this monograph simply as names, without reference to the phylogenetic order of evolution, which is given above. The names of the lower premolar cusps are adapted from the terminology used by Osborn for the lower true molars, but again without reference to the phylogenetic order of appearance.

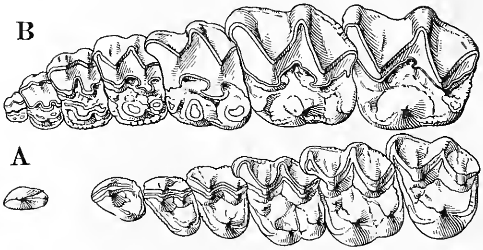


FIGURE 229.—Upper premolar-molar teeth of the earliest (A) and latest (B) known titanotheres

Both tooth rows drawn to the same length. A, *Eotitanops borealis*, Am. Mus. 14887; lower Eocene. Premolars very primitive, a wide diastema behind pm¹. B, *Brontotherium gigas*, Am. Mus. 492; lower Oligocene. The later type, showing the molarized pattern of the premolars and the great size of the molars. Premolars very advanced in pattern, diastema closed.

Summary of premolar evolution of the titanotheres

	Wind River Basin, Wyo. (Wind River B, "Lost Cabin")	Bridger Basin, Wyo.		Washakie Basin, Wyo. (Washakie A, B; B=Uinta A, B)	Uinta Basin, Utah			Titanotherium zone (Chadron A, B, C)
		Bridger A, B	Bridger C, D (=Washakie A)		Uinta A	Uinta B	Uinta C	
P¹ with one cusp, except in later forms; p², p³, p⁴ with three cusps:								
Lambdotheriinae	Primitive; evolving slowly.							
Eotitanopinae	do.							
Palaeosyopinae		Primitive, evolving regularly.						
Telmatheriinae			More advanced.				A little more advanced.	
Sthenodectes						Well advanced.		
Manteoceratinae			More advanced.			But little changed.		
Dolichorhininae			Of high type	Evolving slowly	Evolving slowly			
Metarhinus			do.	Of high type	Of high type			
Rhadinorhininae— Rhadinorhinus			do.		do.			
Intermediate conditions:								
Diplacodontinae— Diplacodon							Advanced.	
Eotitanotherium						Of high type		
P¹–p³ with four cusps; p⁴ with three or four cusps (fourth cusp (te) absent or connected with third cusp (de)):								
Brontopinae								Advanced, but changing very little.
Diploclonus								Do.
Menodontinae— Allops								More advanced, but changing very little.
Menodus								Well advanced and progressing moderately.
P¹–p⁴ with four cusps (p⁴ with fourth cusp very large and not connected with third cusp):								
Megaceropinae								Very advanced, but changing little.
Brontotheriinae								Do.

CORRELATION OF DIMENSIONS OF UPPER AND LOWER TEETH

In considering the generic and specific relations of isolated upper or lower jaws, it is frequently desirable to estimate some of the dimensions of unknown upper teeth from corresponding dimensions of the lower teeth and vice versa. The following table of equations of measurements, prepared by W. K. Gregory, was based primarily upon the type of *Telmatherium cultridens* but has been verified as to other titanotheres.

Dimensions in the upper row of teeth (anteroposterior measurement) approximately equal to dimensions in the lower row

M^1–m^3 = tip paraconid m_1 to tip entoconid m_3.
P^1–p^4 = hinder border p_1 to tip protoconid m_1.
P^2–p^4 = tip protoconid p_2 to tip protoconid m_1.
P^4 = tip protoconid p_4 to tip protoconid m_1.
M^1 = tip protoconid m_1 to tip protoconid m_2.
M^2 = tip protoconid m_2 to tip protoconid m_3.
M^3 = tip protoconid m_3 to tip hypoconulid m_3.
Tip metacone (tritocone) p^4 to tip metastyle m^3 = anterior border m_1 to tip hypoconulid m_3.
Tip paracone m^1 to tip paracone m^3 = tip metaconid m_1 to tip metaconid m_3.
Tip parastyle m^1 to tip parastyle m^3 = tip protoconid m_1 to tip protoconid m_3.

Some of these correlations have been frequently used in the identification of Eocene and Oligocene titanotheres, but they are equally applicable to many other groups of mammals, because they are based upon constant interlocking relations of the cusps in the upper and lower molars.

GEOLOGIC SUCCESSION AND GEOGRAPHIC DISTRIBUTION OF THE EOCENE TITANOTHERES

The following table shows the geologic succession and geographic distribution of the Eocene titanotheres as known in 1914:

Geologic succession and distribution of the species of Eocene titanotheres

[See fig. 41, p. 59]

		Wind River A	Wind River B, Huerfano A	Interval; Bridger A, Huerfano B	Bridger B	Bridger C and D	Bridger E	Washakie A	Washakie B 1	Washakie B 2	Uinta A	Uinta B 1	Uinta B 2	Uinta C 1
51	Protitanotherium superbum													×
50	P. emarginatum													×
49	Diplacodon elatus													×
48	Telmatherium ultimum													×
47	T. altidens													×
46	Manteoceras uintensis													×
45	Sthenodectes incisivus												×	
44	Rhadinorhinus diploconus												×	
43	Dolichorhinus fluminalis												×	
42	D. hyognathus								×				×	
41	D. intermedius												×	
40	D. heterodon												×	
39	D. longiceps												×	×
38	Eotitanotherium osborni												×	
37	Dolichorhinus vallidens								×					
36	D. longiceps											×	×	
35	D. superior											×		
34	Rhadinorhinus abbotti											×		
33	Metarhinus riparius											×		
32	M. earlei								×			×		
31	M. cristatus											×		
30	M. fluviatilis											×		
29	Sphenocoelus uintensis											×		
28	Metarhinus earlei							×				×		
27	Mesatirhinus petersoni					×		×				×		
26	Metarhinus megarhinus					×		×						
25a	Eometarhinus huerfanensis			×										
25	Manteoceras washakiensis							×						
24	Manteoceras manteoceras					×		×						
23	Telmatherium validum					×								
22	T. cultridens					×								
21	Palaeosyops sp					×								
20	P. copei					×		×						
19	P. robustus					×		×						
18	P. leidyi					×								
17	P. grangeri					×								
16	Limnohyops laticeps					×								
15	L. monoconus				×									

Geologic succession and distribution of the species of Eocene titanotheres—Continued

		Wind River A	Wind River B, Huerfano A	Interval; Bridger A, Huerfano B	Bridger B	Bridger C and D	Bridger E	Washakie A	Washakie B 1	Washakie B 2	Uinta A	Uinta B 1	Uinta B 2	Uinta C 1
14	L. matthewi	-----	-----	-----	×	-----	-----	-----	-----	-----	-----	-----	-----	-----
13	L. priscus	-----	-----	-----	×	-----	-----	-----	-----	-----	-----	-----	-----	-----
12	Palaeosyops major	-----	-----	-----	×	-----	-----	-----	-----	-----	-----	-----	-----	-----
11	P. paludosus	-----	-----	-----	×	-----	-----	-----	-----	-----	-----	-----	-----	-----
10	P. fontinalis	-----	-----	×	×	-----	-----	-----	-----	-----	-----	-----	-----	-----
9a	Eotitanops minimus	-----	-----	×	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
9	E. major	-----	×	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
8	E. princeps	-----	×	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
7	E. borealis	-----	×	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
6	E. brownianus	-----	×	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
5	E. gregoryi	-----	×	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
4	Lambdotherium progressum	-----	×	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
3	L. popoagicum	-----	×	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
2	L. primaevum	-----	×	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1a	L. magnum	-----	×	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1	L. priscum	-----	×	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----

SECTION 3. THE LOWER EOCENE TITANOTHERES

ANCESTRAL TITANOTHERES OF THE LAMBDOTHERIUM ZONE OF WYOMING AT THE END OF LOWER EOCENE TIME

The sudden appearance of two forms of titanotheres in the region now known as Wyoming and Colorado at the end of lower Eocene time in the *Lambdotherium* zone is a very striking fact. The two forms are *Lambdotherium*, relatively small, swift, with slender limbs, very abundant (upland type); and *Eotitanops*, larger, with medium-sized limbs, less abundant (lowland type).

No trace of the ancestors of either of these animals has thus far been found in the immediately underlying *Heptodon* zone and earlier beds, although the remains of horses (*Eohippus*) occur there in abundance. The evidence favors the theory that the titanotheres migrated into the ancient mountain region of North America near the end of early Eocene time. The beds in which they first appear belong to what is called the *Lambdotherium* zone, because of the great abundance of the remains of this delicately formed titanothere, which is found there in numbers exceeded only by the remains of horses. In the typical Wind River formation Granger, in his collections made from the *Lambdotherium* zone in 1905 and 1909, assembled out of a total of 727 specimens remains of 191 *Eohippus*, 111 *Lambdotherium*, and 14 *Eotitanops*.

The localities of the *Lambdotherium* zone known up to the year 1912 were as follows:

	Thickness in feet
Wyoming, Wind River Basin, Lost Cabin section	400
Wyoming, Big Horn Basin, Tatman Mountain section	325
Wyoming, Beaver Divide, Green Cove section	265
Colorado, Huerfano Basin, Garcia Canyon	400

The three sections in Wyoming are of nearly uniform thickness throughout. The geology of the *Lambdotherium* zone in Colorado is described in Chapter II. There is also considerable uniformity in the size and character of the remains of *Lambdotherium*. Most of the remains are referred to a single species, *L. popoagicum*, which, however, appears to split up into several subspecies. We know only one phase in the evolution of this animal. Other phases await discovery.

PHYSIOGRAPHIC ENVIRONMENT AT THE END OF LOWER EOCENE TIME

It is especially interesting to picture the geographic, climatic, and biotic conditions surrounding these early titanotheres. The picture may be drawn partly from the study of the rocks in which their remains occur and partly from the remains of the numerous mammals that are found with them in these Wind River deposits. The complete geologic relations of the deposits of the *Lambdotherium* zone have been presented in Chapter II. We comment here chiefly on the geographic and climatic features of the period.

WIND RIVER BASIN, WYOMING

In lower Eocene time (*Lambdotherium* zone) the Wind River Basin was a broad flood-plain valley with mountain barriers to the north, west, and southwest and an easterly drainage. (Sinclair and Granger, 1911.1, pp. 87–103, 105.) The materials of which the beds are composed came from these surrounding mountains. The fine material consists of highly colored clay, in places banded alternately red and blue, interstratified with pale greenish-buff and yellow-brown sandstone in more or less continuous lenses. The sandstone, which is composed largely of quartz sand in which fossils are rare, appears to have been laid down by swift-flowing streams. The deposits of blue clay contain layers of lignite, ranging from mere dark bands to rather thick beds, indicating still water and a humid climate when vegetation was accumulating rapidly. Skeletons of mammals found in this blue clay were evidently swept into still-water areas and covered with river sediment; but fossils are rare in this stratum also. In many of the bands of red clay, on the contrary, or at the contact of the red and blue strata, great numbers of fragments of jaws and scattered teeth are found. Such levels probably represent parts of the basin floor as it was when these creatures died. The beds of red clay, according to Loomis, Granger, and Sinclair, were formed during the drier cycles, when the carbonaceous matter of decaying plants was completely oxidized, when iron compounds were concentrated and oxidized, and when the bones of animals exposed at the surface were weathered and broken before they were entombed. These signs of the alternation of moist and dry climate, indicated respectively by blue and red clays, are not accompanied by signs of excessive aridity, the mammals in the red and blue clay bands being the same. Similar alternations of red and blue clays are now found in the desert basins of Asia.

BIG HORN BASIN, WYOMING

The discovery of *Lambdotherium* by the Amherst College expedition of 1904 under Loomis and its localization by the American Museum expedition of 1911 (Sinclair and Granger, 1911.1) in the uppermost levels of the red-banded clay beneath the lignitic beds of Tatman Mountain demonstrated the deposition of sediments of Wind River age in the Big Horn Basin. The true *Lambdotherium* zone is exposed on all sides of Tatman Mountain and consists chiefly of red-banded beds. Granger and Sinclair observe (1912.1, p. 66) that the lower Eocene sediments of the Big Horn Basin, like those of the Wind River Basin, represent the filling in of a great trough surrounded by mountains. No volcanic ash occurs. The mountain streams have borne down gravel, sand, and clay and deposited them in stream channels or spread them over flood plains. No evidence of wind transportation has been observed. The red and blue banding of the clays occurs in more or less regular alternation.

BEAVER DIVIDE, WYOMING

The discovery of a typical Wind River fauna on Beaver Divide by Olsen, of the American Museum party of 1910, was a most important one, because it extends the range of this fauna many miles to the southwest. The entire fauna was obtained at or near a certain stratum of bluish-green shale resting on a band of red shale, the fossiliferous zone not exceeding 10 feet in thickness. (See Chap. II.) Remains of the animals listed below were obtained:

Reptilia:
    Glyptosaurus (scutes).
    Crocodile (scutes, vertebrae, and teeth).
    Turtles (numerous fragments).
Insectivora:
    Hyopsodus n. sp.
    Hyopsodus sp.
Creodonta:
    Didymictis? altidens.
Primates:
    Microsyops sp.
Equidae:
    Eohippus craspedotus.
    Eohippus? venticolus.
Lophiodontidae:
    Heptodon calciculus.
    Heptodon ventorum.
    Heptodon n. sp.
Titanotheriidae:
    Lambdotherium popoagicum.
Amblypoda:
    Coryphodon sp.

The fish and aquatic reptiles in this fauna indicate plainly that the deposit on Beaver Divide was fluviatile, and, as Granger and Sinclair observe, go far toward establishing the theory that the Wind River shales were flood-plain deposits, a theory that is further supported by the presence of numerous channel fillings of coarse sandstone. All the fossils from the shales are fragmentary and consist mostly of teeth whose roots are worn off, indicative of water transportation and abrasion.

HUERFANO BASIN, COLORADO

The *Lambdotherium* zone was discovered in Colorado by Dr. J. L. Wortman while he accompanied the writer in 1897 (Osborn, 1897.126) on a survey of the Huerfano Eocene deposits, which were first announced by Hills in 1888 (Hills, 1888.1). The zoogeographic significance of this discovery is evident from the fact that it carries the *Lambdotherium* fauna eastward to the foothills of the Rocky Mountains, between the famous extinct volcanoes known as the Spanish Peaks.

Wortman described these beds as follows:

> These beds of the lower division [*Lambdotherium* zone] are indistinguishable, so far as their general appearance and lithological characters are concerned, from those of the upper level [*Palaeosyops fontinalis* zone]. The fossils occur apparently in a single stratum not exceeding 10 or 15 feet in thickness and not more than 30 or 40 feet from the base of the formation. They underlie the beds of the upper division with perfect conformity, and there is at present no means of determining exactly where the one ends and the other begins. That sedimentation was continuous and uninterrupted from the beginning to the close of the whole [Huerfano] deposit, I do not think there can be the slightest question. The exact locality from which the greater number of the fossils of the lower beds were obtained is Garcias Cañon, about 1½ miles south of Talpa or the mouth of Turkey Creek. [Osborn, 1897.126, pp. 253–254.]

The animals associated with *Lambdotherium* in this zone are provisionally identified by Osborn and Matthew as follows:

Titanotheriidae	Lambdotherium popoagicum.
Creodonta	Didymictis altidens. Didymictis leptomylus. Oxyaena lupina.
Insectivora	Hyopsodus sp.
Amblypoda	Coryphodon ventanus.
Artiodactyla	Trigonolestes secans.

SUMMARY

A summary of the life conditions in the Wind River and Big Horn Basins during lower Eocene time shows that there is no evidence of climatic change throughout lower Eocene time; that the conditions through the *Systemodon* zone and the succeeding *Heptodon* zone, into the overlying *Lambdotherium* zone, remain substantially similar. This fact accords with the substantial similarity in the general character of the mammalian fauna throughout the lower Eocene. The fauna evolves during this very long period; old forms give way to new; but it does not change in its general adaptation to conditions.

Thus in the great mountain valleys sediments were being continually derived by erosion from the older rocks of the mountains and deposited in these great basins. Throughout Wind River time fluviatile deposition is indicated by numerous channels filled with coarse sandstones which irregularly traverse the finer clays or interstratify with them in the form of lenses. In the clays are found fish, crocodiles, and turtles, and occasionally beds of *Unio*. Local swamps are indicated by the presence of lignitic areas in the blue clays and in the sandstones, but never among the red clays. The feldspars that wash down from the surrounding granitic mountains are fresh and angular, a fact that suggests rapid transportation of the fragments for short distances and burial beyond the reach of carbonated waters. These conditions do not favor the idea of luxuriant Eocene tropical forests or of a warm, humid climate with the formation of a deeply decaying humus, but suggest rather a dry although not necessarily arid climate, with rapid changes of temperature favorable to splintering the ledges of the granite cliffs. There were no frosts, but the climate may have been stimulating to a vigorous and actively competing fauna. In the Big Horn Basin fluviatile deposition is indicated throughout the entire Eocene epoch. The lignitic shales that cap the *Lambdotherium* zone, as indicated by the fresh-water mollusks and plant contents, are both fluviatile and palustrine.

The above picture of the physiography and the climate of these Rocky Mountain basins of Wyoming in early Eocene time accords thoroughly with the analysis of the chief adaptive types of mammals whose remains are found in the lower Eocene rocks. These mammals are broadly divided into three types—fluviatile, or river-living; river border, or palustrine; upland, or plains-living.

The upland type sought and found hard ground, to which their narrow feet and compressed hoofs were adapted. Conspicuous among these dry-ground forms is *Lambdotherium* itself, a swift-moving, or cursorial animal broadly analogous in structure to the horses of that time (*Eohippus*) and lophiodonts (*Heptodon*), as well as to the archaic condylarths (*Phenacodus*).

The Wind River fauna of the *Lambdotherium* zone represents the closing chapter of lower Eocene mammalian life. It is closely affiliated with the fauna of the typical lower Eocene or *Systemodon* zone, because the two contain 25 genera and 11 species of mammals in common. It is doubtful whether a single family of mammals of the *Systemodon* zone becomes extinct in the *Lambdotherium* zone, yet some of the archaic mammals begin to show a numerical reduction.

On the other hand, the Wind River fauna is progressive; the first appearance of these two genera of titanotheres, *Lambdotherium* and *Eotitanops*, and of seven other new genera of mammals is prophetic of the oncoming middle Eocene or Bridger life.

During this transition of the Wind River mammals from their Wasatch forerunners to their Bridger successors the physiography and the climate apparently remained the same as in earlier Wasatch time, a fact attested not only by the geologic and physiographic evidence just considered but by the similar relative abundance of the adaptive types of mammals found in these two formations.

The extent of the collections in the American Museum, the total number of specimens collected, and the field records of Granger show that fossil mammals are about four times as abundant in the *Systemodon* zone as in the *Lambdotherium* zone.

The relative numbers of the mammals in the *Systemodon* zone of the Big Horn Basin of Wyoming, as indicated by the number of specimens collected, are shown below:

Mammals in the Systemodon zone

	Specimens
Perissodactyla (horses, 1,202; tapirs, 370)	1, 572
Insectivora (Hyopsodus, 254)	306
Condylarthra (mostly Phenacodus)	264
Amblypoda (coryphodons only)	209
Creodonta (various carnivores)	203
Primates (Pelycodus, Anaptomorphus, etc.)	151
Artiodactyla (mostly Trigonolestes)	120
Tillodontia (Esthonyx)	73
Rodentia (Paramys)	16
Taeniodonta (?edentates, Calamodon)	2
Edentata (new type)	1
	2, 917

This table naturally is only approximately representative. The rodents, for example, were probably far more abundant numerically than the horses. The great number of horses, tapirs, and hyopsodonts in the assemblage listed above is due in part to the abundance of these animals in the "red beds." The table is valuable chiefly in expressing the relative abundance of the adaptive types of ungulates.

In the *Lambdotherium* zone the relative abundance of the remains of ungulates undergoes a marked change: both of the archaic types of mammals, the condylarths and the amblypods, are relatively less abundant than in the *Systemodon* zone.

Relative frequency of mammals in the Lambdotherium zone of Wyoming as indicated by the number of specimens collected

	Specimens
Perissodactyla (horses, 191; titanotheres, 124; heptodonts, 56; hyrachyids, 2)	373
Primates (pelycodonts, 42; anaptomorphs, 9; Microsyops, 30)	81
Insectivora (Hyopsodus, 71)	75
Condylarthra (Phenacodus, 47; Meniscotherium, 1)	48
Rodentia (Paramys, 39)	42
Creodonta (various carnivores)	35
Amblypoda (Coryphodon, 29; Bathyopsis, 2)	31
Artiodactyla (Trigonolestes)	20
Tillodontia (Esthonyx)	12
Edentata (Taeniodonta) (Stylinodon, Calamodon)	5
	722

It will be observed that the Condylarthra (*Phenacodus*) here drop to the fourth place in relative frequency, and the Amblypoda (*Coryphodon*) drop from the fourth to the seventh place. This reduction is partly in accord with the reduction of the archaic types of mammals generally, as shown also in the following faunistic comparison; in the *Systemodon* zone both the genera and species of archaic mammals numerically exceed those of modern type, whereas in the *Lambdotherium* zone the genera and species of archaic and of modern types are evenly balanced.

The relative frequency of the various adaptations to cursorial, ambulatory, and arboreal life is still more significant. The comparison of the adaptive types of the *Systemodon* and *Lambdotherium* zones is as follows:

	Systemodon zone	Lambdotherium zone
Ungulates; cursorial, small, light-limbed	1, 692	373
Ungulates; mediportal, medium in size	264	63
Ungulates; graviportal, large, heavy-limbed	209	31
Primates; arboreal, climbing types	194	81
Insectivores; rodents, etc., ambulatory, small terrestrial and fossorial mammals	395	139
Carnivores; larger and smaller creodonts	203	35
	2, 957	722

It will be observed that although the fossils collected from the *Lambdotherium* zone are only one-third as numerous as those of the *Systemodon* zone the relative abundance of the adaptive types is approximately the same, a fact that sustains the inferences as to geologic and physiographic continuity or the absence of any marked changes of environment during lower Eocene time. Also, in the *Lambdotherium* zone, as in the *Systemodon* zone, there is still a numerical predominance among the ungulates of cursorial types, the horses (*Eohippus*), the lophiodonts (*Heptodon*), the titanotheres (*Lambdotherium*). Singularly, no primitive tapirs (*Systemodon*) have been found. Among the mediportal types may be noted the remains of *Phenacodus* and the titanothere *Eotitanops*. The graviportal coryphodonts, which may have been amphibious or partly aquatic in habit, are comparatively rare.

The first author to analyze the Wasatch fauna with reference to adaptive types in their bearing on physiography and climate was Loomis (1907.1), who divided the Wasatch fauna into percentages, substantially as follows:

Terrestrial and arboreal types	75
Aerial	3
Amphibious	12
Aquatic, including crocodiles, turtles, and fishes	10

The present analysis of the adaptations of foot structure in Wasatch and Wind River time combined gives the following relative degrees of abundance among the hoofed mammals:

Ungulates; small, cursorial, light-limbed types	2, 065
Ungulates; medium, mediportal types, proportioned like the tapir	327
Ungulates; graviportal, heavy-limbed types (*Coryphodon*), proportioned like the hippopotamus	240

The analysis both of the geologic and paleontologic evidence appears to show that in Wind River time there was a warm but relatively dry and invigorating climate in the Rocky Mountain region; that there were streams, swamps, and river borders for the coryphodonts, forests and meadow borders for the true titanotheres (*Eotitanops*), and open spaces with harder ground for the diminutive horses, lambdotheres, and heptodonts. In the forests there were numerous lemuroid or monkey types, as well as arboreal rodents, and on the borders of the savannas there were terrestrial and partly fossorial edentate-like mammals. Periods of aridity and areas of drier ground favored the development of the light-limbed ungulates.

CONTRASTS AND RESEMBLANCES BETWEEN LAMBDOTHERIUM AND EOTITANOPS

Geologic and biologic evidence of the existence of areas of dry, hard ground in Wind River time is thus adduced to explain the surprising fact that the feet and limbs of the little *Lambdotherium* are more highly specialized for cursorial locomotion than the feet of any of the known middle Eocene titanotheres. An alternative interpretation is that the ancestral perissodactyls were small cursorial forms with narrow feet like *Heptodon* and *Systemodon* and that the widening of the feet is a secondary adaptation to mediportal habits. (See p. 586.) The skull of *Lambdotherium* is elongate and relatively *Eohippus*-like. *Lambdotherium* was probably an early specialized cursorial member of the great titanothere family, a member that died out without leaving descendants. Under the law of local adaptive radiation it may have lived in the drier uplands; at all events its remains are especially abundant in the "red beds," in which all together no less than 111 specimens have been found in comparison with 14 of the bulkier *Eotitanops*. (See fig. 230.)

Judging by the 14 specimens of *Eotitanops* that have been found in the typical Wind River *Lambdo-*

therium zone, they had already shown considerable specialization both in structure and in size. The smaller and more primitive forms, such as *E. gregoryi*, only slightly exceed *Lambdotherium popoagicum* in size, but species like *Eotitanops princeps* and *E. major* are little inferior to the existing American tapir (*Tapirus terrestris*). The gradations in size between these five or six species and mutations of *Eotitanops* may be judged from the accompanying outlines (fig. 231) of the lower jaws.

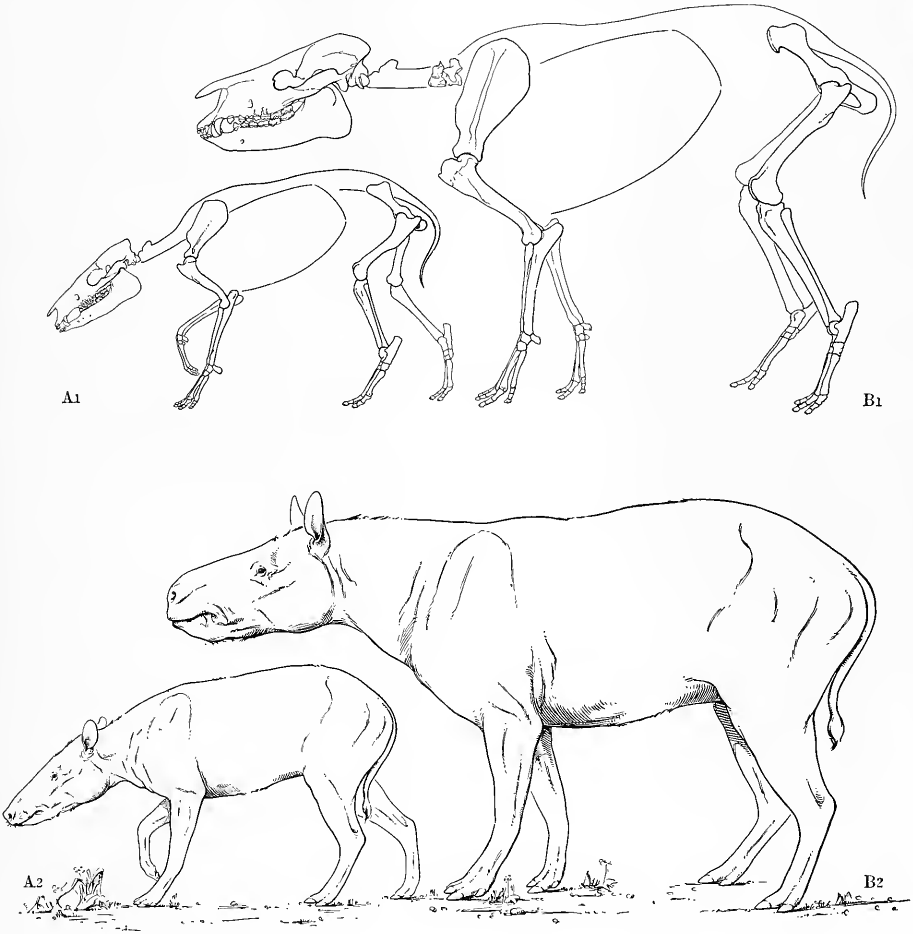


FIGURE 230.—Reconstructed skeletons and restorations of *Lambdotherium popoagicum* (A_1, A_2) and *Eotitanops borealis* (B_1, B_2)

Drawn by E. S. Christman under the direction of W. K. Gregory. About one-tenth natural size. These provisional reconstructions of skeleton and body are based on material in the American Museum.

Eotitanops is a more typical titanothere than *Lambdotherium*. In its limb structure it approaches especially *Mesatirhinus*, of the middle Eocene, although in its mesaxonic foot structure—that is, its enlarged central digit—it still resembles *Lambdotherium*, as shown in Figure 220. Its feet are adapted to softer ground, and we may conjecture that it resembled the tapir in its habits.

The principal contrasts between these two titanotheres are the following:

Lambdotherium	*Eotitanops*
Cursorial, light limbed, small, like *Eohippus*.	Cursorial to mediportal, small to large, almost equaling *Tapirus*.
Face decidedly elongate.	Face moderately elongate.
Muzzle attenuate, pointed.	Muzzle relatively abbreviate, broad.
Cranium abbreviate.	Cranium intermediate.
Three premolars.	Four premolars.
Cropping teeth procumbent.	Cropping teeth more erect.

Both animals possess a number of features in common: (1) They show a similar cone and crescent (or bunoselenodont) pattern of the superior grinding teeth, with either reduced or vestigial intermediate cusps or conules; (2) in both the preorbital (or facial) part of the skull is longer than the cranial (see fig. 232), a primitive characteristic of perissodactyls which at once allies these animals to other primitive perissodactyls and distinguishes them from the middle Eocene titanotheres, in which the cranium is longer than the face; (3) they show enlargement of the median digit (D. III), or mesaxonic structure of the fore and hind feet.

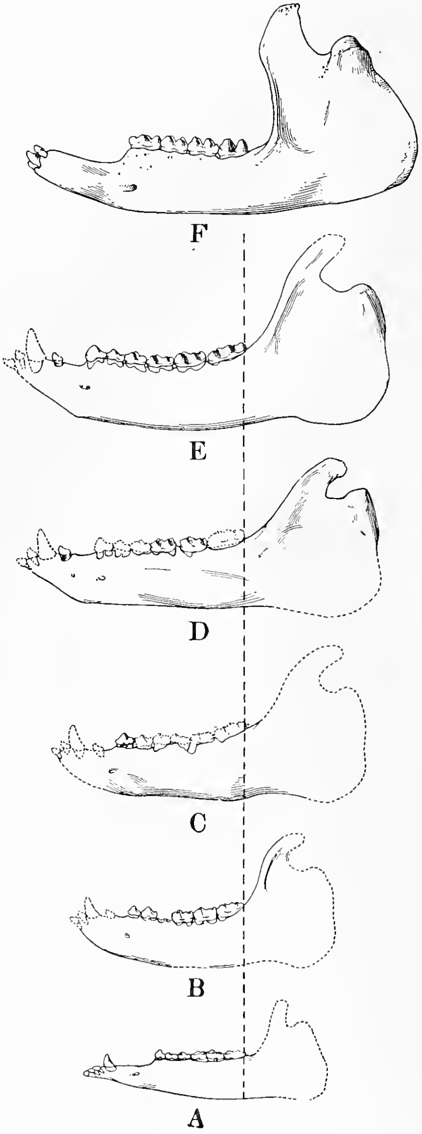


Figure 231.—Lower jaws of *Lambdotherium*, *Eotitanops*, and *Tapirus*

One-fourth natural size. A, *Lambdotherium papoagicum*, Am. Mus. 14906; Alkali Creek, Buck Spring, Wind River Basin. B, *Eotitanops gregoryi*, Am. Mus. 14889 (type); Alkali Creek, Buck Spring, Wind River Basin. C, *E. brownianus*, Am. Mus. 4885 (type); Wind River Basin. D, *E. borealis*, Am. Mus. 14891; west bank of Wind River, 3 miles above canyon (top of banded beds). E, *E. princeps*, Am. Mus. 296 (type); Wind River Basin. F, *Tapirus terrestris*, Am. Mus. 1135; immature specimen.

It is quite possible (see Chap. VIII) that this mesaxonic specialization is itself common among perissodactyls—that is, that all perissodactyls are descended from quadrupeds with narrow feet, as suggested by Gregory. We should interpret this swift-footed structure as an adaptation that enabled the small, defenseless perissodactyls, without horns or tusks, to escape their pursuers.

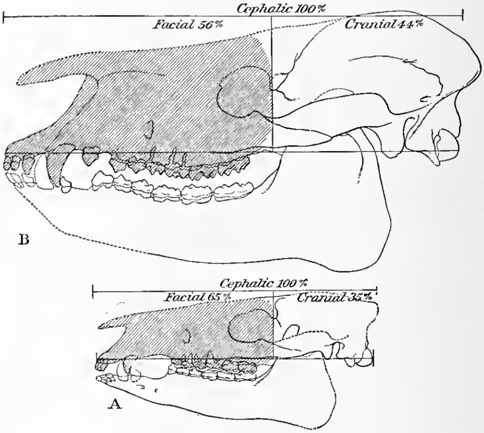


Figure 232.—Restored contours of skulls of *Lambdotherium* and *Eotitanops*

Showing estimated proportions of face (shaded) to cranium. One-fourth natural size. A, *Lambdotherium*, face 65, cranium 35. B, *Eotitanops*, face 56, cranium 44.

The special similarities of foot structure between *Lambdotherium* and *Eotitanops* embrace the following characters: (1) Enlargement of the median digit (D. III), which is provided with a broad proximal phalanx; (2) reduction of digits II and IV, with relative narrowing of the proximal phalanges; (3) reduction of digit V (correlated with this metapodial structure we find that the lunar immediately rests on the unciform, with a narrow (*Lambdotherium*) or oblique (*Eotitanops*) facet on the magnum); (4) small, relatively high and narrow magnum. These points are well illustrated in the accompanying figures of the manus of *Lambdotherium* and *Eotitanops*.

The interpretation of this somewhat specialized form of foot as one derived from a cursorial type is considered in the introduction to the study of the skeleton of the Eocene titanotheres (p. 586).

EXPLORATIONS AND DISCOVERIES

The explorations in the Wind River Basin for remains of titanotheres and the types collected were as follows:

1880. J. L. Wortman, for E. D. Cope; *Eotitanops borealis* (Cope), *E. brownianus* (Cope), and *Lambdotherium popoagicum* (Cope).

1891. J. L. Wortman, for American Museum of Natural History; *Eotitanops princeps* Osborn.

1894. F. B. Loomis, for Amherst College Museum; *Lambdotherium primaevum* Loomis.

1909, 1910, 1911. Walter Granger, for American Museum of Natural History; *L. priscum* Osborn, *L. progressum* Osborn, and *E. gregoryi* Osborn.

The American Museum expeditions of 1909, 1910, and 1911, under Granger and Sinclair, made a series of important discoveries—first, in locating all these titanotheres in the *Lambdotherium* zone; second, in proving that *Eotitanops* and *Lambdotherium* were contemporaneous; third, in collecting the remains of more than eight specimens of *Eotitanops* (Am. Mus. 14887–14894); fourth, in collecting a complete skull and jaws of *Eotitanops borealis*, affording proof that *Eotitanops* is more primitive than the middle Eocene or Bridger forms and belongs to a distinct generic stage.

The Wind River *Lambdotherium* zone is 400 feet thick and may be divided into four levels, each including 100 feet. It is a remarkable fact that nearly all the remains of the 124 specimens of titanotheres found by the American Museum parties were collected between the 250 and 400 foot levels, as shown in the section taken from Granger's field records (fig. 48).

Thus *Eotitanops* and *Lambdotherium* occur contemporaneously. It appears that the mutations or species of *Eotitanops* do not exhibit a continuously graded evolution or succession in ascending levels, for it happens that the smallest and most primitive form known, *E. gregoryi*, occurs on a high geologic level, showing that *Eotitanops* was already polyphyletic in early Eocene time. This is an example of the extreme importance of an exact record of levels.

SYSTEMATIC DESCRIPTIONS OF THE LOWER EOCENE TITANOTHERES

Superfamily Titanotheroidea Osborn

Perissodactyls with bunoselenodont superior molars and selenodont inferior molars. Distinguished from the Chalicotherioidea by normal limbs and hoofs. Distinguished from the Hippoidea by a persistently tetradactyl manus and tridactyl pes.

Family Brontotheriidae Marsh

Related to the type of *Brontotherium*. Evolving between early Eocene and early Oligocene time. Primitively cursorial in gait but early evolving into mediportal and graviportal forms. Terminal phalanges and hoofs progressively reduced. Forward portion of skull originally elongate but early becoming abbreviate; cranial portion progressively elongate. Earlier genera hornless; paired nasofrontal horns developing in middle Eocene time and becoming the dominant character of the skull.

Subfamily Lambdotheriinae Osborn

Lower Eocene titanotheres, small, light limbed, of slender, cursorial proportions. Skull mesaticephalic; facial region elongate; cranial region abbreviate. Superior molars brachyodont, incipiently bunoselenodont, with lophoid paraconules and metaconules; lower molars with pronounced metastylids; premolars $\frac{1}{1}$ absent; lower premolars p_{2-4}, progressively molariform.

Lambdotherium Cope

Plate LIV; text figures 27, 33, 103, 114, 143, 146, 154, 221, 228, 230-242, 244, 483, 484, 486-492, 503, 504, 510, 512, 521, 522, 661, 685, 688, 692, 694, 700, 701, 723

[For original description and type reference see p. 168. For skeletal characters see p. 590]

Generic characters.—Skull of decided proopic dolichocephaly. Anterior premolars wanting. Superior molars broadened transversely, with prominent parastyles and mesostyles, oblique ectolophs, large, free protoconules, and low metalophs; m^3 with prominent hypocone; inferior molars with metastylids; first upper and lower premolars wanting; posterior lower premolars progressive; m_3 with large crescentic hypoconulid. Manus numerically tetradactyl, functionally anisotridactyl; lunar resting chiefly on unciform anteriorly; magnum small, high, and narrow.

We know neither the ancestors nor the descendants of this animal. It is already more highly specialized in many respects than certain of the middle Eocene titanotheres. *Lambdotherium* is readily distinguished by its fine, delicate construction for swift movement, in which it has analogies to the lower Eocene horses. It has a long, slender snout and delicately prehensile jaw. We note especially that (1) the face is much elongated, the faciocephalic index being 65 as compared with 56 in *Eotitanops* and 60 in *Eohippus;* (2) this elongation is correlated with a very slender snout, but the first upper and lower premolars are wanting; (3) the third and fourth lower premolars are more complicated than in *Eotitanops*, p_4 in some forms closely resembling a molar tooth; (4) its sharply piercing canine teeth and chisel-shaped incisors are other features of specialization.

History of discovery of Lambdotherium.—Wortman's discovery in the Wind River valley (1880) and Cope's original description have already been cited. Cope at once recognized the ancestral relationship of this form to the titanotheres. In 1889 he made *Lambdotherium* the type of a distinct family—"Lambdotheriidae"—to embrace all the Eocene titanotheres, a family name that was adopted by Flower and Lydekker. In his "Tertiary Vertebrata" (1885.1, pp. 709,

711) Cope mistakenly referred to this genus the two species *L.* (=*Eotitanops*) *brownianum* and *L. procyoninum.* In the same memoir he placed all the Eocene titanotheres in the family "Chalicotheriidae." In his memoir of 1892 Earle correctly considered this animal a probable member of a side line of titanotheres. In 1893 Osborn recognized the division as a subfamily—"Lambdotheriinae." In 1897 Osborn mistakenly proposed to remove *Lambdotherium* from the titanotheres and related it to the Equidae on the ground of its slender foot structure. The renewal of the demonstration of its relation to the titanotheres is due to W. K. Gregory. In 1907 Loomis discovered five specimens of this genus in the deposits of Buffalo Basin, one of which he selected as the type of the new species *L. primaevum,* believing it to represent a stage somewhat more primitive and perhaps geologically older than *L. popoagicum.* In 1905 and 1909 the American Museum party under Granger finally determined that these animals were geologically contemporaneous with *Eotitanops* but confined to a comparatively narrow geologic zone.

The principal collectors and the areas in which they worked were as follows:

1880. E. D. Cope, J. L. Wortman, for American Museum of Natural History; Wind River Basin, Wyo.
1896. J. L. Wortman, for American Museum of Natural History; Huerfano Park, Colo.
1905. Walter Granger, for American Museum of Natural History; Wind River Basin, Wyo.
1907. F. B. Loomis, for Amherst Museum; Big Horn Basin, Wyo.
1909. Walter Granger, for American Museum of Natural History; Wind River Basin, Wyo.
1916. Walter Granger, for American Museum of Natural History; Huerfano Park, Colo.
1918. Walter Granger, for American Museum of Natural History; Huerfano Park, Colo.

Geologic horizons.—The animals found in four exposures of the *Lambdotherium* zone in the Wind River Basin, the Big Horn Basin, the Beaver Divide, and Huerfano Park, each 300 to 400 feet thick, are not separated by marked differentiation or evolution; in all these basins and on all the levels of each formation the lambdotheres, so far as known, are substantially similar in size but differ markedly in the degree of evolution of the third and fourth lower premolar teeth. The range in size is indicated on page 282. A very striking fact is that the extremes of premolar structure (fig. 234) were found in animals collected around the great Alkali Creek "red stratum," which is such a conspicuous level mark (fig. 47), many of the specimens being just below the "red stratum," or 50 to 100 feet above the base of the Wind River formation. The greater part of the collections have been made within a vertical distance of 200 feet, which would represent time for considerable evolution; but as the stages of evolution do not occur successively in the ascending levels, it does not appear practicable to separate any but the extreme forms as species or mutations, and the systematic order therefore appears as follows:

Lambdotherium progressum Osborn (most progressive).
L. popoagicum Cope, *L. primaevum* Loomis (intermediate).
L. priscum Osborn (most primitive).

Measurements of teeth of Lambdotherium, in millimeters

[The numbers are those of specimens in the American Museum of Natural History]

	L. priscum					L. popoagicum					L. progressum			L. sp., 14922	L. magnum, 17527 (type)
	14916	14912	14914	12822 (type)	14908	4863 (type)	14899	14904	14907	14902	14917 (type)	14918	14919		
P_2–m_3						68. 7	64					69	70. 6		74
P_3–m_3	58		59			60. 9	57					61	62. 3		64
P_2–m_2						50. 9	47				51. 8	51	53. 3		54
P_2–p_4				25		26. 7	25				26. 4	26. 4	27. 4		28. 5
M_1–m_3	39		41		36	42	39	41				42. 4	43. 1		44
P_2 (ap.)						7. 5	7. 6				7. 6		8. 2		8. 5
P_3 (ap.)	8. 5	9	9. 5	8		9. 3	8. 2				9	9	9		9. 5
P_4 (ap.)	9	9	9. 3	9	8. 2	9. 4	9				9. 5	9. 5	9. 3	9. 3	10
M_1 (ap.)	10. 9	10. 8	11	12	10	11. 4	10. 3	11			11. 4	11. 4	12. 8	10. 8	12
M_2 (ap.)	11. 8	12	12. 5		10. 1	12	11. 1	11. 4			12. 5	12. 6	13. 2	12. 5	13
M_3 (ap.)	16		16. 5		15	17. 5	16. 2	17. 7				17. 4	17. 3		18. 5
P^2–m^3										58. 6					
P^3–m^3									50. 6	51					
P^2–p^4										24					
M^1–m^3								36	34	34					
P^2 (ap.)										7					
P^3 (ap.)									7	7. 8					
P^4 (ap.)									8	8. 5					
M^1 (ap.)								11. 5	10. 3	10. 4					
M^2 (ap.)								12	10. 9	11. 1					
M^3 (ap.)								12	11. 4	12					

Lambdotherium popoagicum Cope

Plate LIV; text figures 27, 33, 103, 143, 228, 230, 231, 233–237, 244, 483, 484, 486–492, 503, 504, 512, 521, 522, 661, 694, 700

[For original description and type references see p. 168. For skeletal characters see p. 590]

Type locality and geologic horizon.—Wind River Basin, Wyo.; *Lambdotherium* zone (Wind River B).

Specific characters.—P_2–m_3 69–56 millimeters; p_3 with paraconid, metaconid, and hypoconid intermediate in development. In superior molars the protoconules more or less free and distinct, metaloph low but distinct, cingula not surrounding the crown internally.

Materials.—The type species (figs. 234, H; 236, C) of a series of mutations of specific character is represented by over 70 specimens in the collections of the American Museum, chiefly from the typical Wind River formation, but also from contemporaneous deposits in the Big Horn Basin, Beaver Divide, and Huerfano Basin. These specimens consist mostly of scattered upper and lower teeth and fragments of jaws but include several nearly complete jaws. One specimen (Am. Mus. 4880) affords a limited but significant knowledge of the skeleton.

Skull.—The imperfectly known skull is analogous to that of the primitive horses rather than that of *Eotitanops* or any of the typical middle Eocene titanotheres. There are only two specimens (Am. Mus. 14903, 14907) in which fragments of the skull are associated with the teeth, from which the conjectural restoration (fig. 233) is assembled, the outlines of the anterior part, or premaxillaries and nasals, being inferred from the attenuate structure of the lower jaw. The principal characters are the following: (1) Dolichocephaly of proopic type—that is, long, slender skull, in which the facial greatly exceeds the cranial length, the faciocephalic index being 65, as compared with 56 in *Eotitanops;* (2) sagittal crest rather low and slender; (3) external auditory meatus open inferiorly; (4) infraorbital foramen placed above the second premolar—that is, decidedly anterior in position as compared with that in the typical titanotheres; (5) an attenuated rostrum associated with the elongated symphysis of the jaw, suggesting the conformation of the skull of a ruminant rather than of a perissodactyl.

Comparison.—This skull is very close in its proportions to that of *Eohippus*, and if it were not for the differences in the teeth might be mistaken for it. The faciocranial indices are similar, namely:

	Eohippus	Lambdotherium	Eotitanops
Faciocephalic	58–60	65	56
Craniocephalic	42–40	35	44
Cephalic	41	(?)	(?)

General features of the teeth.—The dental formula, so far as known, is $I\frac{3}{3}$, $C\frac{1}{1}$, $P\frac{3}{3}$, $M\frac{3}{3}$. The inferior incisors, as observed in Am. Mus. 14899, 14906, 14920, represented in Figures 233, 236, 237, are semicircular in arrangement, semiprocumbent, with spatulate or chisel-shaped crowns; the median incisors especially, which are distinctly chisel-shaped, are quite different from those of *Palaeosyops*, which are bluntly pointed. The inferior and superior canines are rounded, slightly compressed laterally, and sharply pointed.

Type premolars.—No trace of p^1 or p_1 is to be found in any of the specimens; this tooth is ordinarily very persistent in the Perissodactyla. In the *L. popoagicum* type premolar series p_2 is an elevated, laterally compressed cone, with a rudimentary paraconid and low, narrow heel bearing a hypoconid; p_3 presents an anterior lobe composed of a low paraconid, an elevated protoconid, a postero-internal metaconid elevated but slightly developed, a somewhat broader posterior heel or hypoconid, with a rudimentary internal crest representing the entoconid; p_4 is a more progressive or submolariform tooth with an anterior transverse crest composed of protoconid and metaconid behind which is a low, incomplete posterior crest supporting an elevated hypoconid and a depressed internal ridge.

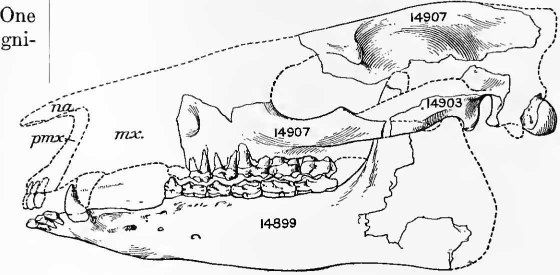


FIGURE 233.—Skull of *Lambdotherium popoagicum*, reconstructed

Made by L. M. Sterling under the direction of W. K. Gregory. About two-fifths natural size. This reconstruction is made from three specimens in the American Museum, collected in the Wind River Basin—No. 14899, Alkali Creek, Buck Spring, lower jaw; No. 14907, Alkali Creek, Wolton, maxilla, malar, and skull top; No. 14903, Alkali Creek, Buck Spring, squamosal and condyle. Missing parts conjecturally restored by comparison with *Systemodon* and *Eohippus*.

Lower premolars, primitive and progressive mutations or specific forms.—The structure of the cusps in p_2, p_3, p_4 is very important. The accompanying diagram (fig. 234) shows the wide range of progressive evolution in the lower premolar teeth which are exhibited in the large number of specimens in the American Museum collection. They embrace stages ranging from far less primitive to stages far more primitive than the lower premolar teeth of the type of *L. popoagicum*. These stages are especially important and interesting because they are recorded as coming from similar geologic levels. These records of geologic levels may be confused, but accepting them as correct, it seems impracticable to divide *Lambdotherium* into a large series of species, although the development of the premolar cusps certainly warrants specific separation.

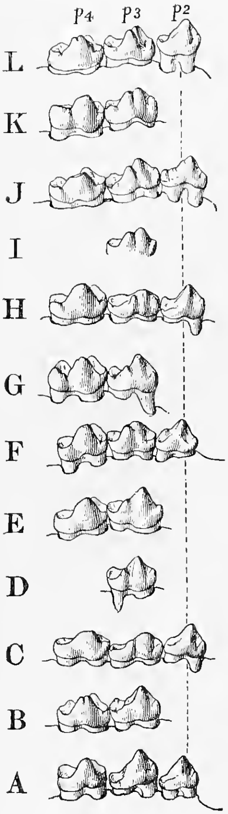


FIGURE 234.—Lower premolars of three "species" or mutations of *Lambdotherium*, illustrating progressive evolution of the premolar crowns

Natural size. Second, third, and fourth lower premolars of the left side, inner side view. A–E, *L. priscum*; F–H, *L. popoagicum*; I–L, *L. progressum*. All American Museum specimens from the Wind River Basin. A, No. 12822 (type), 3 miles east of Lost Cabin; B, No. 14916, Alkali Creek, Buck Spring; C, No. 14900, Alkali Creek, Wolton; D, No. 14912, Dry Muddy Creek, 18 miles above mouth; E, No. 14914, Alkali Creek, Wolton; F, No. 14915, Alkali Creek, Wolton; O, No. 14924, Dry Muddy Creek, 18 miles above mouth; H, No. 4863 (type), Wind River valley; I, No. 14913, Muddy Creek, south side, 18 miles above mouth; J, No. 14919, Alkali Creek, Wolton; K, No. 14918, lower Alkali Creek; L, No. 14917 (type), Alkali Creek, Buck Spring.

These extreme stages are therefore grouped together for the present as mutations between *Lambdotherium priscum*, represented by the simplest type (No. 12822), and *Lambdotherium progressum*, represented by the most advanced type (No. 14917). Halfway between the extremes is the type species *L. popoagicum.*

The cusp evolution is very interesting, including the following elements: Anterior lobe—protoconid (pr^d), paraconid (pa^d), metaconid (me^d), metastylid (ms^d); posterior lobe—hypoconid (h^d), entoconid (en^d).

The series represented in Figure 234, including *L. priscum* at the bottom and *L. progressum* at the top, presents a complete morphologic transition or epitome of premolar evolution, it being essential to note that we do not know whether this corresponds with a real succession in time. At the base p_2 and p_3 are excessively simple, but at the summit p_3 has a large paraconid and metaconid, and p_4 has a paraconid, metaconid, metastylid, and rudiment of an entoconid, which is developed as a distinct cusp in certain specimens (such as Am. Mus. 14924).

Premolars relatively progressive.—It is very important to note that p_3 and p_4 in the progressive forms are much more advanced in evolution than the corresponding teeth in the contemporary *Eotitanops;* in fact, p_4 is submolariform and lacks only the prominence of the metaconid to be like a molar. P_2 in *Lambdotherium* is almost as progressive as p_3 in *Eotitanops.* Even in the middle Eocene species *Palaeosyops leidyi,* p_3, p_4 are not so far advanced as in *Lambdotherium.* We observe also another distinctive character: Whereas in *Palaeosyops* the metaconid arises as a bud or reduplication of the protoconid, in *Lambdotherium* it springs from the posterior side of the protoconid. These details are of importance as demonstrating the accelerated rate of evolution of the premolar cusps as a character of lambdotheres.

Superior premolars.—Comparatively few well-preserved superior premolar series are known, so it can not be determined whether there is a corresponding series of mutations in the evolution of the upper teeth. In the specimens Am. Mus. 14902, 14900, 14911, 14907 the following characters are observed: (1) p^2 very simple, with single external protocone and rudiments of the deuterocone and sometimes of the tritocone; (2) p^3, p^4 with rudimentary parastyle, deuterocone, tritocone, rudimentary crests connecting deuterocone with protocone and tritocone, respectively, faint conules sometimes observed on these crests.

A series of deciduous premolars (Am. Mus. 14934) exhibits dp^2 somewhat more complex than p^2, dp^3 elongate, quadricuspidate, with prominent parastyle and mesostyle.

Molars.—The inferior molars are highly characteristic teeth, distinguished especially by the elevation of their crescents; the protolophid consists of an elevated protoconid, metaconid, and metastylid, or double internal cusp, which is very distinct in unworn teeth. This reduplicate cusp, which develops in the upper Eocene species of horses and also in the true chalicotheres, is not present in the titanotheres of the middle Eocene, such as *Palaeosyops.* A rudimentary hypoconulid is usually observed in m_1 and m_2 and develops into a strong crescentic third or posterior lobe in m_3.

The superior molars, as observed in five specimens in the American Museum (Nos. 14900, 14902, 14904, 14907, 14911), are fairly uniform in character, with very prominent parastyles, mesostyles, variable protoconules, rudimentary or lophoid metaconules. (Pl. LIV, A, B; fig. 235, A.) A very distinctive feature is the large hypocone on m^3. The following characters should also be noted: (1) The transverse diameter always exceeds the anteroposterior; (2) m^1 is a relatively small tooth; m^2 is usually the largest tooth of the series; m^3 is usually intermediate in size but sometimes is the largest tooth of the series.

Measurements of superior molars of Lambdotherium popoagicum, in millimeters

	M^1		M^2		M^3	
	Ap.	Tr.	Ap.	Tr.	Ap.	Tr.
Am. Mus. 4664	10. 5				11. 5	16
Am. Mus. 4880			11. 5	15		
Am. Mus. 14902	10. 5	13	11. 5	14. 2	12	14. 5

Other distinctive characters of the superior teeth are the very oblique ectolophs, the prominent parastyles and mesostyles, the sculptured form of the cusps, especially apparent in the unworn specimens. The protoconule is distinct and usually of subtriangular form; it is connected with the protocone by a low crest. The metaconule proper is rather sessile, indistinct, or wanting; there is, in fact, a depressed metaloph or rudimentary posterior crest. The third superior molar (Am. Mus. 4664) exhibits an especially oblique ectoloph, also a prominent hypocone and low but distinct metaloph.

The jaw.—The type jaw (Am. Mus. 4863, fig. 236) consists of two separate and incomplete rami figured by Cope (Tertiary Vertebrata, Pl. LVIII, *B*). The distinctive feature of the type species is the intermediate condition of the third premolar, which distinguishes this animal from primitive and more progressive specimens.

There are five more complete jaws, namely, Am. Mus. 14899 (figs. 231, 236), 14905, 14906 (figs. 231, 236), 14909, which together afford a full knowledge of the characters of the jaw except the angular and condylar region; the elongate and laterally compressed chin (fig. 236), even more extreme than that of the Eocene horses; the wide diastema between the canine and the second premolar; the incisive border extending somewhat to support the slender, recurved, prehensile canines and the row of chisel-shaped, semiprocumbent teeth; the coronoid process high, vertically placed, sharply defined, with flat anterior face.

The extremes of measurement are shown below.

Measurements of jaw of Lambdotherium, in millimeters

	L. popoagicum, Am. Mus. 4863 (type jaw)	L. progressum, Am. Mus. 14919 (largest jaw)	L. priscum, Am. Mus. 14908 (smallest jaw)
P_2–m_3, anteroposterior	68	70. 6	56
M_1–m_3, anteroposterior	41	43. 1	37
M_1, anteroposterior	11		
M_2, anteroposterior	12		
M_3, anteroposterior	16		
Depth of jaw below m_3	32		

The premolars are 63 per cent of the length of the molars.

Lambdotherium primaevum Loomis

Plate LIV, C, D; text figure 114

[For original description and type reference see p. 178]

Type locality and geologic horizon.—Big Horn Basin, Wyo.; *Lambdotherium-Eotitanops-Coryphodon* zone (Big Horn D).

Specific characters.—Superior molars with crescentic protoconules; cingula completely surrounding the crowns. Measurements as in *L. popoagicum.*

This type is significant as coming from the Big Horn Basin. The type superior first and second molar teeth (fig. 114, p. 178) may be readily distinguished by the greater development of the internal cingulum, which completely surrounds the crown. Another feature is that the protoconules are large and subcrescentic, and the metaconules are lost in the metaloph. These measurements [22] are:

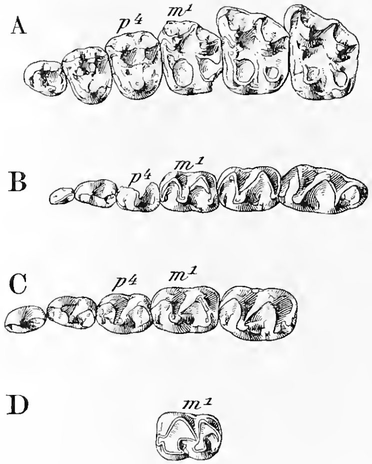


FIGURE 235.—Upper and lower grinding teeth of *Lambdotherium*

Natural size. A, *L. popoagicum*, Am. Mus. 14902, Alkali Creek, Wolton; left upper premolar-molar series. B, *L. priscum*, Am. Mus. 14908, Dry Muddy Creek, 18 miles above mouth; right premolar-molar series. C, *L. progressum*, Am. Mus. 14917 (type), Alkali Creek, Buck Spriug; right lower premolar-molar series. D, *L. progressum*, Am. Mus. 14918, lower Alkali Creek; first lower molar of the left side, crown view. All from Wind River Basin.

Measurements of molar teeth of Lambdotherium primaevum

	Millimeters
M^1 and m^2, combined, anteroposterior	23. 5
M^1, anteroposterior	11
M^1, transverse	13
M^2, anteroposterior	12
M^2, transverse	15
M^2, transverse, maximum along anterior border	18
M_1 to M_3, combined, anteroposterior	41
M_1, anteroposterior	11
M_2, anteroposterior	12. 5
M_3, anteroposterior	17

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[22] The measurements of m^1 and m^2 were accidentally transposed in Loomis' original description.

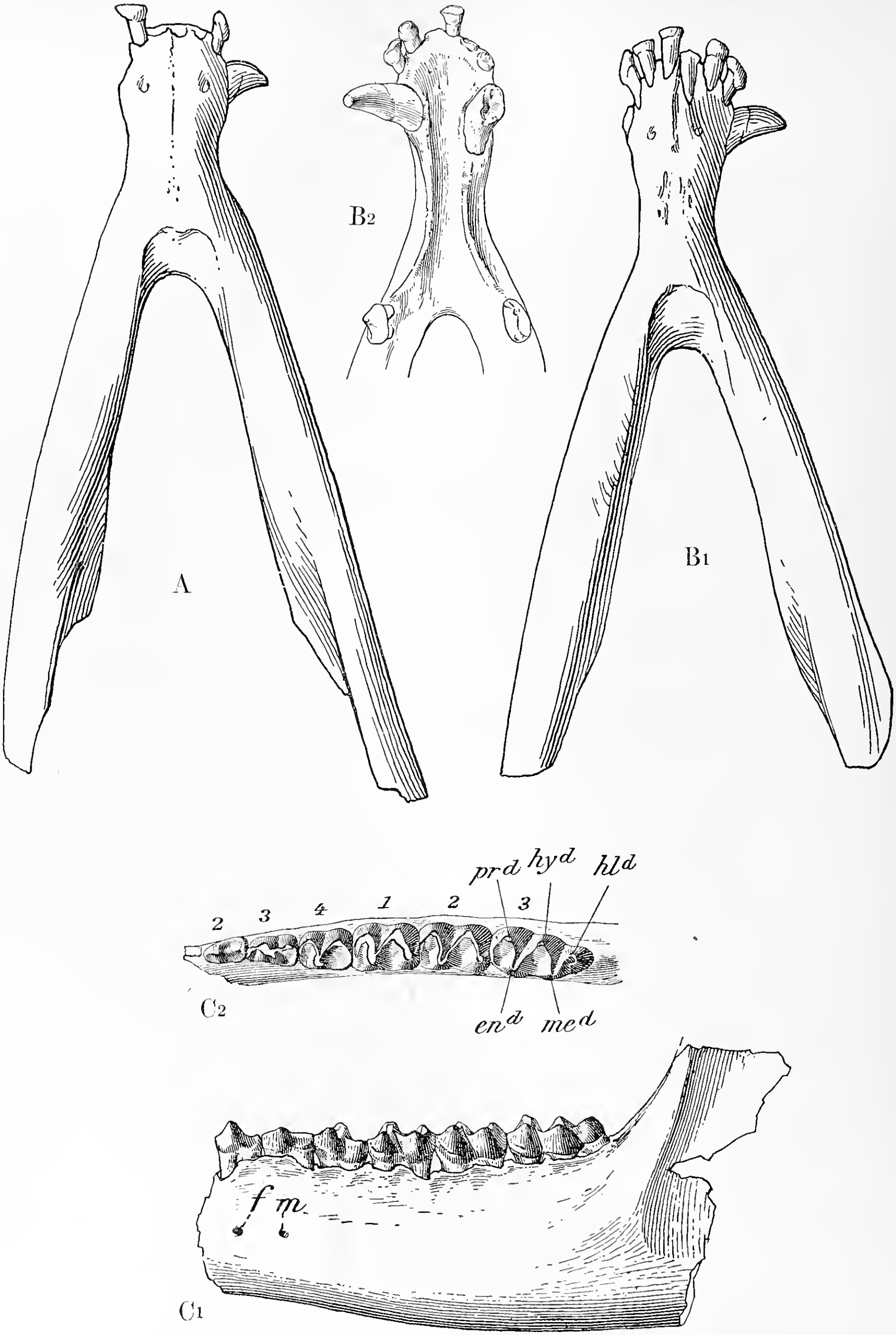

FIGURE 236.—Lower jaws and teeth of *Lambdotherium popoagicum*

Natural size. A, Am. Mus. 14899, Alkali Creek, Buck Spring; lower jaw, inferior surface. B_1, Am. Mus. 14906, Alkali Creek, Buck Spring; lower jaw, inferior surface; an older individual. B_2, The same, showing upper surface of symphyseal region. C_1, Am. Mus. 4863, Wind River valley; type jaw, outer side view. C_2, The same, lower premolar-molar series, crown view.

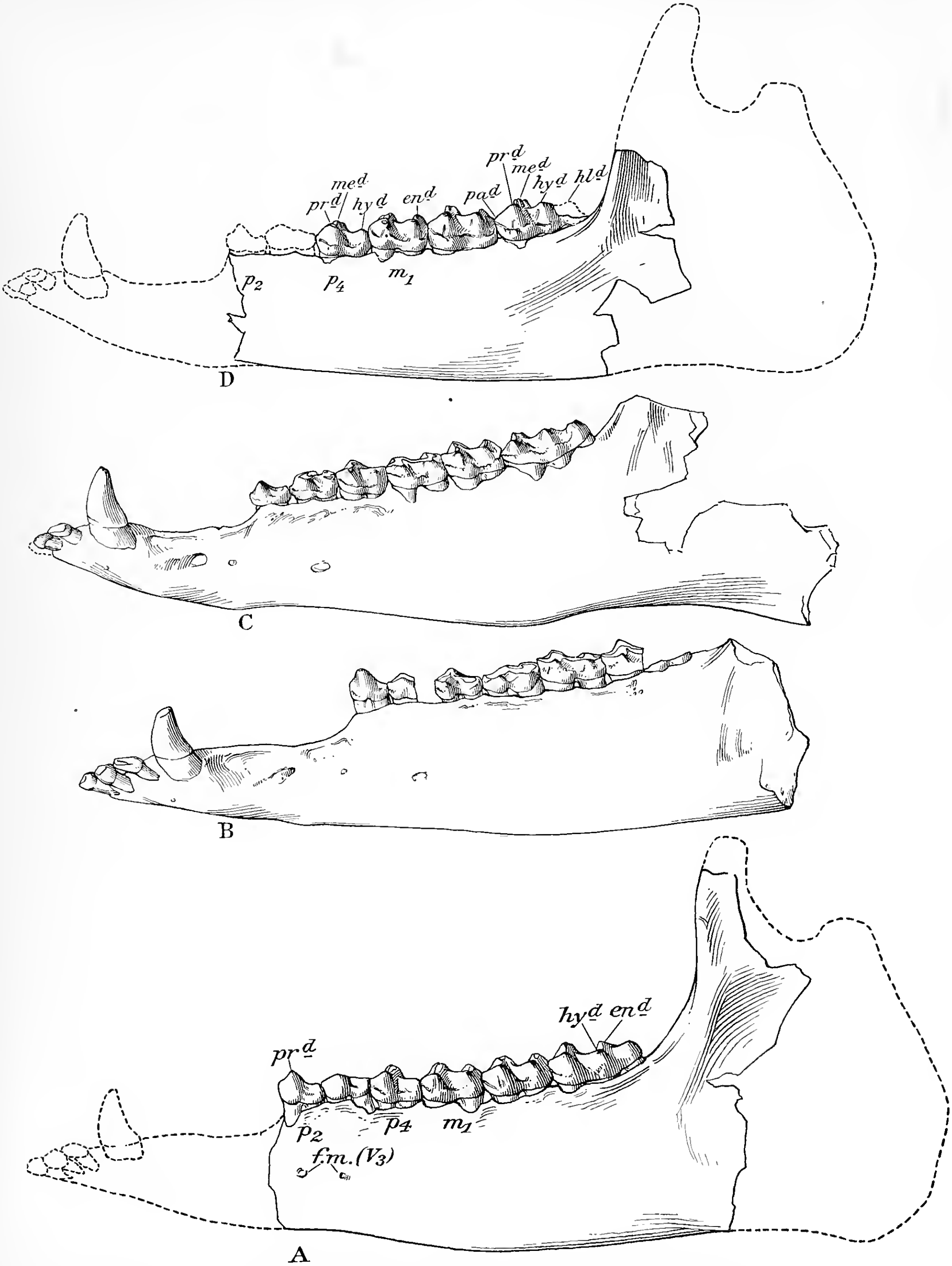

FIGURE 237.—Lower jaws and teeth of *Lambdotherium popoagicum*

Side view. Natural size. A, Am. Mus. 4863 (type); Wind River valley; front part restored from Am. Mus. 14899. B, Am. Mus. 14906; Alkali Creek, Buck Spring; an old individual. C, Am. Mus. 14899; Alkali Creek, Buck Spring. D, Am. Mus. 2989; Wind River valley.

The three inferior molar teeth, m_1–m_3, measure longitudinally 41 millimeters, as compared with 42 in the type of *L. popoagicum.* The external crescents (protoconid, hypoconid), the internal cones (metaconid, distinct metastylid, entoconid), and the crescentic third lobe of m_3 (hypoconulid) are characteristic.

Lambdotherium priscum Osborn

Text figures 146, 234, 235, 238–240

[For original description and type references see p. 194]

Type locality and geologic horizon.—Wind River Basin, 3 miles east of Lost Cabin, Wyo.; *Lambdotherium-Eotitanops-Coryphodon* zone (Wind River B); Granger, collector, American Museum expedition, 1905.

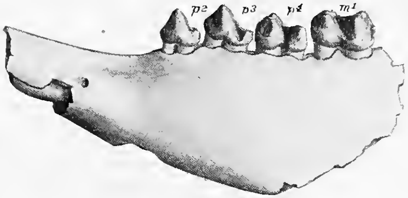

FIGURE 238.—Front part of type lower jaw of *Lambdotherium priscum*

Natural size. Am. Mus. 12822, reversed, showing the long postcanine diastema, the three lower premolars, and the first lower molar. Locality, 3 miles east of Lost Cabin; Wind River formation.

Specific characters.—P_2–p_4, 25 millimeters; m_1–m_3 (referred specimen), 37 millimeters; second and third lower premolars extremely simple, with rudimentary paraconid; p_3, metaconid rudimentary, placed very low upon slope of protoconid, talonid narrow, depressed, with cingular rudiment of entoconid. (See fig. 238.)

The extremely simple or primitive structure of the second lower premolar clearly distinguishes this stage.

A referred specimen (Am. Mus. 14908) collected by Granger (American Museum expedition, 1909), is slightly more advanced in the structure of the second lower premolar (fig. 239) but is still much more primitive than the type of *L. popoagicum.*

The measurements of these two specimens are shown below.

Measurements of Lambdotherium priscum, in millimeters

	12822 (type)	14908 (referred)
P_2–p_4	25	
P_2, anteroposterior	7	
P_3, anteroposterior	8	8
P_3, transverse	5	5
P_4, anteroposterior	9	8. 5
P_4, transverse	6. 5	
M_1, anteroposterior	12	10
M_1, transverse	7. 5	7
M_1–m_3		37

This Wind River species is identified in Huerfano A by a fine pair of jaws from Garcia Canyon (Am. Mus. 17526). The specific character of p_3, without trace of metaconid, is clearly shown in Figure 240. This species is represented by another jaw, with teeth of the same size (Am. Mus. 17528) in which p_3, also without metaconid, is in a slightly more advanced stage of evolution, the talonid being broader.

This species is also doubtfully represented by the imperfect specimen of upper teeth referred to *L. popoagicum* by Wortman (Am. Mus. 2688), as well as by a newly found specimen (Am. Mus. 17529) of approximately the same size. In this new specimen, found 3 miles east of Gardner Butte, the isolated upper teeth of two sides, including p^3–m^3, show the following characters: (1) Molars slightly smaller than in the referred specimen of *L. progressum,* (2) conules and cingulum not so well developed, (3) measurements slightly inferior to those of the type of *L. popoagicum.* (See p. 283.)

The types of *L. popoagicum* and *L. priscum* are both lower jaws from the Wind River, and as there are two lower jaws from the Huerfano positively referable to *L. priscum* and none referable to *L. popoagicum* it seems best to assign these two sets of upper teeth to *L. priscum* also.

Lambdotherium progressum Osborn

Text figures 147, 234, 235, 241, 242

[For original description and type references see p. 194]

Type locality and geologic horizon.—Wind River Basin, Alkali Creek, Buck Spring; *Lambdotherium-Eotitanops-Coryphodon* zone (Wind River B); Granger, collector, American Museum expedition, 1909.

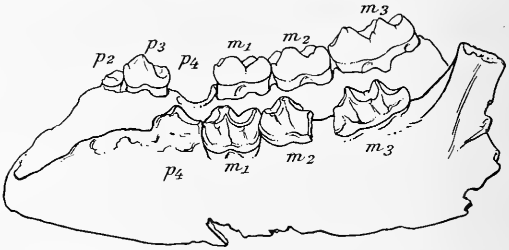

FIGURE 239.—Incomplete lower jaw of *Lambdotherium priscum*

Natural size. Am. Mus. 14908; Dry Muddy Creek, 18 miles above mouth. A referred specimen. Oblique view of dentition.

Specific characters.—P_2–p_4, 16.5 millimeters. Second, third, and fourth lower premolars progressive: rudiment of metaconid on p_2; p_3 with elevated metaconid subequal with protoconid, broad talonid with rudimentary entoconid; p_4 with bifid metaconid and distinct entoconid.

This is readily distinguished from both *L. priscum* and *L. popoagicum* by the advanced condition of p_3, which may be described as submolariform.

Measurements of type of Lambdotherium progressum (Am. Mus. 14917)

	Millimeters
P_2–p_4	26
P_2, anteroposterior	8
P_2, transverse (trigonid)	4. 8
P_3, anteroposterior	9
P_3, transverse	6
P_4, anteroposterior	9. 3
P_4, transverse	7. 3
M_1, anteroposterior	11. 5
M_1, transverse	8. 5
M_2, anteroposterior	12. 5
M_2, transverse	9. 5

This Wind River type is distinguished by p_3, which has a strong metaconid—that is, it is submolariform. A series of molar teeth, p^3–m^3 (fig. 242), from the highest level of the lower Huerfano, is referred to *L. progressum* on the following grounds: (1) The upper teeth fit pretty well those of the type of *L. progressum* from the Wind River; (2) the parastyle is especially prominent at the antero-external angle of m^2, m^3; (3) m^3 has prominent hypocone and cingular hypostyle; (4) the outer cusps of the premolars are approximated, conules prominent; (5) the cingulum is strong on p^4 and m^3.

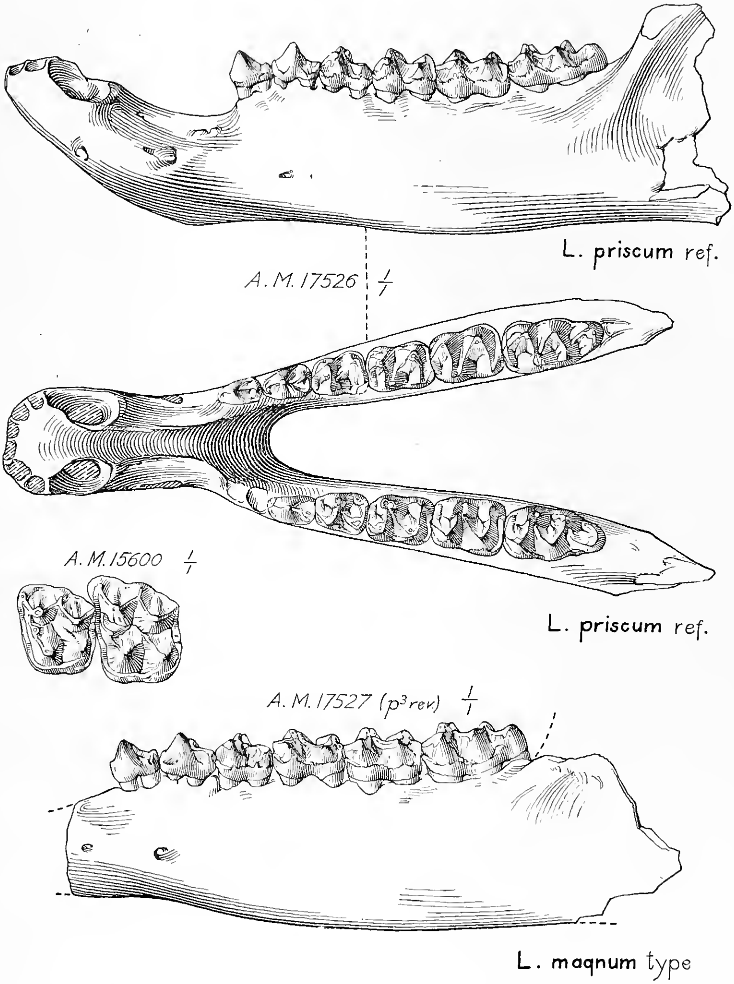

FIGURE 240.—Jaws and teeth of *Lambdotherium*

Am. Mus. 17526, lower jaw of *L. priscum*, referred specimen from Huerfano A, outside and crown views. Am. Mus. 17527, outer view of type jaw of *L. magnum*, Huerfano A. Am. Mus. 15600, first and second upper molars of *L. magnum*, referred specimen from the Wind River horizon of the Big Horn Basin, Wyo. Natural size. After Osborn, 1919.

With these specimens (association doubtful) were found the calcaneum, portion of a tibia, and a proximal phalanx.

Lambdotherium magnum Osborn

Text figures 154, 240

[For original description and type references see p. 199]

Type locality and geologic horizon.—Huerfano Park, Colo.; lower horizon of the Huerfano formation, *Lambdotherium-Eotitanops-Coryphodon* zone (Huerfano A).

Specific characters.—Osborn writes:

> Exceeding in size any other known lambdothere is the type jaw (Am. Mus. 17527) from the Garcia Canyon, lower Huerfano, containing a complete inferior series, p_2–m_3 of both sides, represented in Figure 240. These teeth exceed in length over all (74 mm.) those of the type of *L. popoagicum*, in which the same teeth measure 69. P_3 has a rudimentary metaconid and paraconid, in the same stage of evolution as in *L. popoagicum*. Of similar large size is a referred specimen, Am. Mus. 15600 (fig. 240), from the Big Horn, west end of Tatman Mountain. These referred grinders, m^1, m^2, coincide closely in size with the type of *L. magnum* and may be regarded as a paratype.

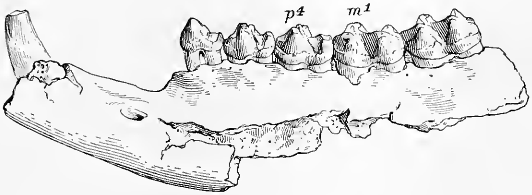

FIGURE 241.—Lower jaw and teeth of *Lambdotherium progressum*

Natural size. Am. Mus. 14917, type, reversed; Alkali Creek, Buck Spring; Wind River formation.

Below are given the measurements of teeth of species of lambdotheres. The numbers following the specific names are those assigned to the specimens in the American Museum of Natural History.

Measurements of teeth of lambdotheres

		Millimeters
P_2–m_3:	Huerfano A, *L. priscum* 17526 (referred)	67
	Wind River B, *L. popoagicum* 4863 (type)	69
	Wind River B, *L. progressum* 14917 (type) (estimated)	71
	Huerfano A, *L. magnum* 17527 (type)	74
M^1–m^2:	Huerfano A, *L. priscum* 17529 (referred)	21.5
	Huerfano A, *L. priscum* 2688 (referred)	22.5
	Huerfano A, *L. progressum* 17530 (referred)	23.5
	Wind River B, *L. popoagicum* 14902 (referred)	25
	Wind River B, *L. magnum* 15600 (referred)	27.5

These measurements show that there is not a great range in size between the smaller and the larger animals referred to this genus (Osborn, 1919.494).

Subfamily Eotitanopinae Osborn

Lower Eocene titanotheres of intermediate size. Body proportions slender, submediportal rather than cursorial. Skull dolichocephalic; facial region longer than cranial region. Superior molars brachyodont; molar tooth proportions much as in the Palaeosyopinae, with reduced paraconules and metaconules. Inferior molars without metastylids. Premolars $\frac{1}{1}$ present; molarization of premolars retarded.

Discovery.—The details of the discovery of *Eotitanops* (*Palaeosyops borealis*) in 1850 and the early history of opinion are in part related above. In Cope's "Tertiary Vertebrata" (1885.1, p. 703, pl. 58a, fig. 3) a full description is given of the type molar teeth and the imperfect radii of the animal that Cope called *Palaeosyops borealis* (Am. Mus. 4892).

Materials.—In 1891 Dr. J. L. Wortman, who had discovered the type, enlarged our knowledge of this genus by the discovery of another specimen (Am. Mus. 296), including a complete lower jaw, two cervical, three dorsal, and one caudal vertebra, the femur, humerus, and the greater part of the fore foot. These bones were described by Osborn and Wortman in 1892 (1892.67) and were referred to the type species, *Palaeosyops borealis*; they are now known as *E. princeps*.

Soon afterward Earle's memoir (1892.1) appeared, in which he treated *Palaeosyops borealis* as probably ancestral to the Bridger *Telmatherium cultridens*. In 1908 Osborn (1908.318) revised the Eocene titanotheres and placed *P. borealis* in the new genus *Eotitanops*.

Granger's explorations in 1909 to 1911 resulted in the discovery of the type of *E. gregoryi* and have enabled us to make a systematic revision of these animals based upon materials in the American Museum collections, which are arranged below according to size and morphologic succession; their geologic succession is shown in Figure 48. The numbers are those assigned to the specimens in the American Museum of Natural History.

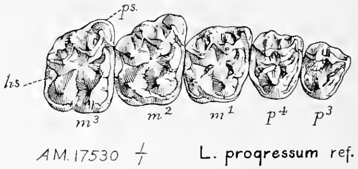

FIGURE 242.—Upper teeth of *Lambdotherium progressum*

Am. Mus. 17530, referred specimen from Huerfano A. Natural size. After Osborn, 1919.

E. major Osborn, 14894 (type), a third metatarsal of the left side (figs. 145, 506).

E. princeps Osborn, 296 (type), jaw, manus, humerus, femur, etc. (figs. 144, 231, 246, 252, 484, 490, 494, 496, 498–500, 512, 686, 692, 700, 724 (Pls. XXVI, LIV).

E. princeps Osborn, 4902 (referred?), fragments of pes.

E. borealis (Cope), 4892 (type), superior molars p^4–m^3, radius, etc. (figs. 102, 497, 498; Pl. LIV).

E. borealis (Cope), 14887 (neotype), skull, jaw, atlas, pelvis, etc. (figs. 229, 232, 244, 250, 251, 494, 495, 501, 515, 721; Pl. LIV).

E. borealis (Cope), 14890, portions of right and left jaws.

E. borealis (Cope), 14891, complete jaws (figs. 231, 248, 249).

E. borealis (Cope), 4886, anterior portion of jaw (figs. 246, 249).

E. borealis (Cope), 14895, calcaneum, astragalus (reference doubtful) (figs. 503, 505, 522).

E. borealis (Cope), 14888, jaws and fragments of skeleton and feet, right pes (figs. 246, 249, 494, 501–503, 521, 701).

E. brownianus (Cope), 4885 (type), jaw fragment (figs. 104, 231, 246, 247).

E. gregoryi Osborn, 14889 (type), jaws, also m^{2-3} (figs. 142, 231, 245–247; Pl. LIV).

E. gregoryi Osborn, 14933 (referred), portions of pes and tibia (fig. 503).

The specimens listed above are arranged not in the ascending geologic order but according to size, *E. gregoryi* being the smallest and *E. major* the largest of the animals represented by these types and other specimens. The specific reference of the separate foot bones (Nos. 14893, 4902, 14895, 14933) is doubtful.

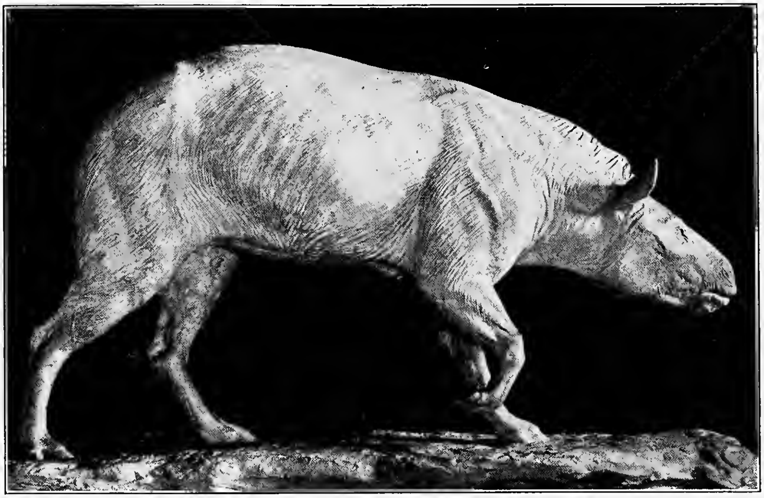

FIGURE 243.—Restoration of *Eotitanops borealis*, of the Wind River formation (Eocene)

About one-twelfth natural size. Made by E. S. Christman in 1917 under the direction of W. K. Gregory.

Eotitanops Osborn

Plates XXVI, LIV; text figures 10, 21, 25, 27, 28, 29, 33 142–145, 155, 210, 212, 219, 229–232, 243–253, 405–408, 482–485, 490, 492–503, 505–507, 512, 515, 521–523, 646, 648, 649, 661, 686, 688, 690, 692, 694, 695, 700, 701, 704, 709, 711, 717, 721–727, 733, 740, 742, 745

[For original description and type references see p. 179; for skeletal characters see p. 591]

Generic characters.—Skull of proopic dolichocephaly. Incisor series obliquely anteroposterior. P_1 with small, compressed single fang; p^2–p^4 with single internal cusps; p^3–p^4 with rudimentary lophoid protoconules; p_4 rather progressive. Superior molars subquadrate and rounded in form; protoconules small; metaconules wanting or rudimentary; inferior molars without metastylids; hypoconulid of m_3 subconic. Manus numerically tetradactyl but functionally tridactyl, with a tendency to mesaxonic structure.

This animal is separated generically from *Lambdotherium* by the possession of full eutherian dentition, including $p\frac{1}{1}$. The fact that the face is longer than the cranium constitutes its principal generic distinction from the middle Eocene titanotheres (fig. 256). As has been shown above, the genus is represented by five specific stages or mutations, which are distinguished partly by size but more clearly, at least in four species, by the development of cuspules on the inferior premolar teeth, as follows:

E. major Osborn, distinguished only by its large size.

E. princeps Osborn, distinguished by size and premolar complication.

E. borealis (Cope), distinguished by intermediate size and premolar simplicity.

E. brownianus (Cope), distinguished by smaller size and premolar simplicity.

E. gregoryi Osborn, distinguished by the smallest size and extreme premolar simplicity.

The range of measurement in the species and mutations is shown in the following tables:

Comparative measurements of Eotitanops, in millimeters

[All specimens in American Museum]

	P_2–m_3	Mtc III	Mts III
E. major, 14894 (type)			103
E. princeps, 296 (type)	[a] 105	87	
E. borealis, 14891 (referred)	98		
E. borealis, 14890 (referred)	96		
E. borealis, 14888 (referred)	94		
E. brownianus, 4885 (type)	90		
E. gregoryi, 14889 (type)	78. 4		
E. minimus, 17439 (type)	[a] 72		

[a] Estimated.

Standard measurements of teeth of the species of Eotitanops, in millimeters

[The numbers are those of specimens in the American Museum of Natural History]

	E. gregoryi, 14889 (type)	E. brownianus, 4885 (type)	E. borealis						E. princeps, 296 (type)
			4892 (type)	14888	14891	14890	4886	14887 (neotype)	
P^1–m^3								108	
P^2–m^3								92	
P^2–p^4									36
M^1–m^3	35. 5							54	
P^4, ap			11					17	
P^4, tr			14. 6					16	
M^1, ap			18					18	
M^1, tr			18. 3					20	
M^2, ap	14							19	
M^2, tr	15. 5							22	
M^3, ap	13. 3							18	
M^3, tr	17							22	
P_2–m_3	78	90		94	98	96			[a]105
P_2–p_4	29. 4	35		36	38	36			39
M_1–m_3	49	55		58	59	60			66
P_2, ap	8. 8					11. 5	12		13
P_2, tr	6. 2					6	6		63
P_3, ap	9. 5					12	12		125
P_3, tr	5. 2					6. 5	7		63
P_4, ap				12		13	12. 5		
P_4, tr				8		7. 5	8		
M_1, ap	14. 5			15. 5	16. 3				183
M_1, tr	8. 5			10	11				12
M_2, ap	15. 5			18	19				21
M_2, tr	10. 5			11. 7	13				14
M_3, ap	19. 5	23		22	23. 2				25
M_3, tr	10. 7			11. 5					14

[a] Estimated.

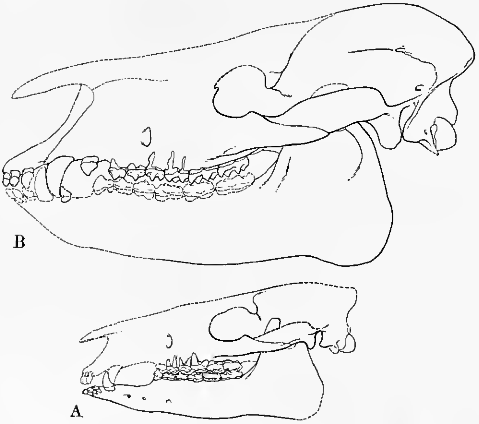

FIGURE 244.—Skulls of the oldest known titanotheres

Reconstructions by L. M. Sterling under the direction of W. K. Gregory. One-fourth natural size. A, *Lambdotherium popoagicum*, Am. Mus. 14907, Alkali Creek, Wolton; 14899 and 14903, Alkali Creek, Buck Spring. B, *Eotitanops borealis*, Am. Mus. 14887, Dry Muddy Creek 12 miles above mouth. All specimens from the Wind River Basin, Wind River formation.

Range of evolution.—As *Eotitanops gregoryi*, the smallest and simplest form, occurs on a high level, having been found 100 feet above the "red stratum" on Alkali Creek (see figs. 47, 48), and as specimens referred to *E. borealis* and *E. princeps* range from the "red stratum" on Alkali Creek, on the 250-foot level, to the 400-foot level, these species and mutations can not be arranged in monophyletic succession, but they afford evidence that even at this time the titanotheres were polyphyletic.

Range in size.—The smallest of the Wind River titanotheres, *E. gregoryi*, measures about 18¼ inches, or 45.6 centimeters, at the shoulders. A larger form, *E. princeps*, measures about 26 inches, or 66 centimeters, at the shoulders. The intermediate form, *E. borealis*, is more slenderly proportioned than the American tapir (*T. terrestris*); it is between 75 and 78 per cent of the height of the tapir, and thus about 75 per cent of the height of *Mesatirhinus* of the upper levels of the Bridger Eocene. *E. major*, judged only by the size of the pes, more nearly approaches *T. terrestris* in size, the median metatarsal of *E. major* measuring 103 millimeters and that of *T. terrestris* 108.

It should be noted that *Eotitanops* includes the only known large lower Eocene perissodactyl. Even *Eotitanops major*, the largest Wind River species, appears to be considerably smaller than *Palaeosyops fontinalis*, the smallest Bridger species.

Measurements of upper teeth of Eotitanops borealis and Palaeosyops fontinalis, in millimeters

	E. borealis from Wind River B, Am. Mus. 14887	P. fontinalis from Bridger A (type), Am. Mus. 5107
M^1, anteroposterior	17. 5	21. 3
M^1, transverse	[a]18. 5	23. 5
M^1, ectoloph, maxilla	19. 5	26
M^1, transverse maxilla	23	27. 2
M^2, transverse maxilla (pr.-pas.)	25. 5	[a]36
Length of left zygoma (anterior border malar to posterior border postglenoid process)	[a]129	[a]137

[a] Estimated.

The measurements given show that in its dentition *P. fontinalis* of Bridger A was much larger than *E. borealis* of the Wind River formation. The relatively small size of the zygoma in the type of *P. fontinalis* is consistent with the fact that the animal was very young, its milk dentition being still functional.

A comparison of *E. borealis* (summit of known lower Eocene) with *P. fontinalis* (lower middle Eocene or lower Bridger) indicates a long period of titanothere evolution between these two species. *P. fontinalis*, although the oldest known Bridger titanothere, differs in two points—the superior dental series is 25 per cent larger than that of *E. borealis;* the cranium is elongate and the face abbreviate.

Eotitanops gregoryi Osborn

Plate LIV; text figures 25, 27, 33, 142, 143, 231, 245–247, 253, 483, 492, 493, 503, 661, 726, 727, 742

[For original description and type references see p. 192]

Type locality and geologic horizon.—Alkali Creek, Buck Spring, Wind River Basin, Wyo.; Wind River formation, *Lambdotherium* zone, horizon Wind River B ("Lost Cabin"), 100 feet above heavy "red stratum."

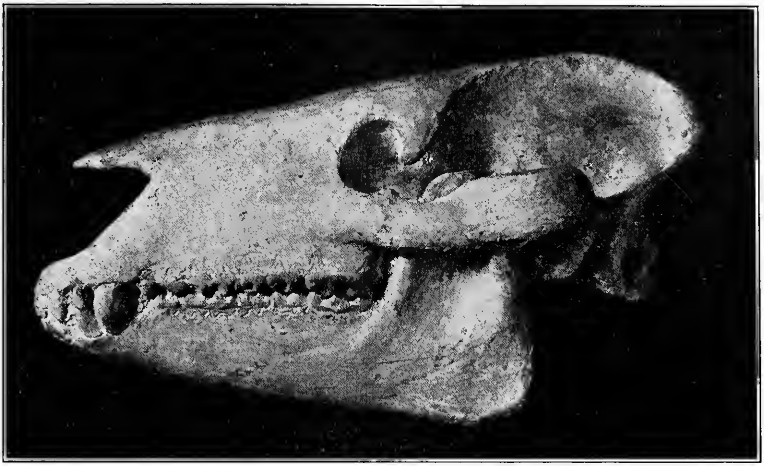

FIGURE 245.—Model of skull of *Eotitanops gregoryi*

Based on type specimen (Am. Mus. 14889) and on *Eotitanops borealis*. One-half natural size.

Specific characters.—Very primitive and of inferior size, p_2–m_3, 78.4 millimeters; m_{1-3}, 49; p_{2-3} with the internal cusps, paraconid and metaconid, consisting of rectigradations in a most rudimentary stage; hypoconulid of m_3 very small; m^3 with a single internal cone, no hypocone.

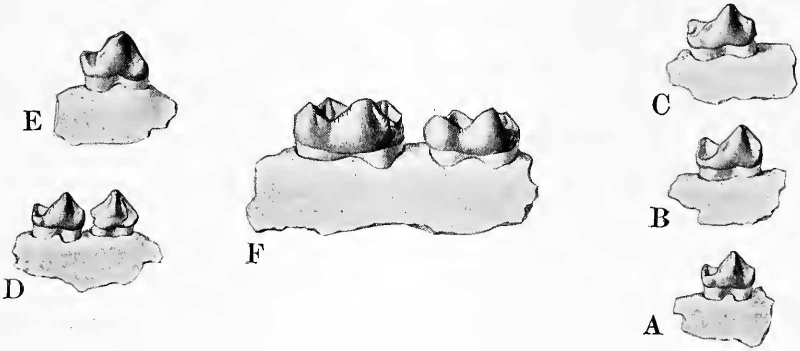

FIGURE 246.—Lower premolars and molars of *Eotitanops*

Natural size. American Museum specimens from the Wind River formation, Wind River Basin. A, B, C, Inner side view of the third left lower premolar: A, *E. gregoryi*, No. 14889 (type), Alkali Creek, Buck Spring, upper level of "Big Red Pocket," 100 feet above heavy red stratum; B, *E. borealis*, No. 14888, Alkali Creek Davis's ranch; C, *E. princeps*, No. 296 (type). D, *E. gregoryi*, No. 14889 (type), left lower premolars (p_2, p_3), inner side view. E, *E. brownianus*, No. 4885 (type), second left lower premolar, inner side view. F, *E. borealis*, No. 14891, west bank of Wind River, 3 miles above canyon (top of banded beds); left lower molars (m_1, m_2), inner side view.

This very sharply defined species is named in honor of Dr. William K. Gregory. Its especial interest lies in the fact that it is the most primitive titanothere known. It represents, however, a persistent primitive stage, because its geologic level, 100 feet above the alkali "red stratum," is higher than that of the typical and relatively progressive *E. borealis*. Its primitive condition is apparent in the comparison of p_3 with the same tooth in *E. borealis* and *E. princeps*. (See fig. 246.)

This third inferior premolar, p_3, is much less progressive than in *E. princeps* or even in *Lambdotherium;* the other premolars are correspondingly primitive, p_2 short, compressed, with a very rudimentary hypoconid, p_3 laterally compressed, hypoconid distinct, paraconid, metaconid, and entoconid extremely rudimentary rectigradations. In the molar teeth, m_{1-3}, the metastylid and entostylid are also in an extremely rudimentary or rectigradational stage. In m_3 the hypoconulid is small, subconic, external in position. (See fig. 235.)

Eotitanops brownianus (Cope)

Text figures 104, 143, 231, 246, 247, 253

[For original description and type references see p. 169]

Type locality and geologic horizon.—Wind River Basin, Wyo.; Wind River formation, *Lambdotherium-Eotitanops-Coryphodon* zone (Wind River B), exact level not recorded.

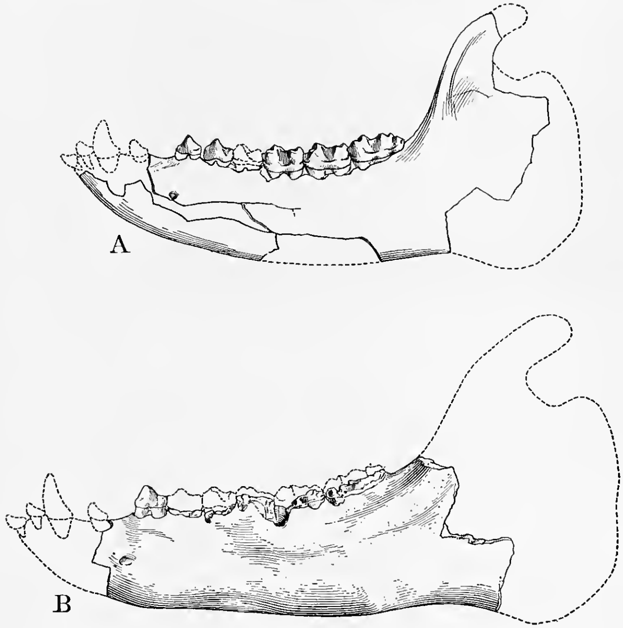

FIGURE 247.—Lower jaws of *Eotitanops gregoryi* and *E. brownianus*

One-half natural size. A, *E. gregoryi*, Am. Mus. 14889 (type), reversed; Alkali Creek, Buck Spring, upper level of "Big Red Pocket"; Wind River formation, upper part (Wind River B, "Lost Cabin"). Contours partly restored from *E. borealis*. B, *E. brownianus*, Am. Mus. 4885 (type), reversed; Wind River Basin. Contours partly restored from *E. borealis* and *E. princeps*.

Specific characters.—Size greater than *E. gregoryi*; p_2–m_3, 90 millimeters; m_{1-3}, 55; fang of p_1 placed in close proximity to the canine; p_2 compressed, hypoconid distinct, elevated, entoconid invisible, paraconid and rudimentary rectigradations placed very low on the crown, metaconid extremely rudimentary if present; metastylid rudimentary.

P_2 (see fig. 246) is in a less advanced stage of evolution than p_3 in *E. gregoryi*.

As shown in the comparative series of the jaws (fig. 231), in the table of measurements (p. 290; see also fig. 483), and in the accompanying figures, the type of this species belonged to an animal in size midway between *E. gregoryi* and *E. borealis*. The ramus of the jaw rather resembles that of *E. borealis* but with a pronounced swelling below m_3; its vertical depth below the anterior face of m_3 is 40 millimeters; the symphysis is decidedly broad and massive.

Eotitanops borealis (Cope)

Cf. *Palaeosyops borealis* Cope

Plate LIV; text figures 10, 28, 29, 102, 143, 219, 229–231, 243, 244, 246, 248–251, 405, 406, 482, 493–495, 497, 498, 501–503, 507, 515, 521–523, 646, 648, 649, 690, 694, 700, 701, 717, 721, 724, 725, 745

[For original description and type references see p. 168]

Type locality and geologic horizon.—Wind River Basin, Wyo.; Wind River formation, *Lambdotherium-Eotitanops-Coryphodon* zone (Wind River B, "Lost Cabin").

Specific characters.—Of larger size; p_2–m_3, 94–98 millimeters; premolar teeth more complicated, as shown in neotype and associated specimens; p_2 with very rudimentary paraconid and metastylid; p^{2-4} with progressively developing tritocones and single internal deuterocones backwardly inclined, crowns subtriangular; m^{1-3} with distinct protoconules.

Materials.—The fragmentary type specimen is the historical *Palaeosyops borealis* (Am. Mus. 4892) of Cope, figured in the "Tertiary Vertebrata," Plate LVIII, A, Figure 3. It is marked No. 16 in the Wind River valley collection of J. L. Wortman, July, 1880. The very fine specimen selected as a neotype (Am. Mus. 14887, figs. 250, 251) consists of the skull and jaws found by Granger in 1909 on Dry Muddy Creek, 100 feet above the alkali "red stratum," and represents a slightly larger and somewhat more progressive mutation.

Incisors of neotype.—The incisors show the characteristic titanothere feature of increase in size from i^1 to i^3, the transverse measurement of the crowns being respectively i^1 6 millimeters, i^2 6, i^3 8 (estimated). The crowns of i^1 and i^2 are bluntly spatulate or chisel-shaped. I^2 has a faint antero-internal cingulum; i^3 is rounded and subcaniniform. The general arrangement of the series is obliquely anteroposterior rather than transverse. The canine is prominent, laterally compressed, the alveolus measuring, transverse, 13 millimeters (estimated); anteroposterior, 17.

Premolars of neotype.—P^1 is placed midway between the canine and p^2, consistently with the relatively elongate preorbital region. The chief features of p^{2-4} are the simple, backwardly directed deuterocones with low crests connecting them with the protocones and tritocones; the tritocones (see figs. 229, 250) increase progressively in p^{1-3}; external cingula faintly indicated in p^3, p^4. The three premolars taken together are subordinate in measurement (36 mm.) to the molars (54 mm.).

Superior molars of neotype.—The superior molars exhibit the characteristic bicrescentic ectoloph with prominent parastyles and mesostyles, and median ridges opposite the paracones and metacones (Pl. LIV, fig. 229); the protoconules are fairly prominent and faintly crescentic in m^{1-3}, forming a vestigial protoloph; the internal cingula festoon but do not surround the inner sides of the crown; m^3 entirely lacks the hypocone; protolophs distinct but sessile are observed on m^{1-3}, also faint rudiments of metalophs on m^1, m^2.

Lower molars of referred specimens.—The valuable series of jaws (Am. Mus. 14887, 14890, 14891, 14888, and 4886) complete our knowledge of the inferior dentition except the incisors, which are unknown (figs. 248–250). The premolar-molar series, p_2–m_3, exhibit progressive gradations of length from 94 to 98 millimeters. (See table on p. 290.) They are thus superior to *E. brownianus* and inferior to *E. princeps* in measurement. The premolars afford the distinctive specific characters or mutations in the progressive stages of the internal cuspules or rectigradations.

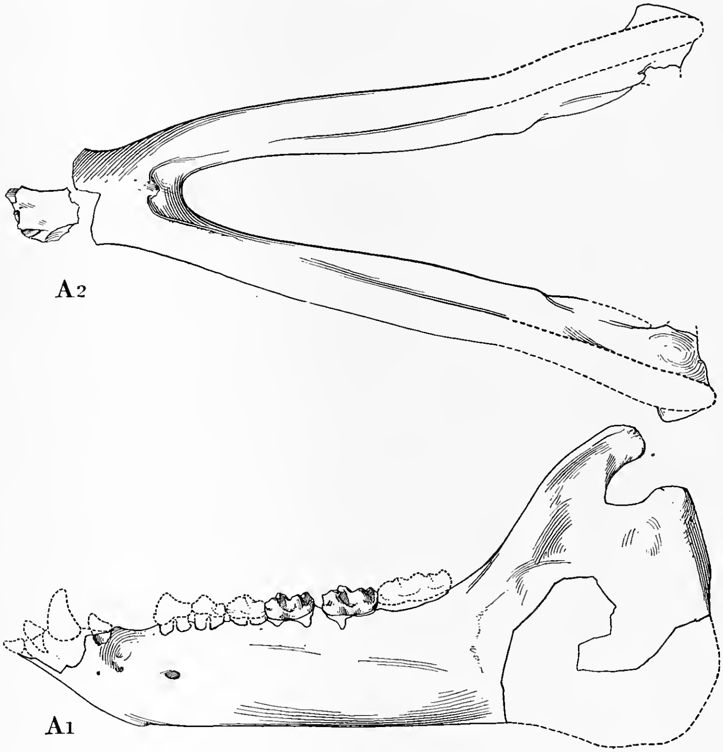

FIGURE 248.—Lower jaw of *Eotitanops borealis*

One-half natural size. Am. Mus. 14891; west bank of Wind River, 3 miles above canyon (top of banded beds); Wind River formation. A_1, Outer side view; A_2, inferior view.

Besides the somewhat arbitrary association of the type and neotype, we also refer to this species the materials listed above, including a number of jaws and portions of the skeleton. (See figs. 231, 246, 248, 249, 494, 501–503, 505, 521, 522, 701.)

Characters of the teeth.—The fourth superior premolar (Am. Mus. 4892; Pl. LIV, H) measures anteroposteriorly 12 millimeters, transversely 14; it exhibits a faint external, distinct anterior and posterior, but no internal cingula, conical deuterocone, small protoconule and larger convex protocone, a somewhat smaller and more plane tritocone and small metaconule ridge. The superior molars exhibit faint external, more prominent anterior and posterior, and incomplete internal cingula; the ectoloph consists of sharply defined parastyle, paracones and metacones with median external ridges, and a prominent mesostyle; the most distinctive feature of the inner half of the crown in m^1 is the sublophoid character of the protolophs and hypolophs, which unite respectively with the distinct protoconule and a much less distinct metaconule to form a low or sessile crest. This rudimentary or vestigial lophoid character is even less evident in the middle Eocene species of titanotheres. M^1 measures 18 by 17 millimeters (ap. by tr.); it is a nearly quadrate tooth, in wide contrast to the transversely expanded tooth of *L. popoagicum.* In m^2 the less worn paracone measures 7 millimeters in height; the ectoloph is thus somewhat elevated in these molars, but its crescents are not strongly concave and incurved as in the Bridger titanotheres; the protoconule is distinct, the metaconule is faint. In m^3 similar characters are observed on the anterior half of the crown; the posterior half is broken away.

FIGURE 249.—Lower teeth of *Eotitanops borealis*

Natural size. A, Crown view of left lower premolars and molars (p_2–m_3); Am. Mus. 14888; Alkali Creek, Davis's ranch, Wind River. B, Crown view of molars (m_1–m_3); Am. Mus. 14891; west bank of Wind River, 3 miles above canyon (top of banded beds). C, Crown view of premolars (p_2–p_4); Am. Mus. 4886; Wind River valley, Wind River formation.

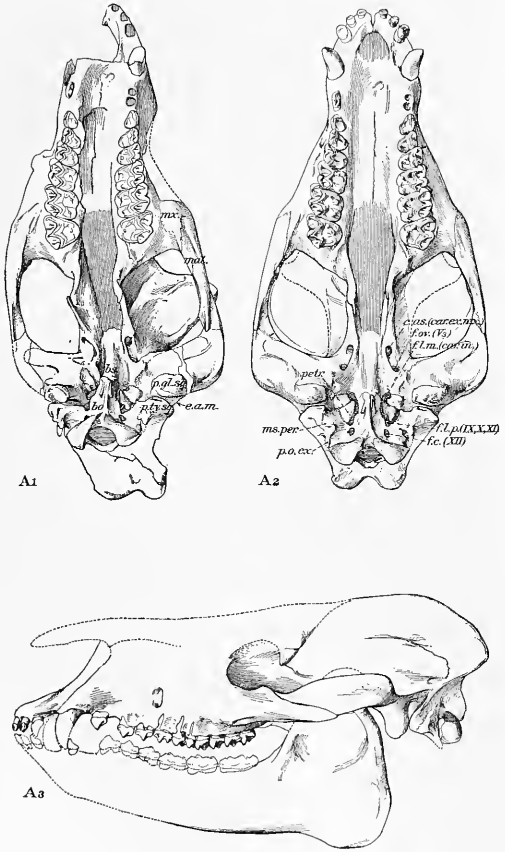

FIGURE 250.—Skull of *Eotitanops borealis*

One-fourth natural size. Am. Mus. 14887, Dry Muddy Creek 12 miles above mouth; Wind River formation. A_1, Palatal view of crushed specimen; A_2, A_3, reconstruction of the palatal and side views of the same skull made by L. M. Sterling under the direction of W. K. Gregory.

The lower molars exhibit low brachyodont crowns, the crescentic external cusps alternating with the subconic internal cusps; extremely rudimentary hypoconulids, metastylids, and vestigial paraconids are observed; external cingula rudimentary, internal cingula entirely wanting, as in all titanotheres; hypoconulid of m_3 central, small, sublophoid.

Skull.—The discovery of the skull of *E. borealis* (Am. Mus. 14887, neotype) was an important event in the work of determining the morphology of the titanotheres because it connected these mammals closely with other early Eocene perissodactyls and separated them from the middle Eocene forms. The chief feature of the skull is that the proopic or facial region is longer than the opisthopic or cranial region, whereas in all the middle Eocene titanothere skulls yet known the face is shorter than the cranium and becoming progressively shorter throughout Eocene and lower Oligocene time. The skull is also relatively long and narrow, and the true molar series is relatively short as compared with the total length of the skull. These characters are well shown in the reconstruction of the skull (figs. 250, 251) and in the model of the head (figs. 646, 648, 649); they are expressed in the following indices, which are estimates only, because the skull is considerably crushed:

Cephalic index 50 (width across zygomata ÷ basal length = 160 millimeters ÷ 313 [estimated]).
Faciocephalic index 56 (length of face ÷ basal length = 185 ÷ 313).
Molar index 17 (length m^1–m^3 ÷ basal length of skull = 54 ÷ 313).

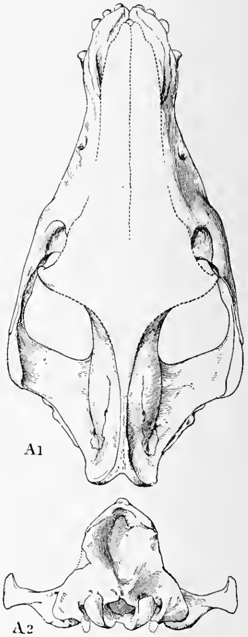

FIGURE 251.—Skull of *Eotitanops borealis*

A_1, Top view; A_2, occipital view. One-fourth natural size. Am. Mus. 14887, Dry Muddy Creek 12 miles above mouth; Wind River formation. Reconstruction made by L. M. Sterling under the direction of W. K. Gregory.

These fundamental proportions give the skull of *Eotitanops* (fig. 250) a striking resemblance to that of other lower Eocene perissodactyls. The type is technically known as proopic dolichocephaly.

Attention may be called to the following details: (1) Premaxillaries slender, symphyseal union very slight, indicating feeble use of superior incisors, premaxillaries joining nasals superiorly, a primitive feature; (2) infraorbital foramen placed above p^3–p^4, widely separate from orbit (closer to orbits in Eocene forms); (3) malars gently rounded, and zygomata moderately projecting; (4) superior profile believed to be plane or gently convex, slightly convex above the orbits; (5) greatest width of skull opposite glenoid fossae; (6) temporal fossae deep, brain case small, surmounted by high, thin parietal crest; (7) occipital crest overhanging condyle superiorly, deeply indented in median line; (8) postglenoid and post-tympanic open below auditory meatus; (9) small exposure of the mastoid between the post-tympanic and paroccipital process; (10) in occipital view (fig. 251) the parietal crest is narrow and flaring superiorly; (11) in palatal view basioccipital and basisphenoid keeled or compressed; (12) typical perissodactyl foramina separate—namely, condylar, lacerum medium and posterius, ovale, and alisphenoid; (13) posterior nares deeply inclosed by pterygoids and pterygoid wings of alisphenoids; (14) posterior borders of palatines not preserved; (15) palate relatively elongate, narrow and arched from side to side; (16) postglenoid process narrow, internal in position; (17) occipital condyles sharply convex, prominent, separated in median line.

Measurements of Eotitanops borealis and E. princeps, in millimeters

	E. borealis, Am. Mus. 14887 (neotype)	E. princeps, Am. Mus. 296 (type)
Basilar length, premaxillaries to condyles (estimated)	313	
Zygomatic or transverse width (estimated)	162	
Width across occipital condyles	52	
Cranial length, postorbital process to occipital condyles	128	
Facial length, postorbital process to maxillary symphysis	185	
Length of lower jaw, symphysis to condyles (estimated)	245	250
Height of jaw, condyle to bottom of angle	97	99
Lower jaw, depth behind m_3	48	50

The jaws are well displayed in the neotype (Am. Mus. 14887) and in the referred specimens, especially in the well-preserved jaw shown in Figure 248 (Am. Mus. 14891).

The chief characters are the following: Ramus elongate, gently convex in vertical section, expanding toward symphysis; lower border suddenly compressed and descending below angle, thin posterior border; delicately retroverted coronoid, ramus slowly ascending behind m_3; symphysis moderately elongate, gently convex, incisive alveoli, indicating progressive increase of size from i_1 to i_3 and semiprocumbent position of the incisors.

Eotitanops princeps Osborn

Plates XXVI, LIV; text figures 27, 33, 143, 144, 231, 246, 252, 407, 408, 483, 484, 490, 492–494, 496, 498–500, 512, 661, 686, 692, 700, 704, 709, 724

[For original description and type references see p. 193. For skeletal characters see p. 590]

Type locality and geologic horizon.—Wind River Basin, Wyo.; Wind River formation, *Lambdotherium-Eotitanops-Coryphodon* zone (Wind River B, "Lost Cabin").

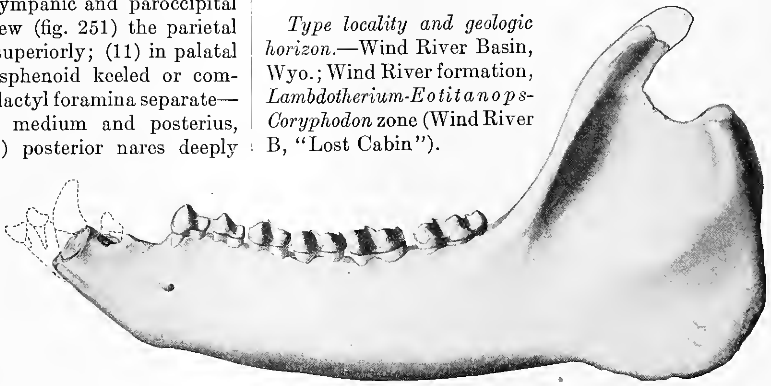

FIGURE 252.—Lower jaw of *Eotitanops princeps*

One-half natural size. Am. Mus. 296 (type), reversed. Wind River Basin; Wind River formation.

Specific characters.—Of still larger size; p_2–m_3, 105 millimeters (estimated). Inferior premolar teeth somewhat more complicated, as shown in the type specimen; p_2 with elevated, distinct, but very rudimentary paraconid and metastylid, entoconid very rudimentary if present, talonid narrow; p_3, paraconid quite distinct, elevated, metastylid small, distinct, entoconid rudimentary, talonid broad; p_4 submolariform, talonid broad, entoconid shelf distinct. Hypoconulid of m_3 rounded, more robust. Ramus larger and more robust.

The more advanced development of the premolar rectigradations, the increased size of the teeth and of the jaw, the larger size of the hind feet in the referred specimen (Am. Mus. 4902) combine to distinguish this specimen as a mutation or subspecific stage between *E. borealis* and *E. major*.

Lower jaw of type.—The well-preserved jaw (fig. 252) of the type specimen (Am. Mus. 296) measures 253 millimeters from the back of the condyle to the symphysis, 99 from the condyle to the bottom of the angle, and 53 vertical depth of the ramus just behind m_3. Its distinguishing features are (1) the elevation of the condyle above the grinders; (2) the rather slender, recurved coronoid with sharply angulated and flattened anterior border, which reminds us of the coronoid of the middle Eocene *Mesatirhinus* and *Dolichorhinus* rather than of that of *Palaeosyops;* (3) the well-defined superior fossa between the angle and the coronoid; (4) the depressed or delicate incurved posterior border of the angle; (5) the elongate (70 mm., estimated) symphysis laterally compressed behind the canines; (6) the slope of the anterior border of the coronoid directly into the fang of m_3; (7) the moderately thick rami (18 mm.). The lower profile or contour of the jaw is convex below the molars, concave below the coronoid, extending backward into the angle.

Inferior teeth of E. princeps (*type; Pl. LIV*).—There were apparently three inferior incisors, the crowns of which are not preserved. The alveoli of the inferior canines are slightly compressed laterally; the estimated measurements are 15 millimeters (anteroposterior) by 13 (transverse). The crown of p_1 is not preserved; its fang is single; the fang is separated from that of the canine by a very narrow diastema (3 mm.); behind it is a continuation of the diastema, 16 millimeters in width. This diastema points to a somewhat elongate character of skull and jaw, since the total length between the canine and p_2 is 31 millimeters. P_2, measuring 13 by 6 millimeters, is an elongate, laterally compressed, bifanged tooth with an elevated paraconid and depressed metastylid or posterior cusp, noncingulate and with the faintest indication of valleys on the inner surface. P_3, measuring 12 by 7 millimeters, is slightly more progressive, with its metaconid externally placed and a more clearly indicated posterior valley. P_4, measuring 13 by 8 millimeters, exhibits a broader talonid and is thus submolariform. The molars are perfectly preserved, aggregating 65 millimeters in length, 14 in maximum width of crown. The individual total measurements (ap. by tr.) are as follows: M_1, 17 by 12 millimeters; m_2, 21 by 13; m_3, 26 by 14.

This progressive increase posteriorly accords with a similar increase of the upper molars posteriorly, as observed also in *Lambdotherium.* The inferior molars exhibit faint external and no internal cingula; rather low but well-defined crescents; a progressive increase in size; paraconids partly defined on m_3. The most distinctive primitive feature in m_3 is the small size, subconic form, and mesial position of the hypoconulid as compared with its backward extension and crescentic form in some of the middle Eocene types.

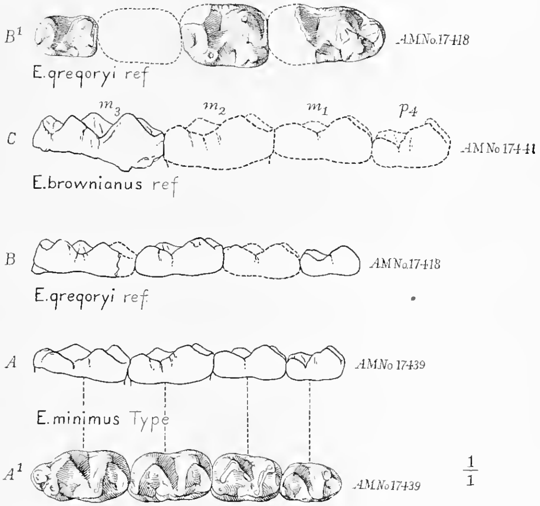

FIGURE 253.—Lower grinding teeth of three species of *Eotitanops* from the upper Huerfano formation (Huerfano B)

Natural size. After Osborn, 1919. A, A^1, *E. minimus* (type), lower level of the upper horizon of the Huerfano formation; B, B^1, *E. gregoryi* (referred specimen), from the upper Huerfano; C, *E. brownianus* (referred specimen), from near the base of the lower Huerfano.

Eotitanops major Osborn

Text figures 145, 483, 506

[For original description and type references see p. 193. For skeletal characters see p. 597.]

Type locality and geologic horizon.—Alkali Creek, Wind River Basin, Wyo.; Wind River formation, *Lambdotherium-Eotitanops-Coryphodon* zone (Wind River B, "Lost Cabin").

Specific characters.—The type and only known specimen (Am. Mus. 14894) consists of a left median metatarsal associated with the distal end of a tibia. It is distinguished from *E. princeps* by its notably larger size (length of Mts III, 104 mm., greatest width, 16). The skull and dentition are not known.

Eotitanops minimus Osborn

Text figures 155, 253

[For original description and type references see p. 199.]

Type locality and geologic horizon.—Huerfano Park, Colo.; Huerfano formation, *Eometarhinus-Palaeosyops fontinalis* zone (Huerfano B; lower level).

Specific characters.—As this is the smallest true titanothere known, Osborn (1919.494, p. 564) assigned to the type lower molar teeth p_4–m_3 (Am. Mus. 17439) the specific name *minimus.* The measurement of p_4–m_3 (53 mm.) is much less than that (58 mm.) of the corresponding teeth in *E. gregoryi*, yet the other characters are so similar to those of *E. gregoryi* as to suggest that this is a related form. Figure 253 exhibits the form and size of three species, *minimus*, *gregoryi*, and *brownianus.* A large number of measurements of Eocene titanotheres show that no single species exhibits so great a range in size.

The discovery of this dwarf titanothere, together with the presence of titanotheres of the same size as *E. gregoryi* and *E. brownianus* in Huerfano B and Wind River B, reveals the existence of what is probably a distinct phylum of diminutive titanotheres separable from the Eotitanopinae. We must, however, await the discovery of the skeletons before this supposition can be confirmed.

SECTION 4. THE MIDDLE AND UPPER EOCENE TITANOTHERES

PHYLA DISTINGUISHED

Some of the middle Eocene titanotheres represented in the lower Bridger beds may have been evolved from forms related to the Eotitanopinae of the Wind River formation. A geologic interval covering a long period (including Huerfano B = Bridger A) separates the titanotheres of the Wind River B from those of Bridger B, and during this period there was a marked transformation in the proportions of the head, for in the titanotheres of Wind River B the face is longer than the cranium (dolichopic), whereas in those of Bridger B and succeeding subdivisions the cranium is longer than the face (brachyopic).

In the titanotheres now to be described this change in faciocranial proportions probably occurred during the deposition of Bridger A and Huerfano B. In the 10 or 12 genera of titanotheres of the middle and upper Eocene the cranium is longer than the face. These animals fall broadly into two large groups, which are more or less theoretically subdivided (1917) into two groups and into six chief phyla or lines of descent as shown in the accompanying table.

Characteristic features of groups of titanotheres

[Compare fig. 219, p. 265]

Palaeosyopine group: Palaeosyops, Limnohyops, Telmatherium, Sthenodectes	Manteoceras-Dolichorhinus group: Manteoceras, Mesatirhinus, Dolichorhinus, Metarhinus, Rhadinorhinus, Diplacodon
Skull brachycephalic to mesaticephalic.	Skull mesaticephalic to dolichocephalic.
Horn rudiments retarded in evolution.	Horn rudiments precocious in evolution.
Occiput rounded or high.	Occiput primitively low and broad.
Zygomata deepened vertically.	Zygomata shallow vertically.
Canines more pointed, erect.	Canines more obtuse, recurved.
Third superior incisor caniniform.	Third superior incisor incisiform.
1. Subfamily Palaeosyopinae (Limnohyops, Palaeosyops), extremely brachycephalic.	3. Subfamily Manteoceratinae = Brontopinae (Manteoceras, Protitanotherium, Brontops), progressively brachycephalic.
2. Subfamily Telmatheriinae (Telmatherium), mesaticephalic to brachycephalic.	4. Subfamily Dolichorhininae (Mesatirhinus, Metarhinus, Dolichorhinus), mesaticephalic to dolichocephalic, facial region downturned.
	?5. Subfamily Megaceropinae = ?Rhadinorhininae (?Rhadinorhinus, Megacerops), mesaticephalic, facial region upturned.
	6. Subfamily Brontotheriinae = ?Diplacodontinae (Diplacodon, Brontotherium), horns precociously developed.

The extreme forms of the two groups—namely, *Palaeosyops* and *Dolichorhinus*—also contrast widely in the detailed characters of the skull, as shown in longitudinal and cross sections in Figure 254.

The subfamilies 1–6, according to the Osborn system (see Chap. I), correspond with the phyla, or vertical lines of descent, which have been established among the Eocene titanotheres, also between the Eocene and Oligocene titanotheres. Thus it is now known that *Manteoceras* and *Protitanotherium* are related to *Brontops* of the Oligocene. *Diplacodon* of the upper Eocene is of uncertain affinities with the lower Oligocene genera. It is possible but by no means demonstrated that *Rhadinorhinus* is related to the Oligocene brontotheres and *Megacerops*, as suggested by Gregory.

SPECIES OF PALAEOSYOPINAE AND DOLICHORHININAE FROM THE UPPER HUERFANO (TROGOSUS ZONE)

The discovery of two very distinct phyla of true titanotheres in the lower Eocene confirms the theoretic separation of the titanotheres into subfamilies as occurring in lower Eocene time. In the Huerfano formation we have evidence of two subfamilies, as follows:

Palaeosyopinae (perhaps derived from the Eotitanopinae)	Dolichorhininae (*Manteoceras-Metarhinus-Mesatirhinus-Dolichorhinus* group)
Hornless.	Osseous horn rudiments at nasofrontal junction.
Slender nasals.	Nasals very stout, laterally decurved.
Subbrachycephalic.	Mesaticephalic.
More robust proportions.	Smaller proportions.

The first subfamily is represented by numerous specimens of *Palaeosyops fontinalis* Cope; the second group is represented by the single type specimen of the new genus *Eometarhinus* (*E. huerfanensis*).

SYSTEMATIC DESCRIPTIONS OF THE MIDDLE AND UPPER EOCENE TITANOTHERES

THE PALAEOSYOPINE GROUP (PALAEOSYOPS, LIMNOHYOPS, TELMATHERIUM, STHENODECTES)

DISTINCTIVE FEATURES AND GEOLOGIC HORIZONS

Osborn finally included the genus *Telmatherium* within the palaeosyopine group, although there are some grounds for placing it closer to the Manteoceratinae. The telmatheres appear to have had a long and independent evolution of their own (see fig. 697) and thus constitute the distinct subfamily Telmatheriinae.

The resemblances and contrasts between the three chief genera included in these two subfamilies are indicated in the following manner, on the principles of proportional and numerical evolution explained on pages 251–262.

Proportional and numerical characters of titanotheres of the palaeosyopine group

Palaeosyops	Limnohyops	Telmatherium
Skull and skeleton very robust; skull decidedly broad and massive; feet short.	Skull and skeleton more slender; skull broad, brachycephalic, less massive; feet narrow.	Skull and skeleton rather slender; skull decidedly elongate, dolichocephalic.
Fore feet short, more paraxonic, the fifth digit larger.	Fore feet short, more mesaxonic, with the fifth digit reduced.	Fore feet long, more mesaxonic, the fifth digit elongate.
Skull rounded, occiput stout, sagittal crest of medium length, forehead protuberant or convex.	A more elevated occiput, higher and thinner sagittal crest; forehead concave, without protuberance.	Occiput very high; sagittal crest elongate; forehead plane, no protuberance.
Jaws robust, chin prominent, angulate; mandibular rami massive below grinding teeth; coronoid at base very broad and concave anteriorly.	Jaws somewhat more slender, chin sloping, rami less massive below grinders, anterior face of coronoid less broadened.	Jaws more slender; chin deep; symphysis elongate.
Premaxillary symphysis short and rounded.	Premaxillary symphysis rounded.	Premaxillary symphysis elongate.
Maxillary splint on side of malars; malar section rounded.	Maxillary splint extending from side to beneath malars; malar section depressed.	Maxillary splint elongate, extending beneath malars; malar section rectangular.
Incisors more transverse; canines sublanceolate to round; premolars compressed anteroposteriorly; molars broad or quadrate, with strong, rounded parastyles.	Incisor series obliquely placed; canines slightly more compressed and ridged; molars with ridged parastyles and ridged conules.	Incisor series more parallel; canines high, sublanceolate; premolars elongate; molars narrow, more sharply crested or hypsodont, with feeble parastyles or none.
Conules on superior molars more or less persistent, rounded.	Conules on superior molars persistent, ridged or lophoid.	Conules on superior molars disappearing early.
Grinders persistently brachyodont.	Grinders persistently brachyodont.	Grinders progressively hypsodont.
Last superior molar usually without hypocone or second postero-internal cusp; crown subtriangular, rounded.	Last superior molar usually with a distinct hypocone; crown more quadrate.	Last superior molar without hypocone; crown quadrate.
Ectolophs of superior premolars in some specimens resembling those of molars (that is, with mesostyles).		

SUBFAMILY PALAEOSYOPINAE (STEINMANN AND DÖDERLEIN)

The Palaeosyopinae consist of the *Limnohyops* and *Palaeosyops* generic phyla. They were abundant chiefly in lower and middle Bridger time, beginning to decline in upper Bridger time. *Limnohyops* is subbrachycephalic to brachycephalic, mediportal; *Palaeosyops* is brachycephalic to hyperbrachycephalic, graviportal. They were larger than tapirs, proportions stout, becoming graviportal; feet of brachypodal type; skull broad, progressively brachycephalic, facial region abbreviate, nasals tapering distally, nasofrontal horns retarded in development; cranial region and zygomata broadening; grinding teeth persistently brachyodont; canines stout, subconical.

They make their appearance at the base of the Bridger or in Bridger A, in the species *Palaeosyops fontinalis*, and the last member known is the species *Palaeosyops copei*, of Bridger D or Washakie A. The Palaeosyopinae thus formed the first titanothere subfamily to appear in the middle Eocene and also the first, so far as known, to disappear geologically.

The subfamily name Palaeosyopinae is taken from the name of the classic genus *Palaeosyops leidyi*, the first Eocene titanothere discovered. These titanotheres are broad-headed, chiefly of lower and middle Bridger age, reaching a climax and beginning to decline in upper Bridger time. The cranial region of the skull is longer than the facial region; the head is short and broad (brachycephalic); the horns are relatively late or retarded in development; the feet are short and broad (*Palaeosyops*), or less broad (*Limnohyops*).

The two phyla, *Palaeosyops* and *Limnohyops*, were contemporaneous, their remains being found in the same deposits.

SEPARATION OF PALAEOSYOPS AND LIMNOHYOPS GENERIC PHYLA

In the middle Eocene of the Bridger region in western Wyoming the animals known as *Palaeosyops* and *Limnohyops* are the earliest to occur geologically—namely, in Bridger A, B, and C. They were browsing animals, with short-crowned teeth and broad heads, which increase in breadth in the successive descendants of the original forms. They exhibit many features in common, yet they seem to represent two distinct contemporaneous phyla. Of these two phyla *Limnohyops* is the more primitive; it is in many features more central or intermediate than the second phylum, consisting of the very massive, broad-headed *Palaeosyops*.

The genus *Palaeosyops* of Leidy was the first known, and the *Limnohyops* of Marsh may be regarded as a subgenus. Although the animals belong to two different lines of descent, the ancestral members of each line (Bridger A and B) are not easily distinguished.

The abundance of remains of *Palaeosyops* is welcomed by the student of evolution because so many intergradations or mutations are found. But this very abundance renders more difficult the definition of species because the sharp lines of specific separation and distinction break down; the forms merge into one another.

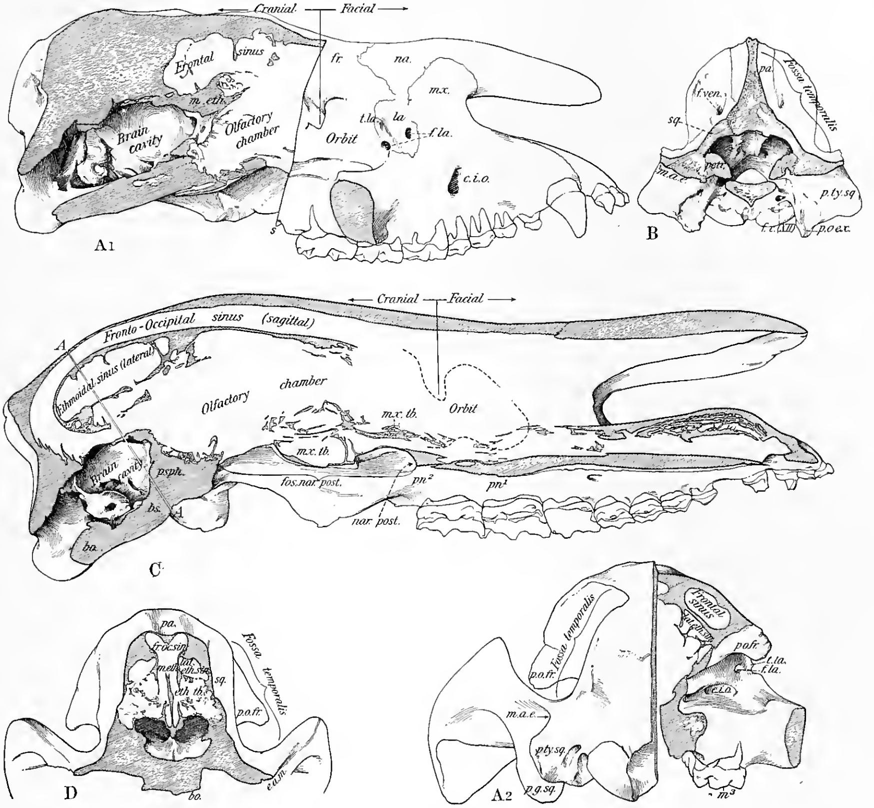

FIGURE 254.—Sections of skull of brachycephalic (A, B) and dolichocephalic (C, D) Eocene titanotheres

One-fourth natural size. A₁, *Palaeosyops leidyi*, Am. Mus. 1544 (type). Median section of cranial region. Note the back part of the olfactory chamber (with remnants of the ethmoturbinals), the cribriform plate, the frontal sinus, and the cellular character of the expanded cranial vertex above the brain chamber. (Section line shown in A₂.) A₂, The same, rear view. The left side shows the widened vertex of the occiput; the right side shows in section the frontal and ethmoidal sinuses. B, *Limnohyops priscus*, Princeton Mus. 10044. Cross section through the basioccipital, periotic, squamosal, and parietal, seen from front. In this primitive form the sagittal crest has not expanded into a flattened cranial vertex, and hence this region is without any large cavities. C, *Dolichorhinus hyognathus*, Am. Mus. 1851. Median section of the whole skull slightly to the right of the median plane, showing the enormous olfactory chamber, the elongate fronto-occipital sinus, and the small brain chamber. The much enlarged maxilloturbinal (mx. tb.) is produced backward and downward, appearing as a prominent swelling in the roof of the narial channel; the primary border of the posterior nares is at pn^1, the secondary at pn^2. D, *Dolichorhinus longiceps?* (*hyognathus?*), Am. Mus. 1852. Cross section through the middle part of the brain chamber (near line *A-A* of figure C) looking forward. Note the fossae for the anterior lobes of the brain, the lateral ethmoid sinus, the mesethmoid septum, the remains of the ethmoturbinal scrolls, and the large fronto-occipital sinus.

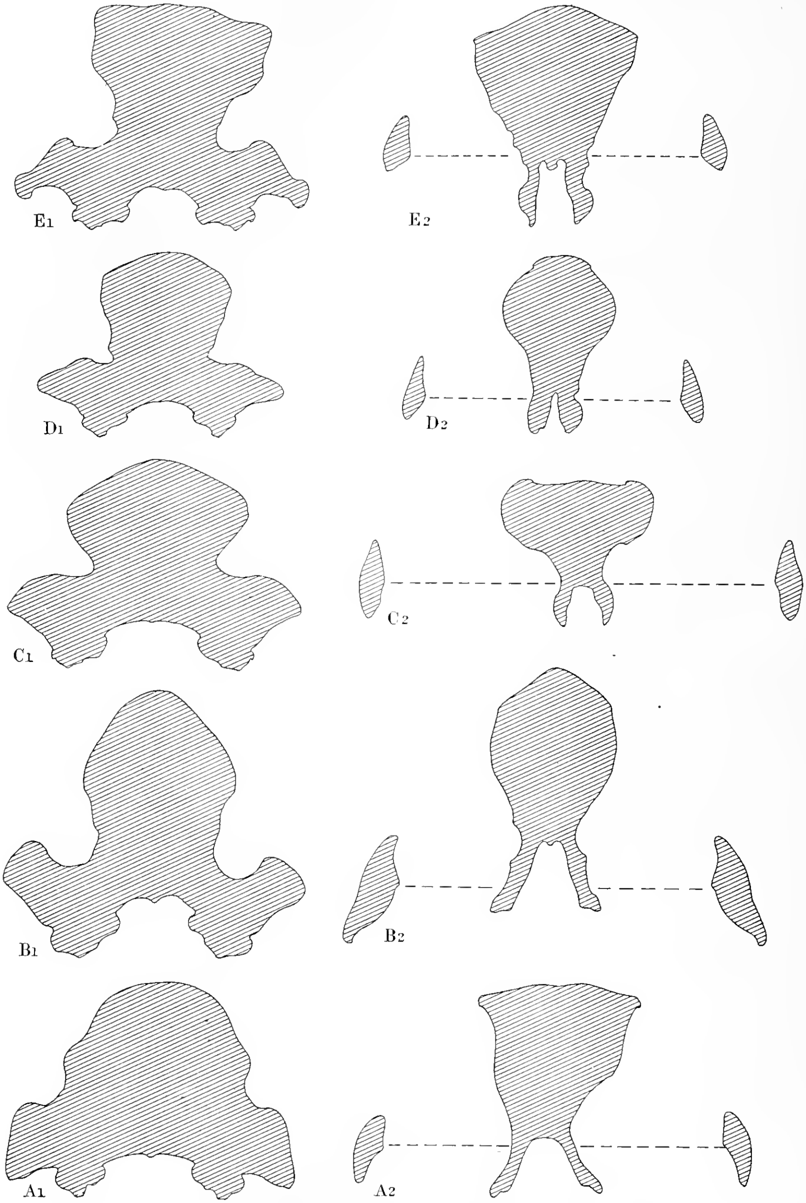

FIGURE 255.—Cross sections of the skull in middle Eocene titanotheres

One-fourth natural size. A_1–E_1, Sections across the face just behind the lacrimal and through the malar and m^2; A_2–E_2, sections across parietals, alisphenoids, and zygomatic process of squamosal. A_1, A_2, *Palaeasyops leidyi*, Am. Mus. 1516; B_1, B_2, *Telmatherium ultimum*, Am. Mus. 2060 (type; crushed laterally); C_1, C_2, *Manteoceras manteoceras*, Am. Mus. 12678; D_1, D_2, *Mesatirhinus petersoni*, formerly Am. Mus. 1556, now in British Museum; E_1, E_2, *Dolichorhinus hyognathus*, Am. Mus. 1851.

Probably the physiographic conditions in this region during the early stages of the Bridger deposition were peculiarly favorable to these animals. Whatever the cause in Bridger B and C their remains are as plentiful as those of other titanotheres are rare. In Bridger D, however, remains of *Palaeosyops* become mingled with those of titanotheres of other kinds, which are equally or even more abundant and include forms that apparently had undergone their antecedent evolution in another part of the mountain region of the continent. (See fig. 257.)

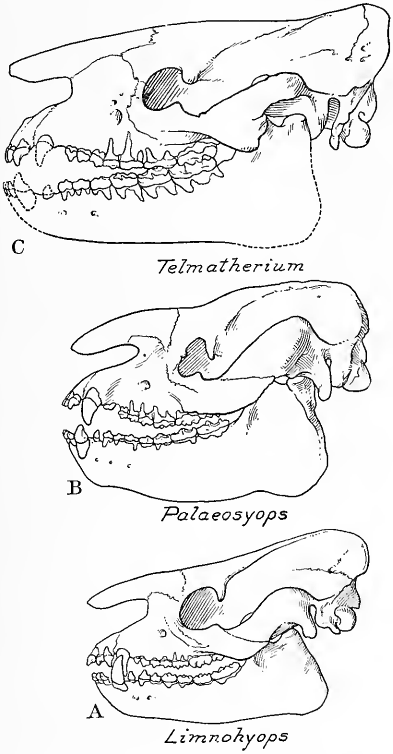

FIGURE 256.—Three skulls typical of the palaeosyopine group

One-eighth natural size. A, *Limnohyops priscus*, Am. Mus. 11687 (type), middle Eocene, lower Bridger; B, *Palaeosyops leidyi*, Am. Mus. 1544 (type), middle Eocene, upper Bridger; C, *Telmatherium ultimum*, Am. Mus. 2060 (type), upper Eocene, Uinta C (true Uinta formation).

COMMON CHARACTERS OF THE PALAEOSYOPS AND LIMNOHYOPS GENERIC PHYLA

The three most distinctive features of *Palaeosyops* and *Limnohyops*, as stated above, are brachyodonty, or persistently short-crowned grinding teeth; brachycephaly, or progressively increasing head width; brachypody, or broad and abbreviated foot structure (less defined in *Limnohyops*).

The members of all the species known in both phyla are thus short-toothed, short-skulled, and more or less short-footed. In the accompanying outline of the parallel geologic distribution of the species belonging to these two phyla in the Bridger formation we observe that in about every 200 feet of sediment there is accu-

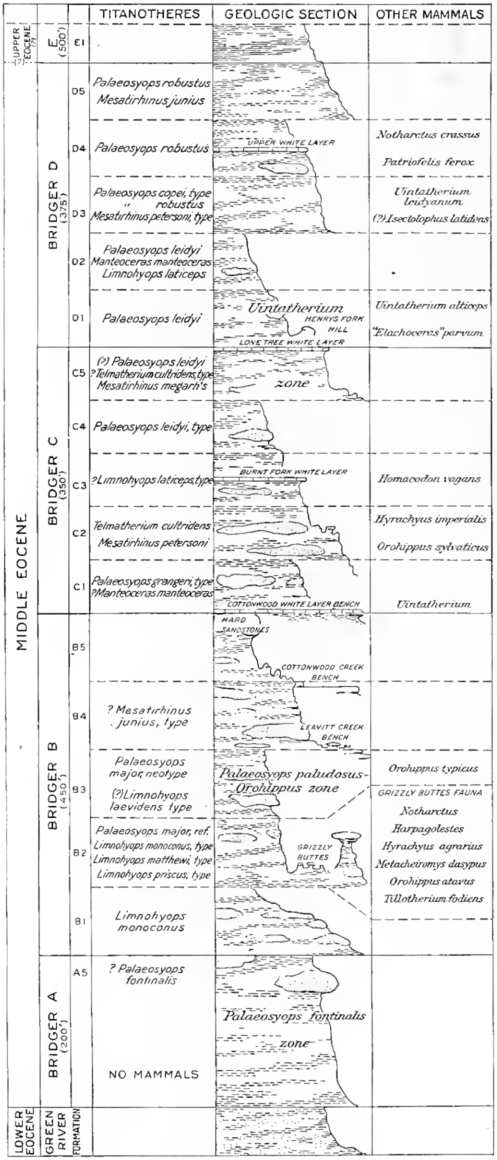

FIGURE 257.—Distribution of the species of *Palaeosyops* and associated fauna in the Bridger formation, Bridger Basin, Wyo.

mulated a change in proportions and in a number of details of cranial and dental structure which we may collectively dignify by the term species, in the neo-Linnaean sense. The transitional or intermediate stages, distinguished by the infinitesimal advance in certain new characters, are mutations in the sense of that term as used by Waagen. The orthogenetic or direct and adaptive origins of single new characters are rectigradations in the sense of that term as used by Osborn. (See p. 812.) The progressive changes in certain characters—for example, in the rectigradations of the premolar teeth and in the rise of the horn rudiments on the frontals—occur nearly contemporaneously in members of the two phyla. In some other characters the progression is dissimilar, or at different rates.

Geologic horizons of Limnohyops and Palaeosyops

Part of formation	Horizon	Limnohyops	Palaeosyops
Upper Bridger	D 3		P. copei.
	D 2	L. laticeps	
	D 1	L. laticeps	
	D		P. robustus.
	C 4	L. laticeps	P. leidyi.
	C 3		P. leidyi.
	C 2		P. leidyi.
	C 1		P. grangeri.
Lower Bridger	B 4		P. major.
	B 3		P. major.
	B 2	L. matthewi L. monoconus. L. priscus L. laevidens	P. major. P. paludosus.
	B 1?–5?		P. longirostris.
	B 1		P. paludosus.
	A?		P. fontinalis.

PROGRESSIVE DISTINCTIONS BETWEEN PALAEOSYOPS AND LIMNOHYOPS

It is extremely difficult—indeed, it may be impossible—to distinguish parts of individuals belonging to *Palaeosyops* from parts of those belonging to *Limnohyops*. Means of recognizing the differences and resemblances have been afforded by the cumulative work of Marsh, Earle, Osborn, and Gregory.

The supposed distinctive generic character (Marsh) of *Limnohyops*, namely, the presence of a hypocone on m^3, is possibly a primitive character, because of its presence in *Lambdotherium*. It prevails but does not appear to be constant in all species of *Limnohyops*. It is typically absent but exceptionally present, by reversion perhaps, in *Palaeosyops*. In the proportions of the skull *Palaeosyops* is more robust and *Limnohyops* is more slender, and this quantitative or proportional contrast prevails throughout all the cranial, dental, and skeletal parts, although it is often difficult to measure or define the finer shades of difference.

When we compare the ancestral members of the two phyla in Bridger B, some of them are difficult to separate. As the successive specific stages of *Limnohyops* are contemporaneous geologically with those of *Palaeosyops* it is well to enumerate the chief known distinctions which gradually develop and become fully apparent only after the two lines of descent have diverged from each other, as observed in the higher geologic levels—for example, in comparing *P. robustus* and *L. laticeps* of Bridger D. These distinctions are as follows:

1. The upper and lower molar teeth of *Palaeosyops* are relatively larger, more rounded, and more robust than those of *Limnohyops*.
2. The vertical striations on the cones of the upper and especially of the lower molars of *Palaeosyops* are more distinctly marked.
3. On the upper molars (m^{1-2}) of *Palaeosyops* the conules are more variable, more rounded, and separate; in *Limnohyops* they are more constant, lophoid, ridged, or conjoined with the protocone and hypocone; this distinction, however, is not invariably reliable.
4. In m^3 of *Limnohyops* the hypocone is typically though not invariably present (*L. laticeps*), and the metaconule is extremely reduced, owing to the large size of the adjacent hypocone. In m^3 of *Palaeosyops* the hypocone is typically absent but sometimes present, as in the type of *P. diaconus*. In m^3 of *Palaeosyops* the metaconule is generally present and in some specimens is so close to the raised posterior cingulum as to appear like a hypocone; thus the m^3 of *Palaeosyops* is generally more triangular, whereas that of *Limnohyops* is more quadrate and sometimes actually bilobed internally.
5. The parastyle in *Palaeosyops* is rounded and obliquely placed across the outer angle of the crown, whereas in *Limnohyops* it is sharp and extends outward as a ridge, analogous to the parastyle of the *Telmatherium* type (Pls. LX, LXIII).
6. The nasals taper toward the extremities and are more pointed in *Palaeosyops*, whereas in *Limnohyops* the sides of the nasals are more parallel and they are more truncate at the extremities.
7. The suborbital bar in the two genera becomes quite different; in *Palaeosyops* the bar is rounded and the overlying maxillary process extends back on its outer side as a broad splint, whereas in *Limnohyops* the bar becomes more depressed and slightly rectangular in section and the maxillary process extends back as a long, slender splint on the lower side; in *Telmatherium* the suborbital bar is distinctly rectangular and the maxillary process extends back as a long, narrow splint beneath the malar projection.
8. In *Limnohyops* the top of the cranium is slightly concave; in *Palaeosyops* there is a strong median convexity near the frontoparietal junction some distance behind the orbits.

9. The sagittal crest of *Palaeosyops* is lower, broader, and passes more rapidly into the temporal ridges, whereas in *Limnohyops* as in *Telmatherium* the crest is higher and thinner and extends well forward before spreading into the temporal ridges.

10. The male jaws of *Palaeosyops* are at once recognized by (*a*) the more prominent, massive chin and, as seen from below, the short, depressed area for the digastric muscle on the posterior symphyseal line, features that contrast with the longer, more sloping chin of *Limnohyops* and its elongate median fossa for the digastric; (*b*) the massive breadth of the *Palaeosyops* rami, as seen from below, in contrast with the somewhat more slender inferior borders of the jaw in *Limnohyops;* (*c*) the extremely distinctive base of the anterior border of the coronoid process which in *Palaeosyops* is very broad and in progressive stages deeply hollowed out in front, whereas in progressive stages of *Limnohyops* it is somewhat narrower, less deeply excavated, and lies more to the outer side of the line of the molar teeth.

Additional means of distinction are set forth in the descriptions of the genera and species.

W. K. Gregory has observed that the above and other differences are in part quantitative; they are differences in the proportion of one and the same character, as in the form of the nasals, of the suborbital bar, and of the sagittal crest. The divergence is far less than that seen in the modern genus *Cervus*, for example. It may be noted also that certain of the numerical differences are variable; for example, the hypocone on m^3. The known forms of *Limnohyops* are rather slender; thus a male jaw of this animal would resemble a female jaw of *Palaeosyops*.

Limnohyops Marsh

Plates LVI, LVII, LX, LXII; text figures 29, 87, 96, 115–117, 219, 254, 256, 258–266, 274, 484, 485, 510–514, 516, 518–523, 525, 527–532, 538, 672, 685, 686, 690, 701, 714, 717, 722, 723, 745, 760

[For original description and type reference see p. 170; for skeletal characters see p. 605]

Generic characters.—Brachycephalic; grinding teeth persistently brachyodont; conules on the molars persistent, usually lophoid; third superior molar subquadrate and usually with distinct hypocone. Proportions of skull and skeleton moderately robust. Manus slender. Five sacral vertebrae (type).

Geographic and geologic distribution.—*Limnohyops* has thus far been found only in the geologic levels B, C, and D of the western or Bridger Basin (see geographic map on p. 8). As compared with *Palaeosyops* the materials representing this genus or subgenus are limited; we can not therefore trace at present the successive stages of its evolution. It is subdivided into five species—*L. laevidens, L. priscus, L. laticeps, L. matthewi, L. monoconus.*

Resemblances to Palaeosyops.—From our present knowledge the geologically early species *L. laevidens* and *L. priscus* are so close to the type of *Palaeosyops* (*P. paludosus*) that they might readily be embraced within one and the same genus. In fact, material at first referred by the present author to *L. priscus* now appears to belong to *P. paludosus*, which is itself so primitive that it may almost be regarded as the ancestor of *Limnohyops*. However, the sum total of the distinctions between these animals—in external form, color, and habits—was probably very considerable, and as we progress into geologically higher stages the cranial and dental differences become more apparent, as summarized below.

Materials.—Besides the admirable type specimen from Bridger C 4 in the Yale Museum, on which Marsh founded the genus and species, American Museum parties have found five specimens of *L. laticeps* in levels Bridger C 4 and D 2. In the lower level of Bridger B 2 occurs the type of *L. laevidens* Cope, and here we have also found two specimens of the somewhat more progressive stage *L. priscus*. At present the species *L. matthewi* and *L. monoconus* are represented only by a single specimen each, and it is noteworthy that these also are of lower Bridger age. Thus our knowledge of *Limnohyops* at present rests on portions of about 16 individuals.

Chief progressive distinctions from Palaeosyops.—(Compare pp. 302, 618, vertebrae; p. 612, limbs and feet.) So far as we know at present *Limnohyops* is distinguished by somewhat more slender proportions. The skull in the larger species is equally broad but less massive; the jaws are decidedly less massive. The long bones of the limbs referred to *L. laticeps* are practically of the same length as those of the contemporary *Palaeosyops leidyi*, but the foot bones of the manus of *Limnohyops* appear to be shorter (figs. 512, 520). *Limnohyops* may be described briefly as a relatively light-limbed, broad-skulled, short-footed type.

As we have already given many of the details by which *Limnohyops* in its advanced stages may be distinguished from *Palaeosyops*, it is only necessary to summarize its chief diagnostic characters.

Cranium: (1) The skull of *Limnohyops* has a concave instead of a convex forehead (fig. 256); (2) it has a high, thin sagittal crest; (3) the nasals are relatively broad anteriorly; (4) the suborbital bridge of the malars is shallow, narrow, and more or less quadrangular in section or broadly depressed, with a rounder outer border, and the flange for masseteric insertion is not extended so far forward as in *Palaeosyops*; (5) the splint of the maxilla extends backward under the side of the malar; (6) only slight prominences indicate the osseous horn areas, and no horn rugosities have been observed; (7) the jaws have more slender rami, the chin is sloping, the digastric fossa is elongate, deep, and sharply defined, the lower border is less thickened below the grinders, the coronoid base is less broad and flaring anteriorly, when seen from the front, and is set on the outer side of the line of the grinders.

Dentition: In the superior teeth we note especially that (1) m^1 is small; (2) the crested metaconules are confluent internally with the hypocone; (3) the parastyle is elongated on the outer side of the ectoloph and somewhat more sharply ridged; (4) the ectolophs of premolars have more sharply defined convex ridges opposite the paraconules and metaconules; (5) the hypoconulid of m_3 is rather sharp and prominent, laterally depressed, and very slightly crescentic.

Measurements of species of Limnohyops, in millimeters

Level in Bridger formation	Species	Basilar length of skull	P^1–m^3	P^2–m^3
C–D	L. laticeps Marsh	^{a} 410	153	139
B 2	L. monoconus Osborn	^{a} 439	156	142
B 1–2	L. priscus Osborn	375	149	133
B 1–2	L. laevidens (Cope)	--------	141	129

^{a} Estimated.

The distinctions in measurement and proportion noted above are based upon our present knowledge and are by no means so full and definite as we should wish.

Comparison of the species.—The known species of *Limnohyops* do not form a progressive phyletic series in the ascending geologic scale, whereas the known species of *Palaeosyops* form a finely progressive phyletic series.

The type of *L.* (*Palaeosyops*) *laevidens* Cope, from Bridger B 1–2, is a relatively small and primitive form, an undoubted *Limnohyops* in skull structure, distinguished by a small p^2 of rounded form. All the teeth in the type are greatly worn.

Considered in ascending geologic order from Bridger B 1 to D the species may be distinguished as follows: The type of *L. priscus* Osborn is recorded as from the same geologic horizon—namely, Bridger B 2—but it is an animal of greater size and has a p^2 of elongate, triangular form.

The large and heavy type of *L. monoconus* Osborn also occurs in Bridger B at Grizzly Buttes. It is named the "single-coned species" in reference to the absence of the hypocone on m^3. Except in this character it is a typical *Limnohyops*.

The type of *L. matthewi* also occurs in Bridger B 2, a surprising fact because of its extremely short and broad skull proportions. It exhibits the extreme of brachycrany.

L. laticeps, the type species of the genus, occurs much higher up—namely, in Bridger C and D. It is less specialized in skull structure than *L. matthewi* and has the generic character of the presence of the hypocone on m^3 very marked.

QUANTITATIVE EVOLUTION OF LIMNOHYOPS

The accompanying table gives the measurements of 29 characters of proportion in 11 specimens, representing 5 species, collected at ascending geologic levels in the Bridger formation.

Evolution of proportions of Limnohyops

[Measurements in millimeters]

	L. laevidens, Am. Mus. 5104 (type); Bridger B	L. priscus		L. matthewi, Am. Mus. 11684 (type); Bridger B 2	L. monoconus		L. laticeps			
		Am. Mus. 11688 (cotype); Bridger B 2	Am. Mus. 11687 (type); Bridger B 2		Am. Mus. 11679 (type); Bridger B 2	Am. Mus. 5102; Bridger B (3–5?)	Yale Mus. 11000 (type)	Am. Mus. 11710; Bridger D 2	Am. Mus. 12201; Bridger C 4	Am. Mus. 12198; Bridger D 2
Skull:										
Condyles to incisive border	--------	--------	^{a} 375	--------	^{a} 439	--------	^{a} 410	--------	--------	--------
Breadth across zygomata	--------	--------	--------	270	^{a} 320	--------	^{a} 310	--------	--------	--------
Tip of occiput to tip of nasals	--------	--------	^{a} 395	--------	--------	--------	452	--------	--------	--------
Height of occiput above for. mag	--------	--------	--------	118	122	--------	118	--------	--------	--------
Total height of occiput	--------	--------	--------	160	--------	--------	--------	--------	--------	--------
Width across postglenoid processes	--------	--------	--------	169	--------	--------	--------	--------	--------	--------
P^1–m^3	141	--------	149	--------	^{a} 156	172	153	--------	--------	--------
P^2–m^3	129	--------	137	--------	142	159	139	--------	--------	--------
P^1–p^4	57	--------	64	--------	--------	--------	64	--------	--------	--------
M^1–m^3	85	--------	87	--------	^{a} 93	103	90	--------	--------	--------
P^4, anteroposterior	15	--------	18	--------	19	20	18	--------	--------	--------
P^4, transverse	21	--------	23	--------	23	26	24	--------	--------	--------
M^1, anteroposterior	23	--------	24	--------	26	27	24	--------	--------	--------
M^1, transverse	27	--------	27	--------	29	33	27	--------	--------	--------
M^3, anteroposterior	31	--------	32	^{a} 30	33	36	33	32	--------	--------
M^3, transverse	34	--------	35	--------	36	40	38	38	--------	--------
Cephalic index	--------	--------	--------	--------	--------	--------	^{a} 75	--------	--------	--------

^{a} Estimated.

Evolution of proportions of Limnohyops—Continued

	L. laevidens, Am. Mus. 5104 (type); Bridger B	L. priscus		L. matthewi, Am. Mus. 11684 (type); Bridger B 2	L. monoconus		L. laticeps			
		Am. Mus. 11688 (cotype); Bridger B 2	Am. Mus. 11687 (type); Bridger B 2		Am. Mus. 11679 (type); Bridger B 2	Am. Mus. 5102; Bridger B (3-5?)	Yale Mus. 11000 (type)	Am. Mus. 11710; Bridger B 2	Am. Mus. 12201; Bridger C 4	Am. Mus 12198; Bridger D 2
Lower jaw:										
Condyle to symphysis	--------	[a] 278	--------	--------	--------	--------	--------	--------	368	357
Length of symphysis	--------	[a] 75	--------	--------	--------	--------	--------	--------	93	[a] 95
Depth of ramus behind m_3	--------	71	--------	--------	--------	--------	--------	--------	93	94
Condyle to angle	--------	123	--------	--------	--------	--------	--------	--------	[a] 175	[a] 153
Lower teeth:										
P_1–m_3	--------	160	--------	--------	--------	--------	--------	--------	191	196
P_2–m_3	--------	146	--------	--------	--------	--------	--------	--------	172	173
M_1–m_3	--------	91	--------	--------	--------	--------	--------	--------	111	116
P_4, anteroposterior	--------	19	--------	--------	--------	--------	--------	--------	22	20
P_4, transverse	--------	13	--------	--------	--------	--------	--------	--------	14	14
M_1, anteroposterior	--------	24	--------	--------	--------	--------	--------	--------	27	28
M_1, transverse	--------	16	--------	--------	--------	--------	--------	--------	17	19
M_3, anteroposterior	--------	41	--------	--------	--------	--------	--------	--------	48	52
M_3, transverse	--------	20	--------	--------	--------	--------	--------	--------	24	25

[a] Estimated.

The foregoing table brings out the following facts:

1. The cranial increases in length and width are not accompanied by proportional dental increases.
2. Relatively large-skulled and extremely brachycephalic animals (*L. monoconus*) occur in the lower Bridger levels.
3. There is no evidence of progressive monophyletic change such as we see in *Palaeosyops*. (See p. 313.)

Limnohyops laevidens (Cope)

Plate LVII; text figures 96, 258, 259

[For original description and type references see p. 163]

Type locality and geologic horizon.—The type specimen represents the smallest, most primitive, and geologically earliest *Limnohyops* at present known. It is somewhat doubtfully recorded from Bridger B 2(?), as represented in the deposits of Cottonwood Creek, Bridger Basin, Wyo. If from this level, it is slightly more recent than the geologically early and most primitive discovered stage of *Palaesoyops*, known as *P. paludosus*, referred specimens of which have been found in Bridger B 1.

Specific characters.—Inferior in all dimensions to type of *L. laticeps;* p^1–m^3, 141 millimeters; p^2–m^3, 129; p^1–p^4, 57; p^2 rounded or transversely oval, with tritocone rudimentary or absent. A large hypocone on m^3.

Materials.—The type specimen of *L. laevidens* (Am. Mus. 5104; see revision of the nomenclature, Chap. III) is a part of an aged skull containing a well-worn dental series, from which it is difficult to determine positively the characters of this animal. The specific name *laevidens* (from *laevis*, *dens* = imperfect tooth) was assigned to this specimen by Cope in recognition of the supposed absence of the tritocone on p^2. It is probable that in the unworn condition this cusp was present but very rudimentary.

Cope's type of Palaeosyops laevidens

Teeth.—The teeth of the type of *P. laevidens* (Am. Mus. 5104), belonging to an aged animal, are especially interesting because they exhibit the influences of age in rounding off the angles, wearing away the cusps, and smoothing down the cingula. Professor Cope was probably misled when he described this type as lacking a tritocone on p^2; we now recognize that the

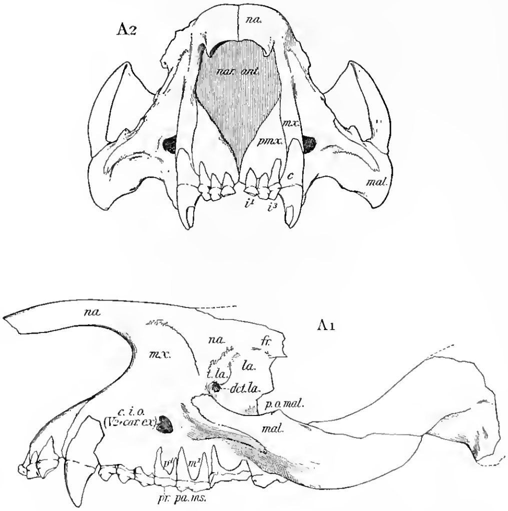

FIGURE 258.—Anterior part of skull of *Limnohyops laevidens*

One-fourth natural size. Am. Mus. 5104 (type), reversed; Cottonwood Creek, Bridger Basin; level Bridger B 3. A_1, Side view; A_2, front view.

apparent absence of this tritocone may be due to age; it probably has been almost completely worn off.

The superior incisors arch gently forward, the total transverse series when in place measuring 56 millimeters; there is a regular increase from i^1 to i^3; the anterior faces of the crowns are slightly crenulate, and a convex swelling or low ridge surrounds the base; the posterior faces are marked off by lateral ridges and by a posterior cingulum, which is irregularly pitted above; the transverse measurements of the anterior portions of the crown are: i^1 10 millimeters, i^2 11 (ap. 12), i^3 12. A narrow diastema (7 mm.), separates i^3 from the canine.

The canine has a stout fang and a crown laterally compressed at the base, the measurements being, anteroposterior, 21 millimeters; transverse, 18; height, 36 (estimated). The crown is defined by faint anterior and posterior ridges; it is slightly retroverted and inverted.

In the premolar-molar series a very narrow diastema (5 mm.) separates the canine from p^1, a tooth which is continuous with the remaining grinders, the total length of the whole grinding series being exactly 141 millimeters, less than in the type of *L. priscus* (149 mm.). In *Mesatirhinus megarhinus* the premolar-molar series ranges from 140 to 147 millimeters. P^1 is a simple, bifanged cone (ap. 11 mm., tr. 8), with faint anterior and posterior concavities on the inner side. P^2 is an obliquely placed oval, measuring (ap. by tr.) 12 (ectoloph 15) by 15 millimeters, whereas in *Mesatirhinus megarhinus* the anteroposterior diameter greatly exceeds the transverse. As Cope pointed out, this tooth is distinguished specifically by the simple rounded protocone, with a more sessile and internally placed tritocone, and a relatively small deuterocone on its lingual side. P^3, measuring 15 (ectoloph 18) by 19 millimeters, is broader than long and exhibits relatively more prominent tritocones and deuterocones. P^4, 15 (ectoloph 18) by 21 millimeters, is also broader than long, the tritocones and deuterocones are still larger, and the external cingulum begins to be defined, as well as the rudimentary anterior and posterior cingula; very rudimentary cingula are also observed in p^2, p^3, except on the lingual side of the deuterocones, which cusps are absolutely smooth and rounded in all these teeth, presenting in this respect a sharp contrast to the condition in *M. megarhinus*, or even (in less degree) to that in the type of *L. priscus*. The entire length of the premolar series is 58 millimeters, as compared with 64 in a small individual of *M. megarhinus*. The molar series measures 84 millimeters. The imperfectly preserved m^1 (ap. 23 mm., tr. 27) exhibits rudimentary external and antero-internal cingula and a subquadrate crown; in m^2, also badly damaged, we observe evidence of sessile conules and a low anterior cingulum; in the better preserved m^3 (ap. 30 mm., tr. 35), also a subquadrate tooth, there are rudimentary external, anterior, and postero-internal cingula, the last giving rise to a low cingulate hypocone; there is some evidence of small, well-worn protoconules and metaconules; the crown, as in the other molars, is singularly smooth.

Skull.—Although only the anterior portion of this cranium is present (see fig. 258), it affords conclusive evidence of ancestral relationship to *L. laticeps* in the rounded shape of the nasals. Its general or palaeosyopine characters are especially seen in (1) the downward V-shaped extension of the nasals on the sides of the face; (2) the prominent antorbital knob of the lacrimals; (3) the backward extension of the infraorbital portion of the maxillaries beneath the malar arch; (4) the narrow median symphysis between the premaxillaries; (5) the comparatively slight lateral decurvature of the nasals; (6) the extreme upward arching of the zygoma as a whole, the mid-depth being 51 millimeters, and the "depression and angulation" of the malar 19 millimeters behind the orbits.

This cranium not only differs in its smaller size but in a number of other proportional characters from that of *L. laticeps*. The nasals are relatively more elongate, narrower posteriorly, and relatively broader anteriorly—that is, the sides of the nasal in front of the narial notch are more nearly parallel, the narrowest midportion measuring 44 millimeters, the broadest terminal portion measuring also 44. From the anterior border of the orbit to the narial notch the measurement is 61 millimeters. The zygomatic bar immediately below the orbit is more angulate and less rounded than in *P. leidyi*, the inferior face of the malars being more flattened and the sharp masseteric ridge defining the malars inferiorly being less extended fore and aft. In palatal view we observe the transverse extension of the glenoid facets for the condyles of the jaw, the opening of the nares behind m^2, the abbreviation of the palatines, and the relative flatness of the palate.

Limnohyops priscus Osborn

Plates LVI, LX, LXII; text figures 29, 115, 219, 254, 256, 259, 260, 266, 274, 690, 717, 745

[For original description and type references see p. 180]

Type locality and geologic horizon.—Grizzly Buttes, west Bridger Basin, Wyo.; Bridger formation, *Palaeosyops paludosus-Orohippus* zone, level Bridger B 2.

Specific characters.—P^1–m^3, 148 (type) to ?161 millimeters. Second superior premolar obliquely elongate with a very rudimentary tritocone. Large hypocone on m^3.

This is apparently a larger and relatively more advanced animal than *L. laevidens*, but, as the specific designation *priscus* indicates, it is still very primitive.

Materials.—*L. priscus* is represented by the type skull (Am. Mus. 11687; see fig. 259), from the Bridger formation at Grizzly Buttes, level B 2, and by the type or cotype jaw (Am. Mus. 11688), found near the same place. An occiput in the Princeton Museum (No. 10044), also from Cottonwood Creek, which was described and figured by Earle (1892.1, p. 353) as *L. laticeps*, may also be provisionally referred to *L. priscus*.

The generic or *Limnohyops* character is shown in the presence of a hypocone on m^3. Divergence from the type of *L. laevidens* is indicated by the elongate form of p^2 as distinguished from the rounded or transversely oval form which this tooth presents in *L. laevidens*. The progressive stage is indicated by the rudimentary condition of the tritocone on p^2 in the type specimen of *L. priscus*.

The type skull.—The skull of the type specimen (fig. 259) is somewhat larger than that of the American tapir. It is extremely interesting to note that it more closely resembles that of the common ancestral form of the titanotheres than does the skull of the contemporary species *Palaeosyops paludosus*. The skull and m^3 are therefore more primitive than those of *Palaeosyops*. The specimen in hand is much crushed laterally, and the restoration represented in Figure 259 is an approximation to the complete form. The estimated total length from condyles to symphysis is 375 millimeters; from the crest of the occiput to the tip of the nasals 395. The cranium shows the typical *Limnohyops* characters enumerated above—namely, short supraoccipital exposure on top of the skull; moderately high, thin sagittal crest, which diverges into the supratemporal crests about 95 millimeters in front of the occiput; occiput moderately high (proportions not to be exactly ascertained owing to its crushed condition). The nasals measure 143 millimeters (ap.) and taper gradually toward the extremities. In the base of the skull the paroccipital processes are separated by shallow grooves from the post-tympanic processes, and the external auditory meatus is apparently open below.

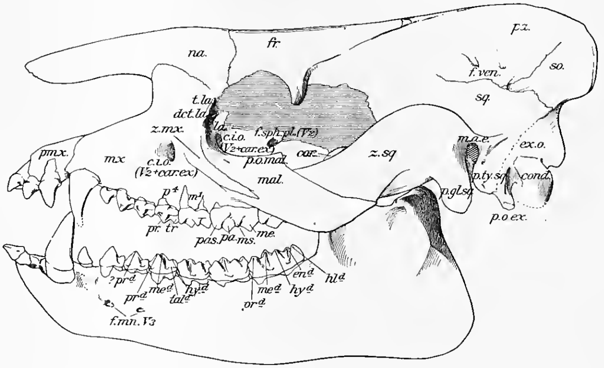

FIGURE 259.—Skull of *Limnohyops priscus*

One-fourth natural size. Skull Am. Mus. 11687 (type); Grizzly Buttes (west), Bridger Basin, Wyo.; Bridger formation, level B 2. Partial reconstruction of crushed skull made by L. M. Sterling under the direction of W. K. Gregory. Lower jaw, Am. Mus. 11688, possibly belonging to same individual. Details of zygoma restored from Am. Mus. 5104 (type of *L. laevidens*); details of occiput from Princeton Mus. 10044, *L. priscus*.

Dentition.—The superior teeth are well represented in the type cranium. The lateral incisor is enlarged as in *Palaeosyops*; the canine is slender, slightly recurved, and followed by a very narrow diastema; the grinding series (Pls. LVI, LX, LXII) is continuous, p^1-m^3 measuring 149 millimeters; pm^2 presents a very large convex protocone and rudimentary tritocone. The inferior teeth are well shown in the cotype jaw (Am. Mus. 11688), found not far from the skull and probably belonging to the same individual. The two incisors preserved are cingulate posteriorly; the canine is rather slender, laterally compressed, and slightly recurved; behind this is a small, simple p$_1$, followed by a narrow diastema; p$_2$ and p$_3$ are comparatively narrow and simple teeth, exhibiting extremely rudimentary paraconids and slightly crescentic hypoconids, and a faint rudiment of the metaconid in p$_3$; p$_4$, on the contrary, is submolariform, exhibiting a well-developed metalophid and a rudimentary hypolophid or posterior crescent which lacks only the entoconid. The three true grinders are simple, with rudiments of vertical striations, with distinct paraconids, and with a sharply pointed subcrescentic hypoconulid on m$_3$. The characters of the jaw are well shown in Figure 259.

Back of the cranium.—The back of a cranium in the Princeton collection (Princeton Mus. 10044) may be provisionally referred to this species. It was found on Cottonwood Creek, Bridger Basin, Wyo., in the Bridger formation, level B 3(?) by Francis Speir, of the Princeton expedition of 1877, and was rightly referred to *Limnohyops* by Earle. The deep (45 mm.) and narrow (9 mm.) sagittal crest is not quite so elongate as that of the Yale Museum type of *L. laticeps*, the supratemporal ridges beginning to diverge rapidly 77 millimeters in front of the crest of the occiput. In addition to the points noted in the type skull above described, we observe in this occiput (1) two large mastoid foramina, (2) two prominences just above the foramen magnum, (3) the broadly extended (48 mm.) post-tympanic processes closely conjoined at the base with the relatively narrow (12 mm.) paroccipital processes; (4) the relatively broad (37 mm.) postglenoid processes. In palatal view the zygomata are seen to have a transverse measurement of 268 millimeters, the post-tympanic and postglenoid processes are slightly (3 mm.) separated; the articular facets for the condyles of the jaw are nearly transverse; a bridge of bone, 19 millimeters in width, separates the foramen ovale and foramen lacerum medium. These features are well illustrated in Figure 260 as compared with similar views of *L. laticeps* and *L. matthewi*.

Limnohyops matthewi Osborn

Text figures 116, 261, 262

[For original description and type references see p. 180]

Type locality and geologic horizon.—Grizzly Buttes (west), Bridger Basin, Wyo.; Bridger formation, *Palaeosyops paludosus-Orohippus* zone, level B 2.

Specific characters.—Type of intermediate size as compared with *L. laevidens* and *L. monoconus.* M^3 small, with large hypocone and quadrate inner half. Occiput very high and narrow. Cranial portion of skull greatly abbreviated, bringing post-tympanic and postglenoid processes into broad union. Temporal openings subcircular as defined by zygomatic arches. (See figs. 261, 262.)

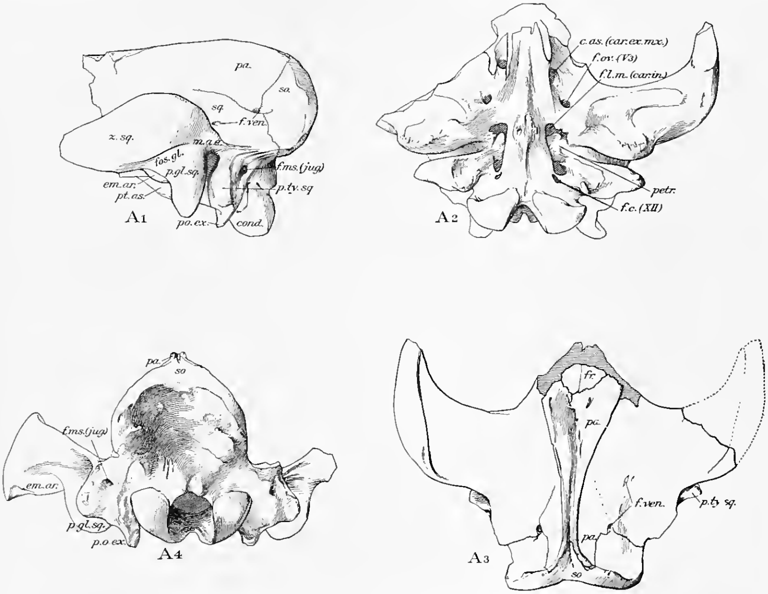

FIGURE 260.—Back part of skull of *Limnohyops priscus*

One-fourth natural size. Princeton Mus. 10044; Cottonwood Creek, Bridger Basin, Wyo.; lower part of Bridger formation. A_1, Side view; A_2, basal view; A_3, top view; A_4, occipital view.

This species is named in honor of Dr. W. D. Matthew, of the American Museum, who has done so much to advance our knowledge of the Bridger fauna and geology.

As compared with the primitive type skulls of *L. laevidens* and *L. priscus,* above described, the cranial region of this animal is surprisingly specialized in its abbreviation, or extreme brachycephaly. This progressive character is difficult to reconcile with the fact that it is geologically recorded in the same low level as that of *L. laevidens.*

Materials.—The type (Am. Mus. 11684), consisting of the posterior portion of a skull which includes the orbits, is the only specimen at present referable to this species. It was found in 1903 by the American Museum expedition.

Distinctive characters.—The brachycranial type of this species is readily distinguished from that of *L. laevidens* by the very specialized condition of the posterior portion of the skull, including the elevated occiput and the firm inclosure of the auditory meatus below. It differs from *L. laticeps* when seen from above in the greater height of the occiput and in the transversely oval form of the temporal openings as defined by the zygomatic arches. It differs from *L. monoconus* in the presence of a large hypocone on m^3 and in the quadrate form of the inner side of this tooth, also in the rounded temporal openings.

In the lateral view of the skull we observe that the zygoma descends rapidly anteriorly and thins out as it passes into the anterior portion of the malar, which constitutes the suborbital bridge; this bridge is depressed in section but exhibits a rounded rather than angulate outer border. This species differs from *Palaeosyops* in that the masseteric insertion ridge is not carried forward any great distance, and that there is a slender splint of the maxillary extending back below the malar bridge. The sagittal crest extends 50 millimeters above the brain case proper; it is even higher and thinner than in *L. laticeps.* As seen from below the temporal openings are transversely oval, the anteroposterior measurement being 82 millimeters, and the transverse measurement from the malars to the alisphenoids 95. The sagittal crest divides these great insertion cavities of the temporal muscles and is thin at the summit, measuring 8 millimeters at the thinnest point; it is also elongate, extending 94 millimeters from the tip of the occiput to the point where it bifurcates into the supratemporal ridges.

The chief feature of the occiput is the foreshortening and compression of its lower portion against the back portion of the squamosals and zygomatic arch, causing a broad junction of the postglenoid and post-tympanic processes and a very characteristic flattening of this region. Seen from behind (fig. 262) the occiput measures 116 millimeters above the foramen magnum, and 157 above the bottom of the occipital condyles. Conforming to the smaller size of the skull as a whole, the condyles measure 86 millimeters transversely as compared with 99 in *L. monoconus*. The width of the occiput across the top is 108 millimeters. At the sides of the exoccipital portion are indistinctly seen the mastoid foramina. Just above the foramen magnum are very faintly indicated the pair of facets characteristic of this genus, more distinctly marked in *Telmatherium*.

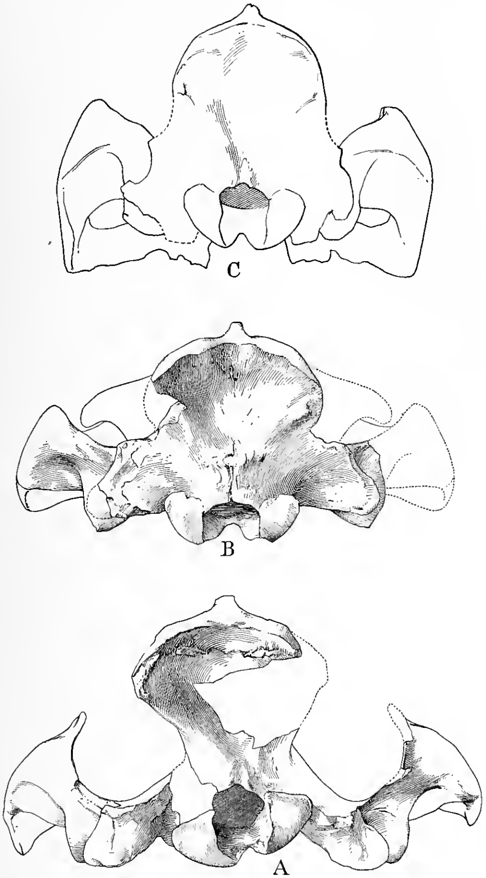

FIGURE 261.—Skulls of three species of *Limnohyops*

Occipital view. One-fourth natural size. A, *L. monoconus*, Am. Mus. 11679 (type); Grizzly Buttes, west Bridger Basin, Wyo.; Bridger formation, level B 2. B, *L. laticeps*, Yale Mus. 11000 (type, vertically crushed); Bridger Basin; upper? Bridger. C, *L. matthewi*, Am. Mus. 11684 (type); Grizzly Buttes, west Bridger Basin; Bridger formation, level B 2.

Limnohyops monoconus Osborn

Plate LXII; text figures 117, 261-263, 484, 485, 510-514, 516, 519-523, 525, 527-530, 685, 686, 701, 723

[For original description and type reference see p. 130. For skeletal characters see pp. 604, 612]

Type locality and geologic horizon.—Grizzly Buttes (west), Bridger Basin, Wyo.; Bridger formation, *Palaeosyops paludosus-Orohippus* zone, level B 2. This specimen was discovered by the American Museum expedition of 1903. It was on the level of *L. laevidens* and *L. matthewi* and thus belongs to a much lower horizon than *L. laticeps*. This specimen may represent, however, the geologic intrusion of a fauna from a higher level, and it is therefore quite possible that it was not contemporaneous with *L. laevidens*. The presence of these specialized forms, *L. matthewi* and *L. monoconus*, on the same geologic level as the primitive forms *L. laevidens* and *L. priscus* is contrary to the general law of succession observed among other forms in the Bridger Basin. It may indicate either some source of error in the geologic records or some deviation from the generally horizontal distribution of the Bridger titanotheres. Another explanation is possible: that *Limnohyops* was evolving more rapidly in other geographic centers, from which these progressive forms may have migrated.

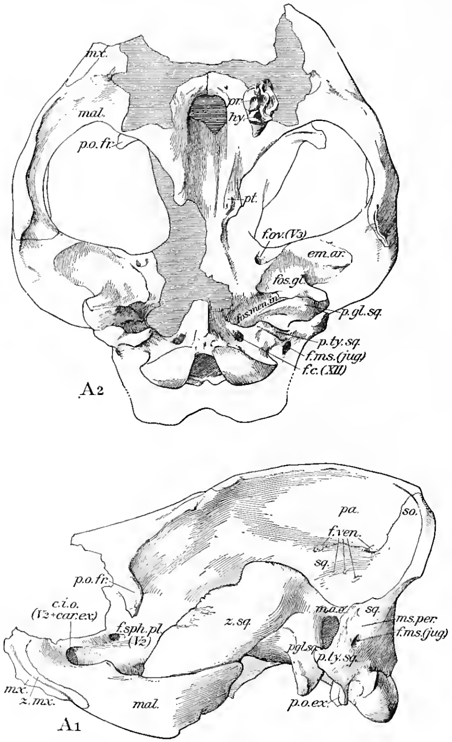

FIGURE 262.—Skull of *Limnohyops matthewi*

One-fourth natural size. Am. Mus. 11684 (type); Grizzly Buttes (west), Bridger Basin, Wyo.; Bridger formation, level B 2. A_1, Side view; A_2, basal view.

Specific characters.—M^3 without hypocone, roundly triangular in form, with broadly extended ectoloph and parastyle. P^2–m^3, 142 millimeters; p^1–m^3, 156. Condyle to incisive border 439 millimeters (estimated);

occiput very high; cranium relatively elongated, with space (4 mm.) between post-tympanic and postglenoid processes; temporal openings as defined by zygomatic arches elongated.

This type (Am. Mus. 11679) is an exception to all the other species referred to *Limnohyops* in the absence of the hypocone on m^3. The specific name, *monoconus*, refers to the existence of but a single internal cusp (protocone) on this tooth. The animal is provisionally referred to the genus *Limnohyops* on strong evidence in five other points of cranial structure which are cited below.

As compared with the type of *L. matthewi*, the animal on which this species is founded is of very robust size; its size is especially robust for the low geologic level from which it is recorded—namely, B 2. Its proportions agree fairly well with those of *L. laticeps*, which is referred to level D 2.

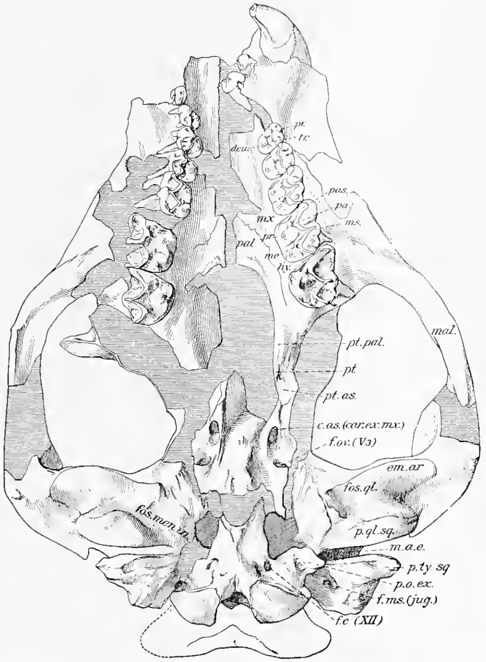

FIGURE 263.—Skull of *Limnohyops monoconus*

Palatal view. One-fourth natural size. Am. Mus. 11679 (type); Grizzly Buttes, west Bridger Basin, Wyo.; Bridger formation, level B 2.

Materials.—The species is certainly known only from the type (Am. Mus. 11679), which consists of the crushed cranium of a robust male specimen, as indicated by the large, recurved canines. Other doubtfully referred specimens (Am. Mus. 5102, 12680) are recorded from B 5.

As the hypocone on m^3 is the alleged "generic" character of *Limnohyops* and is present in the other species *L. laevidens*, *L. matthewi*, and *L. laticeps*, its absence in this form is very exceptional and causes some doubt as to the propriety of the generic reference of this species to *Limnohyops*. The other grounds for referring this animal to *Limnohyops* rather than to *Palaeosyops* are strong, however—namely, (1) the doubly ridged ectolophs of p^2–p^4; (2) the very elevated occiput; (3) the more or less angulate form of the suborbital bridge in the malars; (4) the splint of the maxillary extending on the lower side of the malar bridge; (5) nasals not perceptibly narrowing anteriorly.

Specifically this animal is readily distinguished from all other species of *Limnohyops* by the absence of the hypocone on m^3. As compared with *L. laevidens* it is an exceptionally large form, the measurements (estimated) being, from the condyle to the incisive border 439 millimeters, width across the zygomata 320. It is also distinguished by the very robust and recurved canines. From *L. laticeps* it is distinguished by the higher occiput, by the absence of a hypocone on m^3, and by its supposed lower geologic level. It is distinguished from *L. matthewi* by the more elongate cranium, correlated with which are the oval openings circumscribed by the zygomatic arches, and by the separation between the postglenoid and post-tympanic processes.

The skull is of massive proportions, with widely arched zygomata (320 mm., estimated) as compared with the total length (439 mm., estimated). (See fig. 263.) The anterior portion is too much crushed for recognition, except that the nasals have the form characteristic of *Limnohyops*, with more parallel sides than in *Palaeosyops*. Seen from behind the occiput is more elevated than in *L. laticeps* and resembles that of *L. matthewi*. (See fig. 262.) The extreme height of the sagittal crest above the foramen magnum is 133 millimeters, and above the bottom of the condyles 179; the condyles measure 99 millimeters in width. Seen from above the nasals are narrow and long, measuring 175 to 186 millimeters as compared with 168 in *L. laticeps*. In the region of the frontonasal horn swelling there is a rugose area which may have exhibited a rudimentary frontonasal horn.

Dentition.—The canine is exceptional in its robust size and recurved form, the height being estimated at 41 millimeters and the diameters at the base of the enamel being, anteroposterior, 25; transverse, 25. The crown approaches that of *Manteoceras* in the swelling of the base. The premolars are primitive in lack of complication: (1) there is a small tritocone on p^2, (2) p^2 and p^3 lack the internal cingula entirely, a primitive condition, (3) the double ridging of the ectolophs is a *Limnohyops* character. The molars, m^1–m^3, measuring 93 millimeters, are very distinctive in form, with oblique ectolophs and prominent parastyles. The triangular m^3 especially is of quite different form from that of *L. matthewi*, the tooth narrowing toward the inner side and having a long oblique outer border.

Limnohyops laticeps Marsh

Plates LVII, LXII; text figures 87, 92, 261, 264–266, 511, 531, 532, 714, 760

[For original description and type references see p. 160. For skeletal character see p. 618]

Type locality and geologic horizon.—Bridger Basin, Wyo. Marsh's Fork, the level of which is not certainly known, is the type locality. The American Museum specimens closely resembling the type are from Bridger C 4, D 1, and D 2.

Specific characters.—Of intermediate size; p^1–m^3, 153 millimeters; p^2–m^3, 139; second and third inferior premolars of more advanced type than in *L. priscus;* p^2 with well-developed tritocone; m^3 with a large hypocone (fig. 265). Condyles to incisive border 410 millimeters (estimated); breadth across zygomata 320; smooth and extremely rudimentary horn swellings on nasofrontal sutures. Cephalic index 75 (estimated).

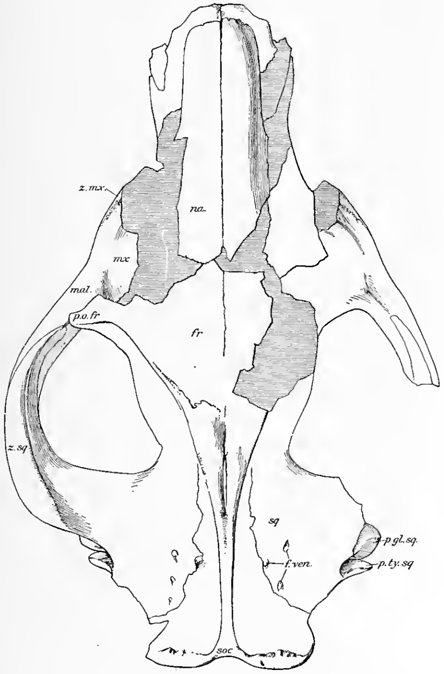

FIGURE 264.—Skull of *Limnohyops laticeps*

Top view. One-fourth natural size. Yale Mus. 11000 (type). Bridger Basin, Wyo.; upper (?) part of Bridger formation.

This was one of the earliest of the Palaeosyopinae to be described, and for a long time it was not clearly separated from the genus *Palaeosyops.* The most distinctive character assigned by Marsh was the hypocone on the last superior molar (fig. 265). Many of the distinctive cranial characters were clearly pointed out by Earle. Additional materials in the American Museum collections enable us to fully define this species, especially from the full characters of the skull, the carpus, and the manus.

Materials.—*L. laticeps* is represented by two specimens—by the type cranium and parts of the skeleton (Yale Mus. 11000), belonging to an individual not fully grown, and by Am. Mus. 11710, a fragment of the maxilla containing two molars, from level D 2, Bridger.

Specific characters of the type.—In addition to the specific characters enumerated above the occiput is moderately high (144 mm. above the condyles, 118 above the foramen magnum); the condyles are moderately broad (95 mm.); the mesostyle on p^4, which is seen as a shadow rudiment or rectigradation in *L. priscus,* is here quite distinct; in p^2 the tritocone is much larger and more distinct than in *L. priscus;* m^1 as in *L. priscus* is small (ap. 24 mm., tr. 27); m^3 is much larger than in that species; the metaconules are larger than in *L. priscus* and confluent internally with the hyipocones; there is little or no diastema behind the canine.

The type skull.—Our knowledge of the skull is based mainly on the crushed but very complete type cranium of *L. laticeps* (Yale Mus. 11000), which gives us the principal characters. (See fig. 264.) (1) The proportions of the skull are approximately the same as in *P. leidyi*—namely, 410 millimeters in length and 310 across the zygomata. (2) The skull of *L. laticeps* is distinguished from that of *L. priscus* and approaches that of *P. leidyi* in the slight narrowing of the nasals anteriorly: posteriorly they measure 53 millimeters in width; anteriorly they diminish to 43 millimeters, being still much broader anteriorly than in *P. leidyi.* Other distinctions from *P. major* and *P. leidyi* are found in the following principal characters: (3) The sagittal crest is very high, extending 65 millimeters above the brain case, and thin at the summit (9 mm.), extending forward a considerable distance (103 mm.) before the crest begins to spread into the supratemporal ridges, whereas in the least progressive specimen of *P. leidyi* described below the thinnest portion of the crest measures 13 millimeters and begins to expand rapidly into the plane of the vertex; (4) the occiput as seen from behind is well defined by a sharp crest and is rounded superiorly, extending 118 millimeters above the foramen magnum and 125 millimeters transversely; (5) the postglenoid and post-tympanic processes are slightly separated; (6) the zygomata arch widely, the malars being compressed inferiorly and

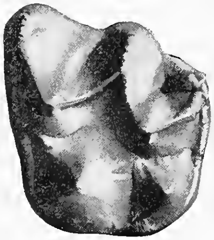

FIGURE 265.—Third right upper molar of *Limnohyops laticeps*

Natural size. Am. Mus. 11710, reversed. Henrys Fork, Lone Tree, Bridger Basin, Wyo.; Bridger formation, level D 2.

forming a sharply convex ridge below the orbits, with a narrow V-shaped union with the maxillaries anteriorly; (7) in lateral view the nasals are slightly decurved anteroposteriorly; (8) the infraorbital foramen is above the third and fourth premolars, or about 34 millimeters below and anterior to the orbit.

Dentition of the type.—The premolars of the type of *L. laticeps* are much more progressive than those of the types of *L. laevidens* and *L. priscus*. The range of progression is parallel with that of *P. leidyi* in the following respects: (1) A larger tritocone is developed on p^2; (2) a distinct mesostyle is observed in the ectoloph of p^4; (3) the protoconule of p^4 is larger. Comparison of these teeth with Leidy's superior premolar and molar types of *P. paludosus* shows that the ectoloph of p^4 is identical in measurement in the two specimens and that the measurements and characters of m^2 are very similar except that in the type of *L. laticeps* the anterior cingulum is somewhat more accented.

In the type of *L. laticeps* p^2–m^3 measures a few millimeters less than in Am. Mus. 2361. The inner side of the crown of p^2 (ap. 11 mm.[23]) is preserved, showing a postero-internal cingulum; p^2 is a transversely oval tooth like that of *P. laevidens;* p^3 (ap. 14 mm., tr. 19) is more progressive than in *L. priscus* in its slightly better developed tritocone, more sharply ribbed protocone, stronger internal cingula; in p^4 (ap. 17 mm., tr. 24) we observe the slightly more distinct development of the conule above mentioned and the presence of a mesostyle on the tooth of the right side, which, however, is wanting in that of the left.

The molar series measures 90 millimeters in length, and the anteroposterior by transverse dimensions of the teeth are, m^1 24 by 26 millimeters, m^2 31 by 35, m^3 33 by 38, the teeth thus being broader than long; the slopes of the cusps are vertically striated but less strongly so than in *Palaeosyops;* both protoconules and metaconules are present, small, of transversely lophoid shape; in m^3, however, the protoconule is more distinct, the metaconule is vestigial, and the cingulum rises into a distinct cingular hypocone (see fig. 265); the vertical ridges of the ectoloph are slightly fainter than in Leidy's cotype of *P. paludosus*, and the external crescents are slightly more open.

Jaw of the type.—The posterior portion of the jaw as preserved shows that the angle descends almost vertically below the condyle and does not extend backward so far as in *Palaeosyops*. The lower border of the angle is 157 millimeters below the condyle. The coronoid is stout, relatively low and broad.

Palaeosyops Leidy

Plates XVI, XXVII, XXVIII, XLIV, L, LIII, LV, LVI LVIII–LXII; text figures 27, 28, 33, 86, 88, 89, 97, 108, 118–120, 210, 214–220, 227, 254–257, 266–288, 305, 405, 407, 482–485, 508–516, 519–523, 528, 533–537, 539–550, 552, 559, 571, 645, 661, 685, 686, 703, 711, 713, 714, 716, 718, 721, 724, 727, 732, 733, 737–742, 745, 760

[For original description and type reference see p. 157. For skeletal character see p. 619]

Type locality and geologic horizon.—Bridger Basin, Wyo., Bridger formation, levels B, C, and D; Washakie Basin, Wyo., *Uintatherium-Manteoceras-Mesatirhinus* zone (Washakie A).

Specific characters.—Brachycephalic. Grinding teeth persistently brachyodont; metaconules on the molars persistent or absent; third superior molar without hypocone. Skull and skeleton robust; feet broad; manus with well-developed fifth digit; lunar resting subequally on magnum and unciform. Four sacral vertebrae.

Geographic and geologic distribution.—This type genus of the family Palaeosyopinae embraces a remarkable series of stages of evolution of animals, which are subdivided into eight species, found in ascending geologic succession—namely, *P. fontinalis*, *P. longirostris?*, *P. paludosus*, *P. major*, *P. grangeri*, *P. leidyi*, *P. robustus*, and *P. copei*. The members of the phylum belong chiefly to the Bridger formation and increase steadily in size from its base to its summit, or from level B to D. *P. grangeri* and *P. copei* are not included in the direct line.

The specimens listed below were collected from the Bridger formation at the levels indicated.

13032, B 1.
10276, B 1 or B 2.
12182, B 3.
13116, B 2.
12185, C 3.
10009, C or D.
12196, C 2.
1544, C 4.
11678, D 4.
5106, D (?).
10282, D (?).
11683, D 3.
12189, C 1.
11708, D 3.
11692, B 2.
11680, B 1.
12181, B 3.
12165, B 2.
12183, B 3.
Type of *P. major*, B 2 (?).
12200, C 4.
12188, C 5.
12205 a, D 1.

Comparatively few specimens of *Palaeosyops* have been found in the more easterly Washakie Basin, only 80 kilometers (50 miles) distant. This fact implies a difference of living conditions, because the deposits of the Washakie Basin are much less rich in fossils and because the greater part of the fossiliferous "Washakie" exposures are of more recent age than the Bridger. Only the lower "Washakie" (horizon A) was synchronous with the summit of the fossiliferous Bridger (horizon D).

The evidence afforded by our present knowledge indicates that the quadrupeds now known as *Palaeosyops* disappeared from this region or died out during or soon after the deposition of Bridger D. *Palaeosyops*

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[23] The anteroposterior measurements given here and elsewhere are taken across the middle of the crown.

was by far the most abundant of the Bridger Basin quadrupeds. The identified materials in the American Museum from the Bridger Basin embrace parts of more than 60 individuals, including 12 more or less complete skulls.

Materials.—Altogether, more than 70 specimens have been examined for this monograph, including those in the collections in the American, Yale, National, and Philadelphia Museums. Most parts of the skeletons are dissociated from skulls; even the jaws are rarely found with skulls; in only three of the specimens of *Palaeosyops* studied are the jaws associated with the skull.

The following table shows the length of the lower grinding series, the length of the upper grinding series, the length along the bottom line of the skull, and the breadth across the zygomatic arches:

Comparative measurements of species of Palaeosyops, in millimeters

Geologic level	Species	P_2-m_3	P^1-m^3	P^2-m^3	Basilar length of skull	Breadth of skull
Bridger D 3	P. copei Osborn	(?)	[a] 170	[a] 153	(?)	(?)
Bridger D	P. robustus (Marsh)	----------	[a] 180	[a] 170	[a] 440	[a] 340
Bridger C 2–4	P. leidyi Osborn	168	174	158	415	310
Bridger C 1	P. grangeri Osborn	----------	180	165	(?)	(?)
Bridger B 2–4	P. major Leidy	164	[a] 155	147	[a] 389–435	[a] 290–335
Bridger B 1–2	P. paludosus Leidy	151	137?	124?	(?)	(?)
Bridger B	P. longirostris Earle	143	(?)	(?)	(?)	(?)
Bridger A	P. fontinalis Cope	(?)	(?)	(?)	(?)	(?)
Huerfano B	P. fontinalis Cope	----------	146	131	----------	(?)

[a] Estimated.

There are steady increases in every dimension measured until we reach the single specimen known of the ultimate species, *P. copei*, from Bridger D 3, in which a sudden falling off in size is observed. (See also detailed table on p. 316.)

Palaeosyops in general steadily evolves from a smaller although very robust animal into a larger, extremely broad-skulled, or brachycephalic animal. Certain characters are persistent in all the species. There are added through orthogenesis other new characters, or "rectigradations," which distinguish the more advanced stages from those found in the lower levels. The chief rectigradations and allometrons are the following: (1) Increase in size and brachycephaly of the skull; (2) steady increase in all dimensions of the grinding teeth; (3) certain cusps in the lower premolars (p_2, p_3) analogous to the paraconid, metaconid, and hypoconid of the true molars; (4) the second cusps (or tritocones) on the outer wall of the second upper premolars (p^2), cusps foreshadowed in the ancestral species; (5) the median ridges (or mesostyles) added on the outer walls of the two posterior upper premolars (p^3, p^4), which happen to be quite distinctive because these ridges do not arise in all titanotheres as they do in all horses; (6) the second postero-internal cusp, or tetartocone, on the superior premolar teeth is late in evolution in all titanotheres and only appears in very rudimentary form in *P. copei;* (7) the horns, or nasofrontal bosses, are rectigradations, which appear to be more retarded in evolution in *Palaeosyops* than in several other phyla.

Summarized, these seven principal cranial and dental changes are shown below.

I. Allometrons (proportional, or metatrophic):
  1. Increase of the skull in size and in brachycephaly.
  2. Steady increase in all dimensions of the grinding teeth (see table on p. 316).
  3. Cusps on the lower premolars p_2, p_3 analogous to the paraconid, metaconid, and hypoconid of the true molars; foreshadowed in *P. paludosus* and increasing progressively in the higher stages.

II. Rectigradations (numerical, or the addition of new elements):
  4. Tritocone on p^2 first occurring in *P. major* and increasing in all higher stages.
  5. Mesostyles added to p^3, p^4, first occurring in *P. leidyi* and characterizing all higher stages.
  6. Tetartocones first appearing on superior premolars in *P. copei* (no higher stages at present known).
  7. Osseous frontonasal horns first appearing in *P. leidyi* and increasing in all higher stages.

Incisors.—The superior incisors exhibit low crowns with irregularly folded posterior cingula; the opposite series are usually separated by a median diastema and from the canines by lateral diastemata. The incisors increase regularly in size from i^1 to i^3; the crowns are convex anteriorly, with a basal subcingulate expansion; the posterior faces slope gradually into an irregularly folded basal cingulum; the lateral incisors i^3 are much the largest and decidedly subcaniniform, with obliquely sloping internal cingulum; i^1 is more symmetrical, with short, compressed root; i^2 is less symmetrical, with longer root; i^3 is very asymmetrical, with a very long, large root. The inferior incisors are readily distinguished by their narrow crown, sharply convex in front, and sloping posterior face divided by a median ridge. As shown in *P. leidyi* the crowns increase slightly but regularly in height from i_1 to i_3. In the lower incisors the opposite i_2 have very long roots nearly meeting in the midline below; i_3 have short roots and are being crowded out by i_2.

Canines.—The superior canines are rounded at the base and when unworn are very slightly recurved and sharply pointed, differing from those of *Telmatherium* in their circular section and strongly convex inner sides. In females the canines are long, pointed, and less robust, while in males they are much more rounded and robust. The inferior canines are of very similar form, nearly erect, with crowns rounded at the base, differing from those of *Manteoceras* in the absence of the marked posterior expansion of the base, and from those of *Telmatherium* in the rounded, nonlanceolate form. A peculiar feature of the lower canines is the directly internal or lingual position of the posterior ridge, the two ridges being thus brought very close together.

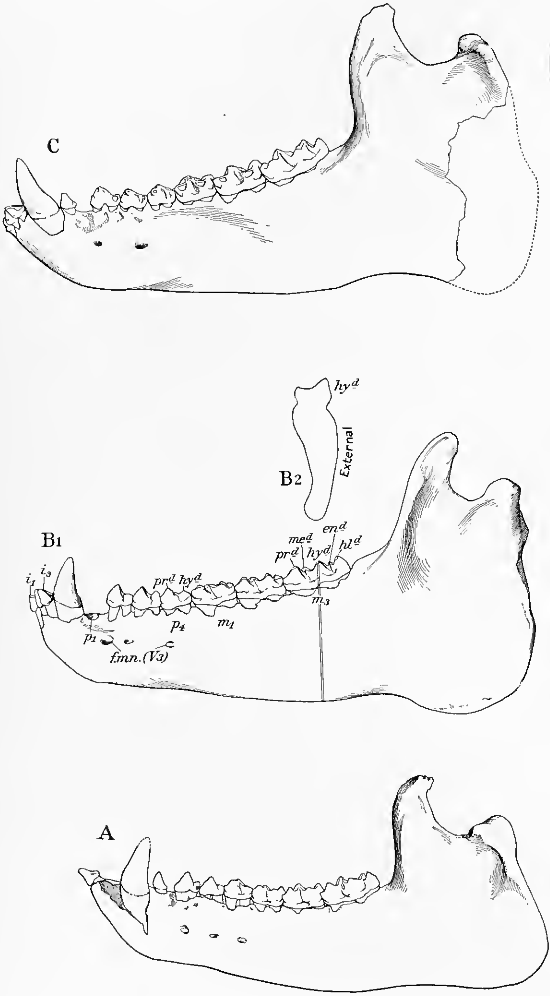

FIGURE 266.—Lower jaws of *Limnohyops* and *Palaeosyops*

One-fourth natural size. A, *L. priscus*, Am. Mus. 11688 (cotype), reversed; Grizzly Buttes (east), Bridger Basin, Wyo.; Bridger formation, level B 2; coronoid and condylar region reconstructed. B_1, *P. copei?*, Am. Mus. 12205a; Lone Tree, Henrys Fork, Bridger Basin; level D 1, 15 feet above white stratum. B_2, The same, section through m_3. C, *L. laticeps*, Am. Mus. 12201, ♀, reversed; Henrys Fork Hill, Bridger Basin, level C 4; angle restored from *P. paludosus*, Am. Mus. 11690

Premolars.—The law of cusp addition in the premolars, which constitutes a most important means of distinguishing the specific stages, is clearly set forth above. In the general brachycephaly the premolars acquire a rounded form rather than the elongate or angulate form seen in *Telmatherium*. P^1 is either slightly separated from the canine or placed immediately behind it, according to the degree of brachycephaly; in form it is either an extremely small, rounded, bifanged tooth or considerably larger, with a posterior internal cingulum in the higher stages. The chief point to note in p^2 is the strengthening and increasing convexity of the tritocone or posterior outer cusp (*P. major*). A very sharp distinction is seen in the progressive transformation of p^3 and p^4 in *Palaeosyops*—namely, in the gradual development of a mesostyle or median ridge separating the protocone from the tritocone (*P. leidyi*), which appears to indicate that in *Palaeosyops* the ectolophs of the premolars are tending to become somewhat like those of the molars, whereas in *Manteoceras* the ectolophs never assume the molar form. The outer cusps of the premolars of titanotheres never become crescentic externally, however, and are thus essentially different from those of the molars.

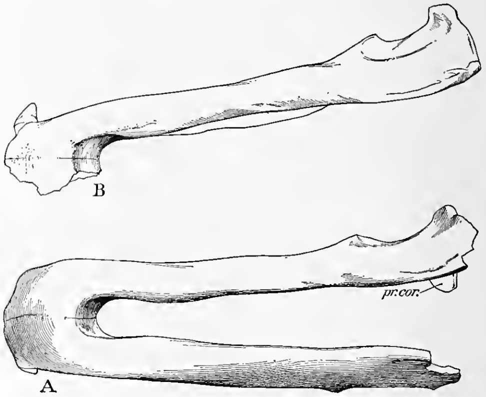

FIGURE 267.—Lower jaws of *Palaeosyops*, male and female

Inferior view. One-fourth natural size. A, *P. paludosus*, Am. Mus. 11680, ♂ (neotype); Little Dry Creek, Bridger Basin, Wyo.; Bridger formation, middle beds, level B 1. B, *P. copei?*, Am. Mus. 12205a, ♀; Henrys Fork, Lone Tree, Bridger Basin; Bridger D 1, 15 feet above white stratum.

In general, the grinding teeth are distinguished by persistent brachyodont or short crowns, and the persistence of the conules is undoubtedly correlated with the persistent breadth of the grinders.

Molars.—The superior molars are progressively distinguished (1) by the increased development of the cingula; (2) by the intensified striations of the sides of the cones; (3) by the robust and rounded form of the parastyle and increasing prominence of this style; (4) by the relative persistence of the conic or sublophoid protoconules; (5) by the more variable, rounded, or lophoid metaconules[24]; (6) by the subtriangular or subselenoid form of the hypocone in m^1 and m^2, the protocone remaining rounded or bunoid; (7) by the fact that in no specimen of *Palaeosyops* has a distinct hypocone on m^3 been observed, although the metaconule is often enlarged and might easily be mistaken for a hypocone, and the posterior cingulum is often elevated. The inferior molars are readily distinguished progressively (1) by the rounded, bulbous character of the sides of the main cusps; (2) by the vertical grooving or striation of the sides of the cusps; (3) by the festooning of the external cingula; (4) by the prominence of the paraconids, the increased development of the metastylid, entostylid, and parastylid; (5) by the increasingly central position and rounded form of the hypoconulid in m_3, a cusp which is subcrescentic when entirely unworn but, as pointed out by Earle, wears into a circle in old age; (6) by the median ridges strengthening the internal slopes of the protoconid and hypoconid crescents, which are evidently dynamically correlated with the presence of the analogous median external ridges on the outer slopes of the paracone and metacone of the upper molars. The internal ridges also serve to comminute the food by pressing against the protocones and hypocones.

Skull and jaws.—The detailed primitive and progressive characters of the jaw and of the male skull may best be indicated under the descriptions of the various species. In general, the skull (fig. 276) is distinguished by (1) nasals tapering anteriorly; (2) a prominent convexity above the orbits covering a large frontal sinus; (3) rudimentary osseous horns which appear on the sides of the face; (4) a relatively short, free sagittal crest; (5) a moderately elevated occiput; (6) deep and outwardly arched zygomatic arches; (7) in earlier stages post-tympanic and postglenoid processes slightly separate; (8) a very large mastoid foramen; (9) occipital condyles moderately expanded; (10) constantly increasing expansion of the masseteric insertion beneath the orbits; (11) premaxillary symphysis short and rounded. In the jaw marked differences are seen between the sexes (figs. 266, 267). In the males the chin is very deep and prominent, correlated with the insertion of the long fangs of the extremely robust canines. In the females the chin is more shallow and more sloping and rather resembles that of *Limnohyops*. The distinctive characters of the male jaw (fig. 268) are (1) the marked curvature of the lower border; (2) the great thickening of the lower border beneath the alveoli of the grinding teeth, which first appears beneath the premolars and then extends progressively backward beneath the molars; (3) the comparatively short digastric fossa for the insertion of the digastric muscle below the posterior portion of the symphysis; (4) the greater distance between the posterior molar and the back of the angle as compared with *Limnohyops;* (5) the breadth of the anterior border of the coronoid, which becomes progressively hollowed out in front; (6) the reduction of the upper portion of the coronoid process, which in some higher stages assumes a more simple form with an abbreviated posterior hook.

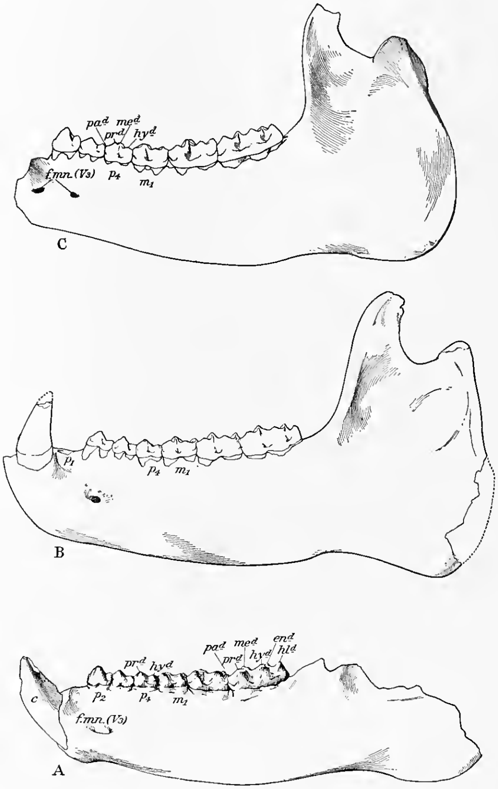

FIGURE 268.—Lower jaws of three species of *Palaeosyops*

One-fourth natural size. A, *P. longirostris*, Princeton Mus. 10275 (type), Bridger Basin, Wyo.; B, *P. paludosus*, Am. Mus. 11680 (neotype), Millersville, Little Dry Creek, Bridger Basin, level B 1; C, *P. major*, Am. Mus. 12181 (neotype jaw), Cottonwood Creek, Bridger Basin, level B 3.

The characters of the skeleton are fully described on page 619.

QUANTITATIVE EVOLUTION OF PALAEOSYOPS

The following table gives the measurements of 28 characters of proportion in 16 specimens, belonging to 6 species, collected at ascending geologic levels in the Bridger formation:

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[24] These cusps appear to be entirely wanting in the primitive species *Palaeosyops fontinalis*, from Bridger A.

Evolution of proportions of Palaeosyops

[Measurements in millimeters. Level, if known, given after specimen number]

	P. paludosus, Am. Mus. 13032; B 1	P. major			P. leidyi					P. robustus					P. grangeri, Am. Mus. 12189 (type); C 1	P. copei, Am. Mus. 11708 (type); D 3
		Princeton Mus. 10276; B 1 or B 2	Am. Mus. 12182 (hypotype); B 3	Am. Mus. 13116; B 2	Am. Mus. 12185; C 3	Princeton Mus. 10009; C ?	Am. Mus. 12196; C 2	Am. Mus. 1516	Am. Mus. 1544 (type); C 4?	Am. Mus. 11678; D 4	Am. Mus. 5106 (type of P. diaconus); D?	Princeton Mus. 10282(b); D	Yale Mus. 11122 (type)	Am. Mus. 11683; D		
Skull and upper teeth																
Condyles to incisive border			[a] 389	435				414	415							
Breadth across zygomata			[a] 290	335				[a] 275	310	[a] 341						
Occiput to tip of nasals								405	397							
Height of occiput									112							
Width across postglenoid processes								188	196							
P^1–m^3	161				162			169	174		[a] 170	174	[a] 180		180	[a] 17
P^2–m^3	144		147	150	150	[a] 150		155	158			163	[a] 170	169	165	[a] 153
P^2–m^2	79		116		115			119	120			127		131	125	118
P^1–p^4	71								73				70		71	70
M^1–m^3	91		94		98	97	96	102	100	94	[a] 102	100	102	[a] 103	107	96
P^4, anteroposterior	18	17	19		18	19	18	18	19	17	19	20	20	20	21	19
P^4, transverse	22	25	24		24	25	26	25	25	24	26	27	27	26	31	26
M^1, anteroposterior	25		27			29	29	29	29	27			29	30	30	
M^1, transverse	26		31		31	[a] 31	32	32	33	31			35	35	35	
M^3, anteroposterior	32	32	33		34	35	32	34	36	33		36	37	37	38	34
M^3, transverse	34	37	40		39	39	41	39	38	37	42	40	42	42	43	40
Cephalic index			74						74							

	P. paludosus		P. major					P. leidyi										P. grangeri, Am. Mus. 12189 (type); C 1	P. copei?, Am. Mus. 12205a; D 1
	Am. Mus. 11692; B 2	Am. Mus. 11680; B 1	Am. Mus. 12181; B 3	Am. Mus. 5101	Am. Mus. 12165; B 2	Am. Mus. 12183; B 3	Acad. Nat. Sci. Philadelphia (type); B 2?	Am. Mus. 1522	Am. Mus. 5103	Princeton Mus. 10009; C or D	Am. Mus. 1544 (type); C 4?	Am. Mus. 1549; ♀	Am. Mus. 1585 [b]	Am. Mus. 1564	Am. Mus. 1546	Am. Mus. 12200; C 4	Am. Mus. 12188; C 5 [b]		
Lower jaw and lower teeth																			
Condyle to symphysis		[a] 340				370					358								344
Length of symphysis		[a] 85				100					93								75
Depth of ramus behind m_3		85	86			97	95	87		91	98		[a] 107	[a] 90	91				91
Condyle to angle		165	157			170		182			174		[a] 170	184					159
P_1–m_3		[a] 169		180		182				189	193	192	190				192		187
P_2–m_3		152	164	169		168					166	171	173	170			178		173
M_1–m_3	98	98	106	109	118	112	[a] 115	105	112	108	107	113	109	113	115	112	115	[a] 126	114
P_4, anteroposterior	19	17	19	19	22	20				20	19	20	21	20	21	20	21		21
P_4, transverse	12	12	13	14	15	14				14	14	15	15	14	14	13	15		15
M_1, anteroposterior	24	26	26	27	29	26		26	29	27	29				29	29			27
M_1, transverse	15	18	17	19	19	19		19	19	18	19				21	19			19
M_3, anteroposterior	41	43	45	47	50	49	[a] 50	45	48	46	46	48	47	50	52	52	50		52
M^3, transverse	22	23	24	27	26	26		25	25	26	25	25	25	28	26		27	31	28

[a] Estimated.

[b] Specific reference doubtful.

The accompanying table brings out the following facts:

1. The law of regular progressive increase in size as we pass from *P. paludosus* (of Bridger B 1) through *P. major* (of levels B 2–3), *P. leidyi* (C 2 to C 4?), to *P. robustus*.
2. The exceptionally large *P. major* skull, Am. Mus. 13116, from B 2 interrupts this regular increase, but its tooth row is not larger than in other *P. major* skulls (that is, the skull and the teeth are differential).
3. So far as the measurements are evidence, the larger specimens of *P. major* overlap the smaller specimens of *P. leidyi*, and the larger *P. leidyi* overlap the smaller *P. robustus*.
4. *P. grangeri*, although it is not so advanced in its stage of premolar evolution as *P. leidyi* and although it comes from a lower level, yet exceeds *P. leidyi* in size.
5. *P. leidyi* seems to be very closely allied to *P. robustus*. It exhibits considerable fluctuation in size.
6. *P. copei*, although more advanced in premolar evolution than *P. robustus*, has a somewhat smaller dentition (differential evolution).
7. While the premolar series remains relatively stationary in length the molar series increases from 91 millimeters in *P. paludosus* to about 102 in *P. robustus* (differential evolution).
8. The fourth premolar and first molar exhibit a marked increase in size, especially in width (differential evolution).

Other conclusions from the measurements are considered under the heading "Differential allometrons," on page 825.

Palaeosyops fontinalis (Cope)

Text figures 97, 269–271

[For original description and type references see p. 165]

Type locality and geologic horizon.—Bridger Basin, Wyo.; Bridger formation, level not clearly recorded but probably *Eometarhinus-Palaeosyops fontinalis* zone (Bridger A), as the type skull is recorded from Green River. Also recorded from Huerfano Park, Colo., in Bridger formation, horizon Huerfano B (=Bridger A). The six specimens from Huerfano B (see below) range from 250 feet to 500 feet below the top of the Huerfano formation.

Specific characters.—Of relatively small size. Superior molars with sharply defined crescents and cusps; m^1 extremely small (ap. 22 mm., tr. 25), with protoconule and no metaconule.

This little-known animal resembles *Palaeosyops* in its cranial structure but differs quite widely from any known species in the form of the cusps of its grinding teeth. It is the smallest, probably the most primitive, and certainly the oldest Bridger titanothere known, and these facts in connection with the very low geologic level give it great importance.

Materials.—This species is represented in Bridger (A?) merely by the very immature skull (Am. Mus. 5107) collected on Green River near Big Sandy Creek. In Huerfano B it is represented by six specimens in the American Museum of Natural History, as follows:

17411. Superior dentition and portion of palate (fig. 271, A), Huerfano-Muddy divide, 2 miles west of Gardner, Colo., 414 feet below the top of the Huerfano formation.

17413. Two upper molars and incisor (fig. 271, C), 3 miles north of Gardner, 400 to 500 feet below the top of the Huerfano formation.

17414. Three superior molars, fragmentary, 3 miles north of Gardner, 400 to 500 feet below the top of the Huerfano formation.

17417. M_1, p^1, and milk teeth (fig. 271, B), 2 miles north of Gardner, 400 to 500 feet below the top of the Huerfano formation.

17425. Series of right upper grinders, p^3–m^3 (fig. 271, D), 2 miles north of Gardner, 400 to 500 feet below the top of the Huerfano formation.

17450. Lower canine and fragment of m_3, Huerfano-Muddy divide, 2 miles west of Gardner, about 250 feet below the top of the Huerfano formation.

The geologic horizons of these specimens range rom 250 to 500 feet below the top of the Huerfano formation.

The immaturity of the type specimen is determined by the fact that only one true upper molar (m^1) has come into use, the second molar (m^2) being still deeply embedded in the jaw. In superior view (fig. 269, A_3) the cranium is valuable as exhibiting the suture between the supraoccipital and the parietals, a suture which closes very early in *Palaeosyops*. Similarly in the lateral view (fig. 269, A_1) the maxilla sends out a broad, spurlike process directly on the outer side of the malar as in *Palaeosyops*, instead of on the under side as in *Limnohyops*. The infraorbital bridge is rounded as in *Palaeosyops*, rather than angulate as in *Limnohyops*. The depressed or sessile character of the supratemporal crest is probably due to immaturity. Behind the post-tympanic process the mastoid is exposed as a narrow strip.

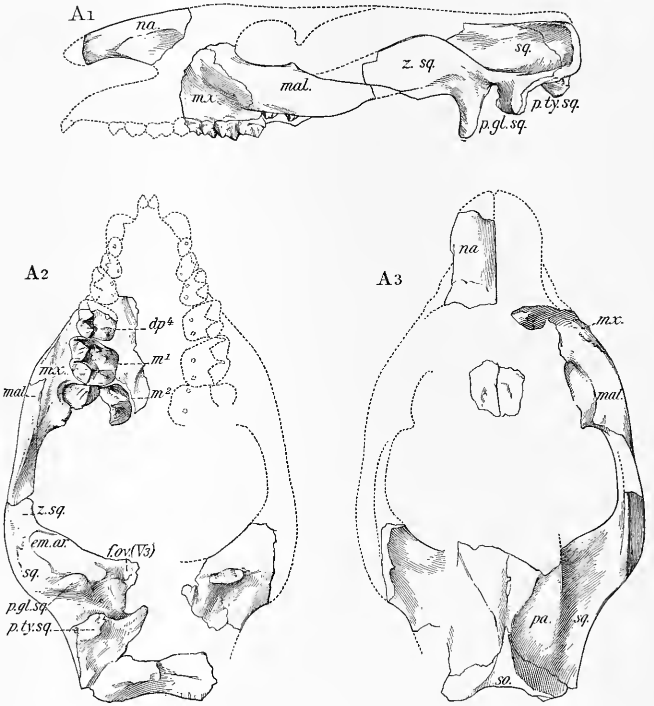

FIGURE 269.—Young skull of *Palaeosyops fontinalis*

One-third natural size. Am. Mus. 5107 (type). Green River near mouth of Big Sandy Creek, Bridger Basin, Wyo.; Bridger formation, level A?. A_1, Side view reversed; A_2, palatal view; A_3, top view.

The specimen thus probably pertains to the genus *Palaeosyops*, though its grinding teeth are not entirely of the typical *Palaeosyops* form; its specific distinction from the larger and more robust forms is readily determined from the teeth.

Dentition.—The part of the crown of dp^4 that is preserved exhibits the protocone more internally placed than the hypocone; this tooth is therefore fully quadrate though not precisely molariform. The well preserved first superior molar (m^1) exhibits trenchant or pointed main crescents and cones; the ectoloph is divided by small, sharply ridged parastyles and mesostyles; a protoconule but no metaconule is present; in size this tooth is diminutive, measuring (ap. by tr.) 22 by 25 millimeters. The anterior half of the second molar (m^2) is preserved; it measures 35 millimeters from the outer side of the parastyle to the inner side of the protocone; the protocone and paracone are prominent; the protoconule is reduced; the metaconule is not preserved.

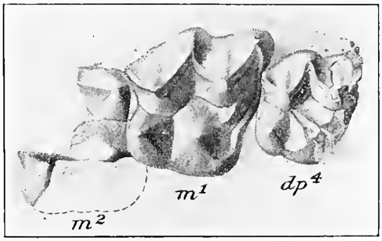

FIGURE 270.—Upper molars of *Palaeosyops fontinalis*

Natural size. Am. Mus. 5107 (type). Green River near mouth of Big Sandy Creek, Bridger Basin, Wyo.; level Bridger A?

As compared with the molars of *P. leidyi*, we note the following differences: (1) Ectolophs and cusps more trenchant and flatter; (2) outer border of the metacone ectoloph more inclined; (3) styles more sharply ridged; (4) hypocone of dp^4 projecting more internally than in corresponding tooth of *P. leidyi*. This species is certainly not a typical *Palaeosyops* in its dentition, as stated above. Measurements may be taken from the natural-size figures of the teeth in Figure 270.

Of the six specimens from Huerfano B (see above) a finely preserved palate (Am. Mus. 17411; fig. 271, A) of an aged individual and the unworn upper teeth (Am. Mus. 17425, fig. 271, D) of a young individual afford a close comparison with the two permanent teeth of the type of *Palaeosyops fontinalis* from Bridger A and are very similar both in characters and in measurement.

Comparative measurements of teeth of P. fontinalis, in millimeters

	Am. Mus. 5107 (type); Bridger A	Am. Mus. 17425; Huerfano B	Am. Mus. 17411; Huerfano B	Am. Mus. 17414; Huerfano B	Am. Mus. 17413; Huerfano B	P. paludosus Am. Mus. 13032; Bridger B 1
M^1–m^3	------	83	77	------	------	91
P^4, anteroposterior	------	16. 5	16. 3	------	------	18
P^4, transverse	------	21. 5	21. 5	------	------	22
M^1, anteroposterior	22	23	22. 5	------	23. 5	25
M^1, transverse	26	26	26	------	[a]26	26
M^3, anteroposterior	------	29	27	30	28	32
M^3, transverse	------	34	31. 5	34	32. 5	34
P^1–m^3	------	[a]146	141	------	------	160
P^1–p^4	------	[a]63	63	------	------	71

[a] Estimated.

General specific characters of P. fontinalis.—The distinctive specific characters of *P. fontinalis* are (1) parastyle very prominent; (2) protoconules reduced; (3) meta- and hypocones closely compressed; (4) no trace of metaconules; (5) no hypocone on m^3; (6) premolars very simple; (7) restored palate of considerable breadth; and (8) the maxillaries send back a splint on the outer side of the malars, as in typical *Palaeosyops*.

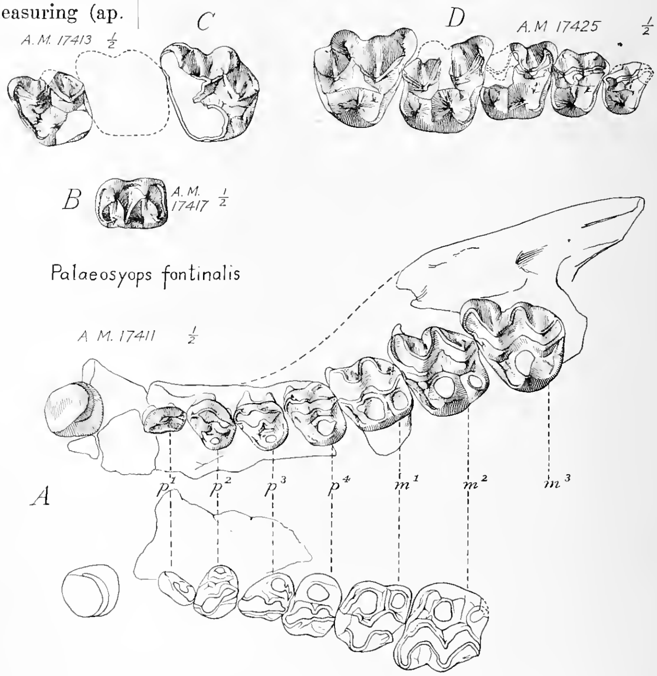

FIGURE 271.—Teeth of *Palaeosyops fontinalis*

One-half natural size. Referred specimens from Huerfano B. (See p. 317.)

Since all these six individuals from Huerfano B agree closely in size with each other and with the type of *P. fontinalis,* they establish Huerfano B and Bridger A as the *Palaeosyops fontinalis* zone, distinguished by true ancestors of *Palaeosyops* inferior in size to any known members of this genus in Bridger B.

Palaeosyops longirostris Earle

Plate LVI; text figures 108, 268

[For original description and type references see p. 172]

Type locality and geologic horizon.—Cottonwood Creek, Bridger Basin, Wyo; Bridger formation, *Palaeosyops paludosus-Orohippus* zone (Bridger B).

Specific characters.—P_1–m_3, 156 millimeters (estimated); p_2–m_3, 143; m_{1-3}, 90; p_4 rather simple. Wide posterior extension of the ramus of the jaw behind m_3. Canine large, semiprocumbent. Mandibular symphysis elongate.

This little-known form appears to be closely related to but somewhat smaller than the typical *P. paludosus.* The type specimen, the left ramus of a lower jaw (fig. 268, A), was well described by Earle in his memoir of 1892. No other known material has been referred with certainty to this species.

Palaeosyops paludosus Leidy

Plates LII, LVI, LVIII, LIX, LXII; text figures 86, 88, 267 A, 268 B, 405, 407, 732

[For original description and type references see p. 157]

Type locality and geologic horizon.—Bridger Basin, Wyo.; *Palaeosyops paludosus-Orohippus* zone (Bridger B). Bridger B 1, as represented by the base of the section of Church Buttes, is apparently the type geologic level. The Bridger B 2 specimen is from the lower portion of the Grizzly Buttes deposition.

Specific characters of type and of referred specimens.—Of small size; p_2–m_3, 152 millimeters; p^2–m^3, 144; m_2 (ap. by tr.), 33 by 20.5; second and third superior and inferior premolars more primitive than in succeeding stages; p^2 with a single external cone—that is, no tritocone; p^3 with a rudimentary tritocone; superior molars subquadrate and premolars without mesostyles. No rudiments of osseous horns.

Joseph Leidy, over 50 years ago, aptly characterized this animal specifically as "swamp or marsh loving" (*paludosus*) because its teeth are manifestly adapted to the softer kinds of herbage.

By Leidy himself and by subsequent authors the term "*paludosus*" was erroneously applied to the more progressive species which are classified in this monograph under *P. major*, *P. leidyi*, and *P. robustus.*

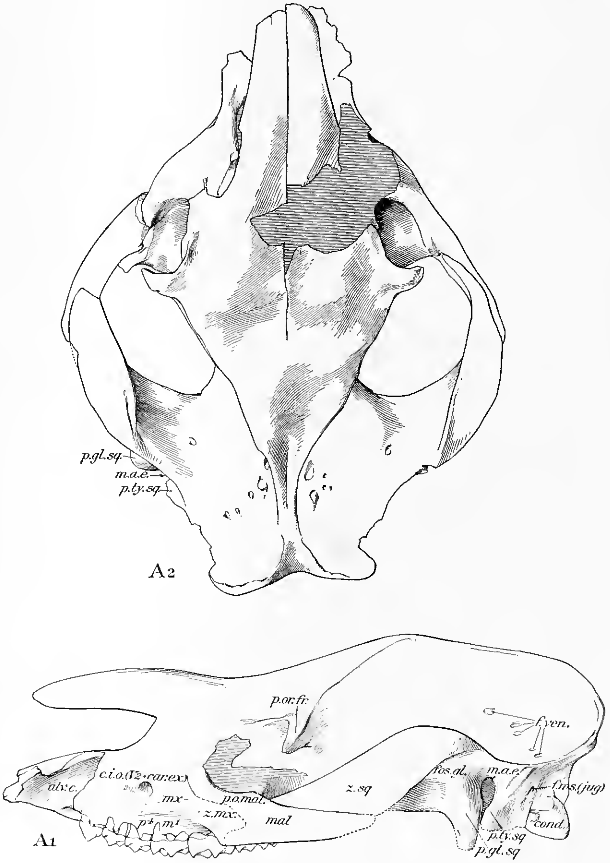

FIGURE 272.—Skull of *Palaeosyops major*

One-fourth natural size. Am. Mus. 12182 (neotype skull). Cottonwood Creek, Bridger Basin, Wyo.; Bridger formation, level B 3. Crushed downward but slightly reconstructed from Am. Mus. 1516 (*P. leidyi*), especially in the infraorbital region. A_1, Side view; A_2, top view.

Materials.—Many of the specimens other than the type which were referred to this species in the voluminous literature belong on higher geologic levels, such as those from upper Cottonwood Creek (Bridger B 4 and 5) and from Henrys Fork (Bridger C and D), and consequently to higher stages of evolution. *P. paludosus* in the restricted sense is represented by Leidy's isolated type teeth in the National Museum (No. 762 in part), which are carefully distinguished in Chapter III of this monograph. An upper dental series probably preserved in the Philadelphia Academy collection was also referred by Leidy to *P. paludosus* (Leidy, 1873.1, pl. 4, fig. 3) and may possibly be conspecific with the type. In the same stage of evolution apparently is the fine lower jaw (Am. Mus. 11680) from Millersville, Bridger Basin, level B, which may be regarded as a neotype. Agreeing well with this neotype lower jaw is the finely preserved upper dentition Am. Mus. 13032, also from Bridger B 1. Three other jaws (Am. Mus. 11692, 11711, from Grizzly Buttes, Bridger B 2, and 13118, from Mountain View, Bridger B 2, Grizzly Buttes) may also be referred to this very primitive species.

The inferior molar, m_2, of Leidy's original type, now taken as the lectotype, measuring (ap. by tr.) 33 by 20.5 millimeters, exhibits crescents with striated sides, very low antero-internal cusp, very rudimentary metastylid, prominent entoconid, with a distinctly developed entostylid, also anterior and posterior cingula wanting, even between the valleys.

The superior premolar type (Nat. Mus. 762, in part) consists of the ectoloph of p^4 of the left side and of the inner half of the crown of p^4 of the right side, two teeth conjoined by wax. The accurate transverse measurement of the crown, therefore, can not be given; the ectoloph measures 19 millimeters anteroposteriorly and 13 millimeters (estimated) from the base of the crown to the tip of the partially worn protocone; it consists of a prominent anterior style, a protocone, sharply convex externally, spreading into an external cingulum which surrounds the less convex tritocone, a cone which is slightly smaller than its fellow the protocone. The inner half of the crown of p^4 of the opposite side consists of a deuterocone, a faint ridge extending anteriorly toward the protocone, measuring 16 millimeters anteroposteriorly; on either side are anterior and posterior cingula which rise gently toward the apex but do not tend to surround the smooth inner side of the protocone; this condition is exactly intermediate between that observed in *L. laevidens* and *P. major*.

As remarked above, the association of these upper teeth with the lower is doubtful; the upper teeth may belong to *Limnohyops*. The second superior molar (Nat. Mus. 758) consists only of the anterior half of the tooth, estimated at 35 millimeters transversely; it exhibits a stout parastyle, a median rib opposite the paracone, a distinct and somewhat transversely elongated protoconule, a low, conical protocone, a low and slightly worn cingulum which rises at the antero-internal edge of the protocone. The anterior cingulum is incomplete at a point anterior to the tip of the paracone (cf. *P. major*, Am. Mus. 12182). The slopes of the cusps, like those of the molars of *P. major*, are vertically striated. The anterior crescent is considerably smaller, whereas in higher stages the two are subequal.

Specific characters of the types.—It is difficult to define this species clearly from the lectotype specimens which are described in detail above. Reference should be made to the very carefully prepared natural-size drawings of these teeth on Plates LII and LIX. The following is a provisional definition:

Second inferior molar (lectotype) with distinct but depressed entoconid, and metastylid and entostylid folds; median ridges within the crescents; cingula not prominent; dimensions, anteroposterior, 33 millimeters; transverse, 20.5; superior premolars without trace of internal cingulum at base of deuterocone; subequal protocone and tritocone on p^4, no mesostyle; superior molars with moderately developed cingula and protoconule, moderately open external crescents.

The superior teeth referred by Leidy to this species are the principal ones among those described by Leidy as *P. paludosus* which possibly belong to this primitive species. The figure copied herewith is taken from Leidy's memoir of 1873 (pl. 4, fig. 3). The specimen is recorded from Grizzly Buttes, Bridger Basin, Wyo., probably Bridger B 2. It is seen at once to belong to a small animal in a very simple stage of evolution. The premolar teeth are readily distinguished specifically, as shown in the figure, by the extremely simple character of the ectoloph of p^2; it exhibits not even a rudiment of the tritocone, a cusp which is strongly developed in the geologically successive *P. major*. The measurements of the teeth as figured on Leidy's plate, said to be of natural size, are suspiciously small—namely, p^1–m^3 137 millimeters, p^2–m^3 133—and may indicate, if the drawing is correct, that the specimen belongs to a smaller form, such as *P. longirostris*.

Osborn's neotype and other referred material.—The neotype jaw (Am. Mus. 11680, fig. 268, B) is referred to the same species as the lectotype (see above) on account of the absolute similarity in form and size of the second inferior molar (m_2) in the two specimens. Although small it belongs to a male animal, as indicated by the very deep and prominent chin and robust canines, which measure (ap. by tr.) 24 by 22 millimeters at the base of the crown. The lower borders of the rami are especially thickened beneath the premolar series, the vertical depth of ramus in front of p_2 being 60 millimeters and behind m_3 81 or 84. While broad, the anterior face of the lower portion of the coronoid process lacks the concavity which distinguishes *P. major*. The grinding series, p_2–m_3, measures 152 millimeters as compared with 163 to 169 in *P. major* and 174 in *P. robustus*. P_2 is in a simple stage, not showing the distinct rudiments either of the paraconid or of the crescentic conformation of the hypoconid. In p_3 faint rudiments of the paraconid, of the metastylid, fold, and well-developed hypoconid crescents are seen. In p_4 all these characters are strongly accented, but this tooth can not be described as molariform, as it still lacks the entoconid, the elevation of the hypoconid, and the equalization of the two lobes. The outline form of this jaw is represented in Figures 267, 268, B, and the detailed characters of the teeth are shown in Plates LVI, LXII, Figure 268.

Another jaw (Am. Mus. 11711) from the bluff above Mountain View, Bridger Basin, Wyo., Bridger formation, level B, has the same general characters but is of smaller size and unfortunately lacks the teeth.

In a third, rather young jaw (Am. Mus. 11692) from Grizzly Buttes, level B 2, the molars are only a shade smaller than those of the type, with which they agree in most details; but this younger jaw is slightly more progressive in the structure of p_4, of the paraconids, and of the metastylid folds in m_1–m_3.

In a fourth jaw (Am. Mus. 13118), from B 2, the characters and measurements agree perfectly with those of the type and neotype.

In a fifth jaw (Am. Mus. 12679), from B 3, the dental measurements are slightly smaller than in the neotype.

The finely preserved upper teeth (Am. Mus. 13032) fit exactly with the neotype jaw. These upper teeth represent one of the oldest (level B 1) and certainly most primitive Bridger titanotheres known. They differ from the type of *L. priscus* in the following respects:

1. They are from a lower level, very low in B 1 (Granger).
2. They are larger.
3. The premolars are far more primitive—the most primitive known, in fact, among Bridger titanotheres.
4. The hypocone-cingule on m^3 is imperfect.

They agree well with the neotype lower jaw of *P. paludosus* in the following respects:

1. They are from the same general level (B 1).
2. They correspond in general size.
3. They show exact fitting of upper teeth (Am. Mus. 13032) with lower teeth (neotype of *P. paludosus*, Am. Mus. 11680)—that is, certain measurements between cusps in the upper jaw agree with corresponding measurements between interspaces and valleys of the lower teeth. The accuracy of this correspondence is highly significant.
4. They show correspondingly backward development in the upper premolars of No. 13032 and of the lower premolars in the neotype of *P. paludosus*.
5. The canines are large and rounded and are characteristic of the genus *Palaeosyops*.

In short, this specimen, No. 13032, appears to fill the great want of an upper dentition of *P. paludosus*. The presence of a cingule-hypocone on m^3 does not necessarily excluded it from *Palaeosyops*, because this cusp is more or less variable, a fact shown by its absence in *L. monoconus* and its presence in *P. diaconus* (= *robustus*).

Specific characters of the neotype and other referred specimens.—Although the first of the Eocene titanotheres to be discovered and constituting the classic type of the genus *Palaeosyops*, and also the oldest in point of evolution, this primitive species is still imperfectly known because of the rarity of the specimens on this low geologic level. A vast amount of confusion has attended the previous description of *P. paludosus*. We are now for the first time enabled to characterize it sharply as a stage in which the second and third superior and inferior premolars are extremely simple in point of cusp evolution. Referring the reader to the previous systematic discussion in Chapter III, we may here summarize our knowledge of the neotype and the referred specimens. The lower jaw (Am. Mus. 11680) is taken as the neotype, in which m_2 agrees exactly with that of the type. This jaw exhibits the following specific characters: P_2–m_3, 151 millimeters; p_2 extremely simple, with faint trace of paraconid fold and noncrescentic hypoconid; p_3 with rudimentary paraconid, metastylid fold, and crescentic hypoconid; p_4 with very decided paraconid, elevated metaconid, distinct metastylid fold, broadly crescentic hypoconid, extremely rudimentary entoconid; m_2 closely agreeing in form and measurement with that of the type; m_3 with a narrow, subcrescentic hypoconulid, median in position.

The following measurements of two specimens referred to *Palaeosyops paludosus* should be compared with the table of measurements on page 316:

Measurements of Palaeosyops paludosus

Upper teeth, Am. Mus. 13032, Bridger B 1:	Millimeters
P^1–m^3	102
P^2–m^3	144
P^1–p^4	71
M^1–m^3	91
P^4, ap. by tr	18×22
M^1, ap. by tr	25×26
M^3, ap. by tr	32×34
Neotype lower jaw, Am. Mus. 11680, Bridger B 1:	
Condyle to symphysis (estimated)	340
Length of symphysis (estimated)	85
Depth of ramus behind m_3	85
Condyle to angle	165
P_1–m_3 (estimated)	169
M_1–m_3	98
P_4, ap. by tr	17×12
M_1, ap. by tr	26×18
M_3, ap. by tr	43×23

Palaeosyops major Leidy

Plates LVIII, LXII; text figures 89, 215, 268 C, 272, 279, 515, 516, 533–535, 546, 550, 686, 721, 741

[For original description and type reference see p. 158. For skeletal characters see p. 620]

Type locality and geologic horizon.—Bridger Basin, Wyo.; Bridger formation, levels B 2 to 4, *Palaeosyops paludosus-Orohippus* zone. Leidy's type jaw is simply recorded from Grizzly Buttes, equivalent to Bridger B 2. The geologic range of this species, as exposed in the upper portions of Grizzly Buttes and the lower portions of the Cottonwood Creek section, covers Bridger B 2, B 3, and probably B 4.

Specific characters.—Of intermediate to large size; total length of skull (estimated), 389 to 436 millimeters; p_2–m_3, 164; p^2–m^3, 147; lower premolars somewhat more progressive; superior premolars without mesostyles; p^2 with two external cones—that is, both protocone and tritocone. No rudiments of osseous horns. Cephalic index 74 to 77.

In 1873 Leidy named this quadruped *P. major*, in reference to its larger size as compared with *P. paludosus*, but he was unable to characterize it fully.

At least six rudimentary new characters, or rectigradations, may now be observed in the grinding teeth alone of this mutation, or subspecific stage—so much for numerical change. The quantitative or proportional changes (allometrons) are equally significant of progressive evolution.

Type and neotype.—Finding it impossible to define this species from Leidy's type specimen, which consists of an incomplete and abnormal fragment of a ramus only, a neotype jaw and skull were selected by Osborn from the same geologic level—namely, Am. Mus. 12181 and 12182, from middle Cottonwood Creek, level B 3 in the Bridger Basin. From these specimens discovered by the American Museum expeditions the species is defined as above. In continuation of the systematic description above, *P. major* may be clearly distinguished as an important early stage of evolution, successive to *P. paludosus.*

Materials.—This species is represented by Leidy's pathologic and fragmentary type ramus (Philadelphia Acad. Nat. Sci. collection, fig. 89) and by six referred specimens in the American Museum from levels B 2 and B 3 of the Bridger Basin, as follows: A crushed but finely preserved skull (Am. Mus. 12182), probably belonging with the mandibular ramus (Am. Mus. 12181), both from Cottonwood Creek, Bridger Basin, level B 3; a still finer specimen (Am. Mus. 13116), from middle Cottonwood Creek, level Bridger B 3; a skull (toothless) and excellent limb bones (Princeton Mus. 10276); an imperfect palate from Smiths Fork, probably from level B 3 of the Bridger Basin; lower jaws (Am. Mus. 12183) from middle Cottonwood Creek, level Bridger B 3; a fine set of lower teeth (Am. Mus. 12165) from the same locality, level Bridger B 2; fine jaws (Am. Mus. 5101), locality and level unknown. The measurements of the jaws indicated above agree approximately with the few measurements that may be taken from Leidy's very imperfect type, and there is consequently little doubt about the final identification of this species, which, like *P. paludosus*, has been confused with species belonging to higher stages and higher geologic levels.

Specific characters of type.—The only specific characters that can be drawn from the fragmentary type specimen (fig. 89) are the measurements of the lower jaw (97 mm. below m_3) and the length of the inferior molar series (m_{1-3}, 115 mm.).

P. major can not, however, be distinguished specifically by characters taken from the type, such as the length of the true molar series or the depth of the ramus behind m_3, because specimens of *Palaeosyops leidyi* having the same measurements are found at higher levels. It must therefore be distinguished by the characters of the neotype specimens found at the same geologic level as the type.

Characters of neotype jaw.—The jaw (Am. Mus. 12181, fig. 268, C), from Bridger level B 3, middle of Cottonwood Creek, is taken as a neotype, although it belongs to a young adult or a female and is somewhat less robust than the type. This jaw was found near the skull (Am. Mus. 12182) and may belong to it. It affords, however, the following distinctive characters as compared with the referred jaws of *P. paludosus:* P_3–m_3 164 millimeters; p_2 with rudimentary paraconid, metastylid fold, and subcrescentic hypoconid (characters all of which are wanting in *P. paludosus*); p_3 with distinct paraconid, very rudimentary metaconid, with metastylid fold subcrescentic and elevated hypoconid; p_4 with broadly prominent metaconid, metastylid fold, hypoconid low, broad, and relatively elevated. More in detail, in p_2 we see a tooth slightly more progressive than that of *P. paludosus* in the following respects, as shown in Plate LXII: It exhibits a very rudimentary paraconid and rudimentary metastylid fold and the beginning of a hypoconid crescent, yet these rectigradations are in their very inception. In p_3 the paraconid, metastylid fold, and hypoconid crescents are accompanied by the entoconid in its most rudimentary form. In p_4 in the unworn condition (Am. Mus. 12165) we see a distinct entoconid and a relatively more elevated hypoconid than in *P. paludosus. P. major* is therefore distinguished as a mutation or higher stage than *P. paludosus* by a number of rudimentary cusplets on p_{2-4} and by the general progress of these teeth toward the molar form. Similarly, in the molar teeth, paraconids, striations on the sides, ridges within the crescents, and festoonings of the external cingulum seem more clearly defined, as well as the entostylids. A very distinctive character also is the hollowing out or concavity of the base of the coronoid process behind m_3, not observed in *P. paludosus;* the free portion of the coronoid process is still quite high and recurved, not having assumed the triangular form seen in *P. leidyi;* the thickening of the lower borders of the rami now extends back below the first molar.

The characters of the jaw of *P. major* are also exhibited in Am. Mus. 12183 and 5101. They are distinguished by the following principal features: (1) The decided curvature of the lower border; (2) the posterior thickening of the symphysis (ap. 89 to 103 mm.); (3) the depth of the ramus behind m_3 (86 mm., cotype, female; 96, type, male; 97, Am. Mus. 12183); (4) the slight reduction of the free portion of the coronoid process; (5) the deep excavation of the anterior border at the base of the coronoid process.

Characters of the neotype skull.—The fine skull, Am. Mus. 12182 (figs. 272, 279), from level B 3 of the Bridger Basin, top of Grizzly Buttes, may also be taken as a neotype and possibly belongs with the neotype jaw above described. It exhibits the following characters, which are well displayed in Plates LVIII, LXII: Superior teeth, p^2–m^3, 147 millimeters; no mesostyles thus far observed on p^3, very faint shadow rudiment of a mesostyle on p^4, cingulum not completely embracing inner sides of superior premolars, tritocone on p^2 small, no external cingulum; ectolophs of molars with "wide-angle" or open crescents; parastyle buttresses not very prominent; rudimentary external cingula opposite valleys; the protoconules very large, angulate; the metaconules small.

The skull is that of a young adult; in an old adult the masseteric ridge below the zygoma would be more strongly developed. It exhibits clearly the convexity of the forehead, the abbreviated sagittal crest, the broad, low occiput, the separation of postglenoid and post-tympanic processes, the absence of even a rudiment of the frontonasal horn; and these characters in connection with its inferior size indicate a decidedly lower stage of development than that of the skull of *P. leidyi* or *P. robustus*. (See table on p. 316.)

The superior cutting teeth are unknown.

Superior premolar-molar series.—This series is well represented in the neotype skull (Am. Mus. 12182), possibly also in Am. Mus. 5105, Cope's paratype of *P. laevidens*, and in Princeton Mus. 10276. The molars are readily distinguished from those of *P. leidyi* and *P. robustus* by their smaller dimensions. (See table, p. 316.) As pointed out above, the premolars are distinguished by the absence of well developed mesostyles in p^{3-4} and by the smaller size of the tritocone of p^2.

Measurements of another specimen.—A beautifully preserved superior premolar-molar series (Am. Mus. 2361, Pls. LVIII, LXII), probably from level A of the Washakie Basin, is in a more advanced stage of premolar evolution than *P. major* and differs from the neotype of that species in having a larger tritocone on p^2, a larger deuterocone and stronger "protoconule ridges" on p^{3-4}, more prominent protoconule ridges on m^{1-3}, and a well-marked metaconule ridge on m^3. The specimen also differs in details from those referred to *P. leidyi*, *P. robustus*, and *P. copei*, and it may represent a new species or subspecies characteristic of Washakie A. Comparative measurements of this specimen are as follows:

Comparative measurements of species of Palaeosyops, in millimeters

	Palaeosyops sp., Am. Mus. 2361	P. major		P. copei?, Am. Mus. 13177	P. copei, Am. Mus. 11708 (type)
		Am. Mus. 5105	Am. Mus. 12182		
P^1–m^3	155	------	------	------	[a] 170
P^2–m^3	145	[a] 145	147	------	[a] 153
P^2–m^2	112	112	116	------	118
M^1–m^3	94	95	94	------	96
P^4, anteroposterior	17	17	19	17	19
P^4, transverse	24	24	24	26	26
M^1, anteroposterior	26	26	27	26	24
M^1, transverse	30	------	31	29	27
M^3, anteroposterior	33	[a] 31	33	------	34
M^3, transverse	35	38	40	------	40

[a] Estimated.

Palaeosyops leidyi Osborn

Plates XVI, XXVII, XLIV, L, LIII, LVI, LIX–LXII; text figures 27, 28, 33, 118, 217–220, 227, 254–256, 273–283, 305, 482, 483, 485, 511–513, 520, 522, 523, 536, 537, 539, 540, 543, 546, 552, 559, 645, 661, 703, 713, 716, 727, 737, 741, 742, 745

[For original description and type references see p. 181. For skeletal characters see p. 620]

Type locality and geologic horizon.—Henrys Fork, Bridger Basin, Wyo.; Bridger formation, *Uintatherium-Manteoceras-Mesatirhinus* zone. Bridger levels C 2, C 3, C 4, and C 5?, as exposed on Henrys Fork in the Bridger Basin, are the geologic levels of this species, which is well above that of *Palaeosyops major*—approximately 200 feet.

Specific characters.—Of larger size; total length of skull 415 millimeters; p^2–m^3, 158; p_2–m_3, 168. Diastemata behind canines. Posterior superior premolars with mesostyles. Barely defined swellings representing the rudiments of osseous frontonasal horns. At least four new numerical characters, or rectigradations, in the grinding teeth. Cephalic index, 74.

This species is named in honor of Joseph Leidy, the founder of American vertebrate paleontology and first contributor to our knowledge of the titanotheres. *P. leidyi* is noteworthy as the earliest form to have the visible beginnings of horns (Pl. XVI, fig. 281). It is the only species of which the bony structure is known in nearly every part; this knowledge is obtained chiefly from materials collected by the American Museum expeditions under Dr. J. L. Wortman.

The form of the occiput in the type skull (figs. 277, 279, B_1) is very exceptional and may be an individual variation. The premolars of *P. leidyi* are more advanced than those of *P. major*, but this and the incipient horn bosses are about the only decisive characters separating the two. The average size of the skull in *P. leidyi* was larger than in *P. major*, but exceptionally large individuals of *P. major* are actually larger than small individuals of *P. leidyi* (see table on p. 316); in fact, *P. major* and *P. leidyi* might by some systematists erroneously be regarded as successive mutations (in the sense used by Waagen) from *P. paludosus* rather than as species in the Linnaean sense, and this conception might be conveniently expressed by trinominal names, such as *P. paludosus paludosus*, *P. paludosus major*, and *P. paludosus leidyi*.

In the opinion of the present author we should hold a heredity conception—that of germ evolution through the independent advance of a very considerable number of single characters, including new rectigradations, such as cusplets on the teeth and horn bosses on the skull; and new proportions or quantitative characters (allometrons). Expressed in another way, *P. leidyi* succeeded *P. paludosus* after a vast interval of time, as indicated by the intervening 400 to 600 feet of sediment. In the long series of generations that separated these stages new tendencies of character and proportion, such as brachycephaly, were one by one added in heredity, so that the offspring of *P. leidyi* were born on a more specialized heredity plane than those of *P. paludosus*. *P. leidyi* was by no means the same animal; it was an enriched stock; it possessed in its germ substance a number of characters not found in its ancestor, and probably it lost some other germ characters.

Materials.—This species is by far the most richly and abundantly represented in remains of skull, tooth, and skeleton. The American Museum collections contain the following principal specimens: No. 1516, a perfectly preserved female skull, level not definitely ascertained, probably C 4; No. 12185, a male skull transitional between *P. leidyi* and *P. major,* level C 3; No. 1581, a laterally crushed skull with a convex forehead and faint rudiments of the horns, associated with portions of the skeleton (possibly *P. robustus*), level probably Bridger C; No. 1544, the type of *P. leidyi,* a broad-topped skull with lower jaw from Henrys Fork, with a large part of the skeleton associated, level probably upper C. Also the following superior teeth: No. 12208, m^2–m^3, level C 4; No. 1552, c–m^3 left, p^2–m^2 right, a small female, very progressive, level probably upper C; No. 12196, p^2–m^3 of right side, level C 2; also No. 1565, milk premolars and m^1–m^2, from Henrys Fork, level probably C; in the Princeton Museum, skull and jaws, No. 10009, level probably upper C.

FIGURE 273.—Skull and head of *Palaeosyops leidyi*

Restoration by Erwin S. Christman made under the direction of W. K. Gregory.

The best specimen of a lower jaw is that associated with the type skull (No. 1544), certainly a male. There are also Am. Mus. 1585, 1522, 1564, 12200, all probably males; 12197, which is in the milk stage, corresponding closely in size with the upper milk teeth (1565); 5103, possibly a female; and 1549, a female; also Leidy's cotype of *P. major* (Acad. Nat. Sci. Philadelphia). None of the foregoing lower jaws are positively recorded as to level.

Specific and age characters.—The materials enumerated above exhibit a considerable range of measurement (see table on p. 316), as well as progressive development of all the mutational characters. The skull form in Am. Mus. 12185 is the most primitive of the series and in many respects takes a position intermediate between that of *P. major* and that of *P. leidyi;* on the other hand, the type skull (Am. Mus. 1544) has an extremely broad cranial roof and differs from all known specimens of *Palaeosyops* in this respect. In addition to these differences, which are due to actual progressive stages of development, there are apparent differences due to age. For example, as explained above, the rudimentary cusplets (such as the paraconid and metastylid), seen especially on the unworn premolar teeth of young individuals, disappear on the worn premolar teeth of old individuals. Another very important age character is the faint frontal rugosity prophetic of a horn seen in old male skulls such as Am. Mus. 1581 but absent in all the younger male and female skulls. With these exceptions *P. leidyi* may be provisionally characterized as follows:

Specific characters of P. leidyi based on the type.—Premolars, especially in specimens from the upper levels, slightly more complex than in *P. major;* paraconid distinct and metaconid rudimentary on p_2; metaconid distinct on p_3; entoconid distinct on p_4; tritocone larger on p^2, becoming convex or ridged; p^3 with mesostyle rudimentary or variable; p^4 with mesostyle distinct, sometimes large. Superior molars with parastyle somewhat more prominent, ectoloph consequently more oblique, external cingula more distinct, all cingula heavier in specimens from the upper levels, valleys of the external crescents somewhat narrower; conules variable, often reduced, sometimes very large; metaconules lophoid on m^1 and m^2, often much reduced, sometimes very large on m^3. In the skull, sagittal crest variable, sometimes narrow, in the type broadened into a flat crest (figs. 276–279), occiput confluent with cranial roof superiorly (in type), posttympanic and postglenoid approximated, almost touching, coronoid process of jaw broadly concave inferiorly.

Incisors.—The superior series measures 70 millimeters from side to side (Am. Mus. 1544); the incisor teeth increase in size from i^1 to i^3, transversely measuring i^1 11 millimeters, i^2 12, i^3 16. Similarly the inferior incisors increase slightly but regularly in height and breadth, the lateral teeth being either continuous with or slightly separated from the canine. There are superior diastemata between the grinding series and the canines, also between the lateral incisors and the canines.

Canines.—The canines are more slender in females, measuring vertically 32 millimeters (Princeton Mus. 10009); the superior canines in this specimen measure 34 millimeters. In the males the canines are more robust, the fangs at the base measuring (ap. by tr.) 21 by 20 millimeters, and when unworn are very slightly recurved, sharply pointed, differing from those of *Telmatherium* in their circular section and strongly convex inner sides. In one specimen (Am. Mus. 1549) the posterior base of the crown is horizontally grooved, apparently as a result of use of this tooth in uprooting plants or pulling down twigs.

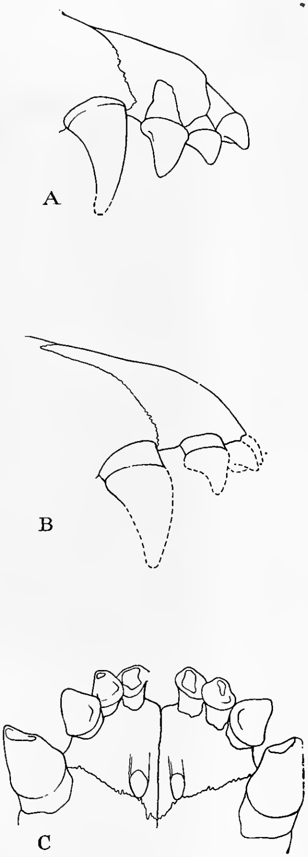

FIGURE 274.—Incisors and canines of *Limnohyops* and *Palaeosyops*

One-half natural size. A, *L. priscus*, Am. Mus. 11687 (type); Grizzly Buttes, west Bridger Basin, Wyo.; Bridger formation, lower beds. B, *P. leidyi*, Am. Mus. 1516; Sage Creek, Bridger Basin. C, *P. leidyi*, Am. Mus. 1544 (type); Henrys Fork, Bridger Basin; probably Bridger upper C or D.

Superior grinding teeth in the type and other specimens.—P^1 exhibits diastemata both in front and behind (see Pls. LX, LXII), whereas in the more progressive specimens of *P. robustus* the diastema behind p^1 is closed; p^1 is occasionally large (Am. Mus. 1552, 5102). The succeeding premolars are distinguished by sharply convex protocones, flattened or very slightly convex tritocones, internal cingula variable, mesostyle wanting on p^3, variable, often very distinct on p^4; external cingula of the premolar and molar ectolophs are variable but especially strong in progressive specimens; in general, more sharply marked than in *P. major.* It is a striking fact that in all the typical specimens (Am. Mus. 1544, 1516; Princeton Mus. 10009) referred to this species the metaconules are wanting, while the protoconules are quite distinct. M^3 is a large tooth but still inferior in measurement and especially in development of the parastyle to that of *P. robustus.* The series p^2–m^3 measures from 150 to 159 millimeters, as compared with 145 to 147 in *P. major* and 163 to 170 in *P. robustus.*

Inferior grinding teeth.—The most distinctive characters of the lower grinding teeth (Pl. LVI) are the prominence of the paraconid, the distinctness of the metaconid, and the crescentic form of the hypoconid on p_2 as compared with that of *P. major;* in more progressive specimens of *P. leidyi* p_2 is almost as progressive as p_3 in *P. major.* Similarly, p_3 and p_4 are much more advanced than the corresponding teeth of *P. major.* In the true molars a marked feature is the more conic form of the hypoconulid of m_3. All these specific characters, however, exhibit fluctuations either toward a more primitive or a more progressive type.

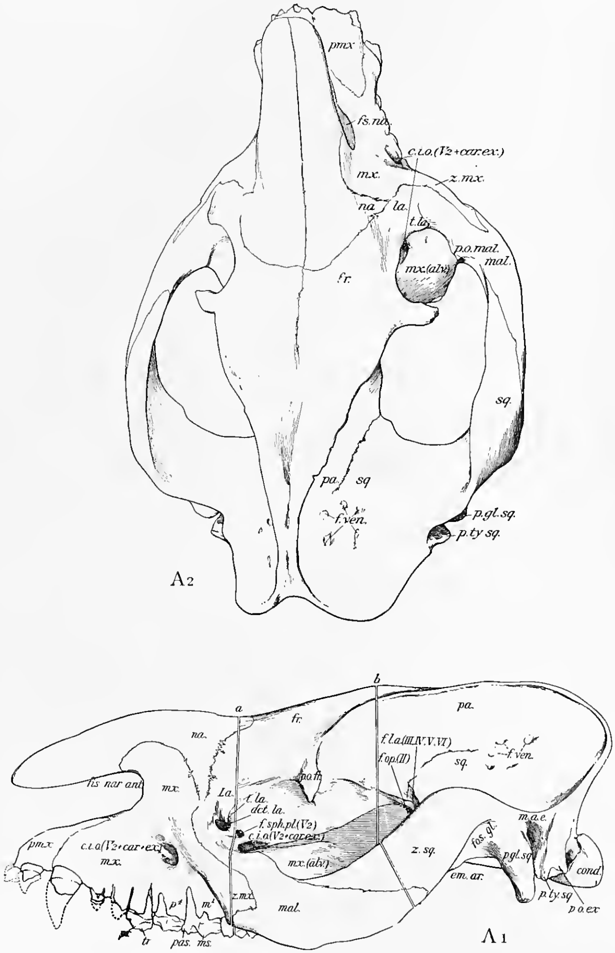

FIGURE 275.—Skull of *Palaeosyops leidyi*

One-fourth natural size. Am. Mus. 1516; Sage Creek, Bridger Basin, Wyo.; level probably Bridger C or D. A1, Side view, reversed (canines from Am. Mus. 12185); A2, top view.

Stages of evolution represented by the skulls.—All the characters of the cranium of *P. leidyi* are more progressive than those of *P. major,* and several stages are represented in the five skulls described below.

Some of these stages belong to animals related to the type of *P. leidyi;* others are intermediate between *P. leidyi, P. major,* and *P. robustus.* Of paramount interest is the origin of the osseous horns.

First stage: Transitional skull (Am. Mus. 12185) from level Bridger C 3, found at the mouth of Summers Dry Creek, appears to be the most primitive in its dentition, p_3 lacking the mesostyle, p^2 comparatively primitive, and the premolar-molar series measuring 162 millimeters, yet the sagittal crest is much broader (17 mm. at narrowest part) than in the *P. major* hypotype skull; the zygomata are more massive and widely expanded, and the measurements throughout are more robust. In this specimen the protoconules are greatly reduced and the metaconules are small and lophoid. It is apparently a male, the canines measuring 36 millimeters vertically and 20 across the base of the crown. The molar crescents are of the "wide-angle" type seen in the hypotype of *P. major.*

Second stage: A higher stage is represented by the female skull Princeton Mus. 10009, in which as a progressive feature a very distinct mesostyle is observed on p^4 and a rudimentary mesostyle on p^3; p^2–m^3 estimated at 150 millimeters. The superior molars exhibit very distinct protoconules but no metaconules. The lower jaw exhibits the more oblique chin of the female type, and the mandibular ramus measures 87 millimeters behind m_3, in which the hypoconulid is progressively conic in form. In this specimen, however, m_2 is very simple.

Third stage: The third stage exhibits the horn swellings without rugosity. It is represented by the finely preserved, apparently female skull Am. Mus. 1516 (fig. 275), in which the zygomata are moderately expanded and the sagittal crest has a minimum breadth of 13 millimeters. More in detail, the superior aspect represents an adult but not aged animal. Although practically of the same size in its length (415 mm.) it is somewhat narrower (275 mm. as against 310) than the type (Am. Mus. 1544) and appears to be in a stage only slightly advanced beyond that of skull Princeton Mus. 10009, because the sagittal crest is just beginning to broaden out into the plane of the vertex, the vertex of the crest measuring 13 millimeters transversely. The supratemporal crests are very prominent, sharply overhanging the temporal fossae and terminating anteriorly in prominent postorbital processes. Between the orbits the skull is broadly convex. The nasals extend 175 millimeters anteroposteriorly; posterolaterally they send down a broad flange beneath the adjoining parts of the maxillaries, lacrimals, and frontals. This flange is not (as in *Manteoceras*, etc.) largely covered by the forward extension of the frontals but appears in side view as a V-shaped area lying between the frontals and the maxillaries, a feature which is very characteristic of *Palaeosyops* and *Limnohyops*. The maxillaries rise in front of this point and arch over the maxillary notch. Another characteristic feature is that the nasals diminish toward the tips both in width and in the depth of the lateral decurvature. Still another feature is the broad entrance of the maxillaries below the anterior portion of the zygomatic arch.

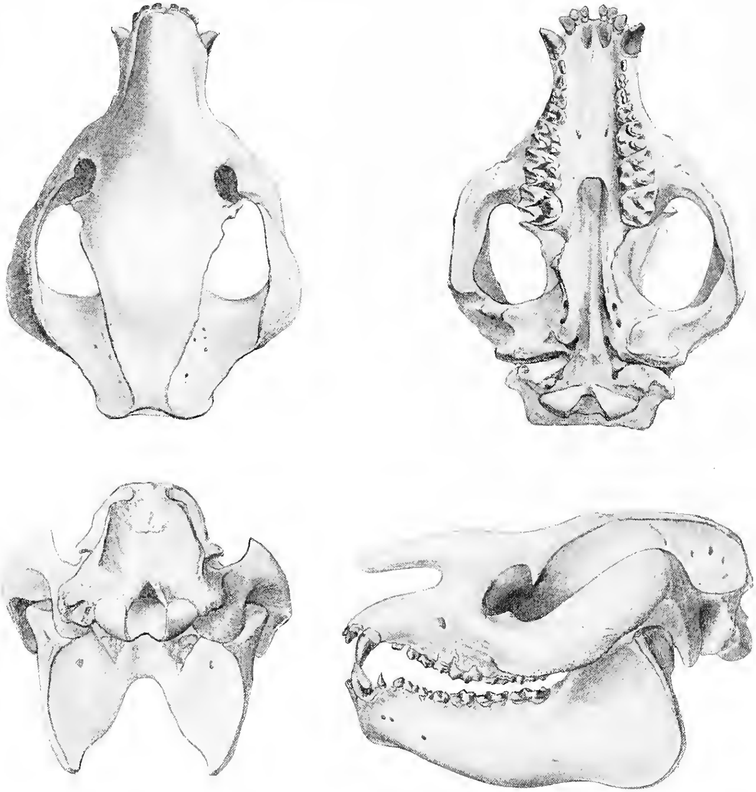

FIGURE 276.—Type skull of *Palaeosyops leidyi*

Am. Mus. 1544; upper part of Bridger formation, level C or D. Drawings by R. Weber. One-sixth natural size.

Horn swellings: By far the most important feature of this skull is the lateral horn swelling (fig. 275) on each of the frontals behind the nasofrontal sutures, which are entirely smooth. They would certainly never have been observed if attention had not been directed to this particular region of the skull by the distinct and rugose horn rudiments seen in a subsequent stage (*P. robustus*).

The type stage (mutation): A more progressive stage is the type cranium, Am. Mus. 1544. In this male skull the frontonasal horn swellings are so slight that they can barely be distinguished. This is a very important point because in the female skull just described the horn swellings are quite apparent. This fact, in connection with corroborative evidence in other phyla, tends to prove that in their inception the horns are not sexual characters. The supratemporal crests at the narrowest point are separated 36 millimeters by the broadly plane vertex of the skull, which passes uninterruptedly into the occiput by a gentle curve, there being no definite supraoccipital border. Immediately behind the orbits the vertex measures 136 millimeters transversely; between the orbits, 119 transversely. The frontoparietal, interfrontal, and frontonasal sutures are all closed by age. The nasals narrow from 76 millimeters at the broadest point posteriorly to 47 at the tips. In the palatal aspect we observe that the palate is relatively short and broad and not decidedly arched, the horizontal plates of the palatines being abbreviated. The postnarial space is relatively short and deep but less excavated than in *Telmatherium ultimum*. A relatively narrow bridge of bone (14 mm.) separates the foramen ovale from the foramen lacerum medium. The postglenoid processes are transversely extended but less decidedly so than in *T. ultimum*. A very characteristic feature is the broad triangular plate formed by the basioccipital and basisphenoid, slightly keeled in the median line, with a prominent rugosity (insertion of rectus capitus and constrictor muscles) at the junction of the basioccipital and basisphenoid and a very narrow bridge between the condylar foramen and foramen lacerum posterius. This is very different from the more elongate and laterally compressed region in *Tel-*

matherium ultimum. The post-tympanic processes are broadly oval, and the paroccipital processes are more slender and acute than in *T. ultimum.* A distinctive feature is the relatively sharp ridge constituting the inferior border of the malars from the point where the arch leaves the skull to their junction with the squamosals. The occipital view of the skull reveals a large mastoid foramen. This is also observed in *Limnohyops laticeps* and appears to be a distinctive feature of this series of crania. Unlike that of *L. laticeps* (figs. 261, 264) the summit of the occiput is not defined by a crest but passes directly into the vertex.

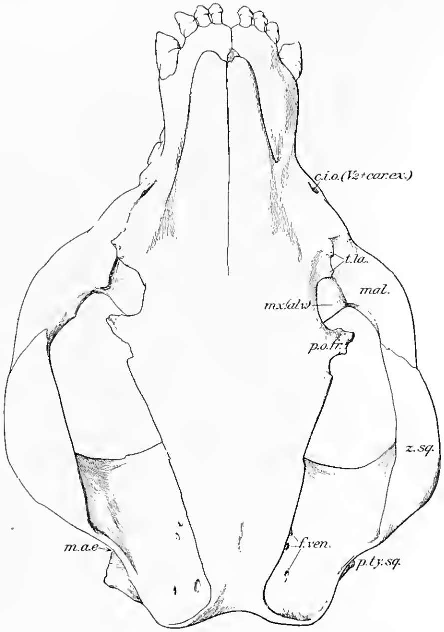

FIGURE 277.—Type skull of *Palaeosyops leidyi*

Top view. One-fourth natural size. Am. Mus. 1544 (type). Henrys Fork Bridger Basin, Wyo.; Bridger formation, level probably upper C or D.

In the lateral view, in addition to the features already mentioned, attention should be called (1) to the prominent antorbital knob or process on the lacrimals, to the abbreviation of the face, the space between the orbit and narial notch measuring but 70 millimeters; (2) to the absence of any horn rudiment; (3) to the convexity of the maxillaries as seen in side view; (4) to the abbreviation of the premaxillaries; (5) to the semicircular section of the malars below the orbits, which passes into the deep and laterally compressed section, with the inferior masseteric ridge beneath and behind the postorbital processes. The anterior and superior views of the cranium (figs. 277, 279) illustrate the characteristic rounded premaxillary symphysis and the abbreviation of these elements and the correlated rounding and depression of the maxillaries below the narial notch.

Type lower jaw: The perfectly preserved jaw of this specimen (fig. 280, C) exhibits the massive chin of the male form. On the lower surface we see the short (24 mm.) digastric fossa, the massive thickening of the mandibular rami (35 mm.), now extending back below m_2, the curvature of the lower border of the ramus, the increased depth (98 mm.) behind m_3, the triangular form of the free portion of the coronoid process, the broadly transverse expansion of the base of the coronoid process behind m_3, the transverse extension (74 mm.) of the condyles, the great elevation (175 mm.) of the condyles above the bottom of the angle, the extension of the angle backward to a less degree than in *Manteoceras,* also on the outer surface the subdivision of the masseteric fossa by a horizontal ridge extending forward and downward from the condyle.

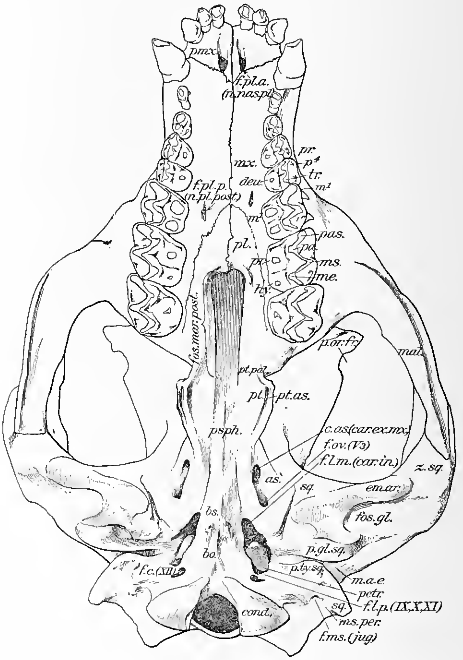

FIGURE 278.—Type skull of *Palaeosyops leidyi*

Palatal view. One-fourth natural size. Am. Mus. 1544 (type). Henrys Fork, Bridger Basin, Wyo.; Bridger formation, level probably upper C or D.

Dentition of the type: Diastemata appear between the opposite incisor series and behind both the incisors and the canines. P^4 is too much worn to show the mesostyle. On the molars the conules are almost completely worn off. External cingula are well marked, especially on m^3. In the lower jaw the incisors exhibit a compact transverse series measuring 53 millimeters. In p_2 the paraconid is well marked. The worn grinding teeth, although perfectly preserved, in such a specimen as the type do not present the distinctive characters of the series; but they demonstrate most conclusively that every element in the crown finally comes into some degree of use in the comminution of food and therefore has an adaptive significance; the styles, the cingula, the cones, the crescents, the conules, all are distinctly worn and blunted either by opposing elements in the lower teeth or by attrition of the food. The crown in this stage of wear presents an ineffective grinding and cutting apparatus and serves little more than a crushing function, because the low crenulated crescents and cones exhibit none of the hypsodont tendency so characteristic of the *Telmatherium* series.

Fifth stage: Mutation transitional to *P. robustus:* The male skull, Am. Mus. 1581 (represented in fig. 281), exhibits as its most interesting and important feature a rugosity and a very slight elevation of the frontals just behind their junction with the nasals, which represents the horn rudiment in this species in the incipient rugose stage. Viewed from above (fig. 281, A_2) this rugosity is seen to be very slightly convex—that is, it rises above the surrounding surface as an elevation involving the posterior border of the nasals and a portion of the nasofrontal suture. This horn is thus slightly posterior to the position which it occupies in the skull of the allied genus *Telmatherium.* In this skull the facial convexity is very prominent. Although m_3 is well worn, the conules are persistent and very slightly affected by the wear. The mesostyle on p^4, originally present, has been worn away.

Comparison with dentition of other forms: The measurements of several other maxillary series are given in the table on page 316. Among the large number of specimens examined some (such as Princeton Mus. 10009) are smaller and are more primitive in structure, approaching *P. major*, whereas others, such as Am. Mus. 5102 (*P. leidyi* advanced, but no mesostyle on p^4) are larger and more progressive. In the former the ectoloph and styles of the premolars are less strongly developed; in the latter the ectoloph, styles, and cingula are very strongly developed. In Am. Mus. 12208, from C 4, the protoconules are present in the second and third molar teeth. In Am. Mus. 5102, an aberrant form, the third and fourth superior premolars are without mesostyles but at the same time exhibit a very marked tendency toward molarization and have strongly pinched ridges opposite the protocones and tritocones. This specimen is progressive in the great prominence of the parastyle.

Fluctuations and progressive characters in the inferior teeth: In the several fine jaws referred to this species (Am. Mus. 1585, 1564, 1546, 1549) we observe fluctuations or individual variations of mutative and specific characters. In p_2 the paraconid is always distinctly marked; in p_3 the protolophid and hypolophid crests are very well defined; in p_4 the metaconid appears in a rudimentary cuspule; in m_3 the hypoconulid varies from a rounded (progressive) to a more crescentric (primitive) form; No. 1549 exhibits the triangular form similar to that seen in the type jaw; in No. 1585 we observe the more recurved form seen in *P. major.*

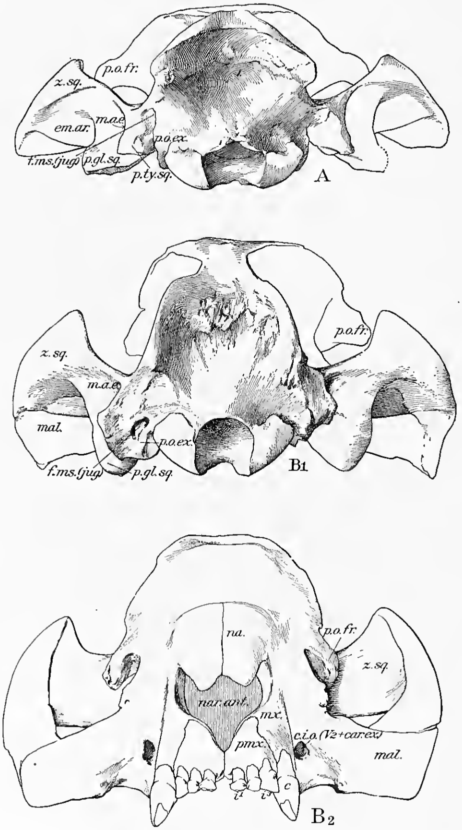

FIGURE 279.—Skulls of *Palaeosyops major* and *P. leidyi*

One-fourth natural size. A, *P. major*, Am. Mus. 12182 (neotype skull); middle Cottonwood Creek, Bridger Basin, Wyo.; Bridger formation, level B 3; occipital view, crushed downward. B_1, *P. leidyi*, Am. Mus. 1544 (type); Henrys Fork, Bridger Basin; Bridger, level probably upper C or D; occipital view. B_2, The same, front view.

Juvenile dentition and crania: In many ungulates the deciduous premolars are more molariform than their permanent successors, and this law is well illustrated in *Palaeosyops*, as in the milk dentition referred to *P. leidyi* (see below) dp^2, dp^3, and especially dp^4 are more molariform than their successors p^2, p^3, p^4. It seems not impossible that p^1 in the titanotheres represents a persistent milk tooth, or dp^1. In the milk dentition under discussion (Am. Mus. 1565) the first premolar (dp^1) is about as large as in the adult Princeton Mus. 10009. The large alveolus of the canine appears to leave no room for the formation of a permanent successor, or p^1. The evidence is still insufficient, however. In the Oligocene titanotheres p^1 may also be a persistent milk tooth (dp^1), as it is in recent horses.

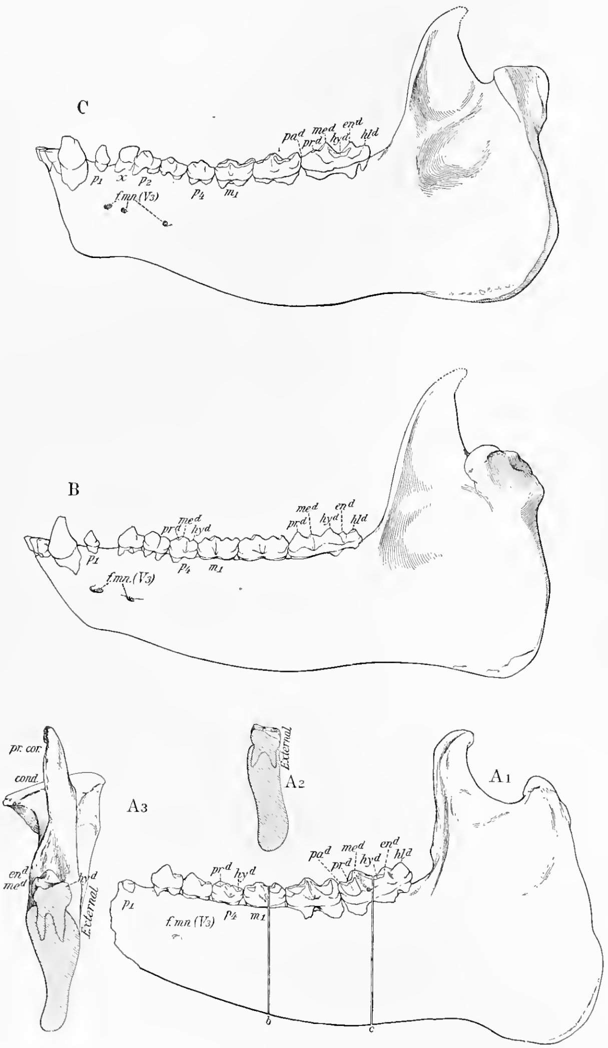

FIGURE 280.—Lower jaws of *Palaeosyops leidyi*

One-fourth natural size. A_1, Am. Mus. 1546 (reversed); Bridger Basin, Wyo.; side view; condyle restored from Am. Mus. 5103, angle from Am. Mus. 1522. A_2, The same, anterior view of section through line b. A_3, The same, anterior view of section through line c, with coronoid and condyle. B, Am. Mus. 1564; Henrys Fork, Bridger Basin; upper Bridger; coronoid and chin supplied from Am. Mus. 1585, incisors and canine from Am. Mus. 1544. C, Am. Mus. 1544 (type); Henrys Fork, Bridger Basin; Bridger, level probably upper C or D. *x*, Abnormal, extra premolar.

Stage with milk teeth and one permanent molar in use: This stage is represented by a maxilla (Am. Mus. 1565, Pl. LIX, figs. 282, 283), probably referable to *Palaeosyops leidyi*, and by a lower jaw (No. 12197, level C 2) belonging to another individual of the same size. In these specimens the length of the ramus is estimated at 300 millimeters. In the upper jaw two upper milk incisors and the milk canines are in place; dp^1 is a simple, conical tooth, smaller than its successor p^1; dp^2 exhibits two external crescents, a parastyle and mesostyle, and two internal cones, but the crown is oblong and not molariform; dp^3 exhibits the same elements more fully developed, the crown small and more quadrate in form, small conules, submolariform; dp^4 is entirely molariform, with protoconules and metaconules and fully quadrate contours; m^1 is also in use.

The juvenile jaw, Am. Mus. 12197, belonging to an animal of exactly the same size as that to which the above-described maxilla pertained, exhibits the following characters: Dp_2 is of small size but similar in form and not more progressive than its permanent successor p_2; dp_3 and dp_4 are in every respect fully molariform.

Leidy's type of *Palaeosyops humilis:* The single tooth from the "Dry Creek beds," Bridger formation, figured in Leidy's memoir of 1873 (1873.1, pl. 24, fig. 8) is the third superior milk molar (dp^3) of the left side of the jaw, belonging to an animal slightly inferior in size to *P. leidyi*. Its agreement in all essentials with dp^3 of the milk dentition, Am. Mus. 1565, above described, makes it clearly referable to the genus *Palaeosyops*, but geologic evidence for this reference is lacking, as its exact level is unrecorded; it might therefore belong to *P. major*, *P. leidyi*, or *P. robustus*. Hence it seems best to regard *P. humilis* as an indeterminate species.

Conclusions.—(1) There is evidence in *Palaeosyops* of the presence of at least two upper milk incisors, one milk canine, and three milk premolars on each side above, or 12 deciduous teeth above all together; (2) the first upper and lower premolars ($p\frac{1}{1}$) are simple, conical teeth, which are retained in the adult dentition—that is, they are probably without predecessors, or milk teeth; (3) the second lower deciduous premolar (dp_2) resembles in form its successor p_2 except that the posterior lobe is better developed; (4) in correlation with the submolariform shape of the corresponding upper teeth, the third and fourth lower deciduous premolars (dp_3 and dp_4) are more molariform than their successors p_3, p_4, especially in having large posterior lobes with high entoconids, which latter are lacking in the permanent teeth; (5) the second and third upper deciduous premolars are quadricuspidate, not fully quadrate, and may be described as submolariform; (6) the fourth upper deciduous premolar (dp^4) is fully molariform.

Palaeosyops robustus (Marsh)

Plates LV, LVI, LVIII, LXII; text figures 94, 284–288, 508–511, 521–523, 542, 544–546, 571, 685, 714, 718, 724, 737, 741, 760

[For original description and type references see p. 161. For skeletal characters see p. 626]

Type locality and geologic horizon.—Bridger Basin, Wyo., especially the upper exposures of Henrys Fork; Bridger formation, *Uintatherium-Manteoceras-Mesatirhinus* zone (Bridger D).

Specific characters.—Of massive breadth and proportions; slightly more brachycephalic than *P. major* and *P. leidyi;* measurements (all estimated), total length of skull, 440 millimeters; basilar length, 440; zygomatic breadth, 340; p^2–m^3, 163–170; mesostyles variable on p^3, more constant on p^4; molars with oblique ectolophs; m^3 enlarged, with prominent parastyle, ectoloph oblique, molar conules strong; distinctly rugose frontonasal horn swellings.

This stage is less perfectly known than *P. leidyi*, our knowledge being confined to the structure of the cranium, of the superior dentition, of a few of the vertebrae and of numerous fragmentary limb bones.

Materials.—The type maxillary teeth are in the Yale University collection (No. 11122). In the American Museum collection the following are the principal specimens: No. 11683, Bridger level D 3, canines to m^3, progressive, close to *P. robustus*, type; No. 1580, crushed skull with rudimentary horns and associated skeletal fragments, from Henrys Fork; No. 1554, skull with rudimentary horns, same stage as type; No. 11678, Bridger level D 4, a broad skull with smaller teeth; No. 5106, Cope's type of *Palaeosyops diaconus*, from Henrys Fork, progressive; Princeton Mus. 10282b, maxillary from Henrys Fork. Also the following less progressive forms: Am. Mus. 1584, palate and teeth; Am. Mus. 1552, palate and teeth, from Twin Buttes, level Bridger C or D; Am. Mus. 1558, also Twin Buttes, level Bridger C or D, palate with p^2–m^3; Am. Mus. 1586, i^1–m^3, unprogressive; and Am. Mus. 1590, fragments of lower jaw, m_{1-3}. We still lack the complete lower jaw.

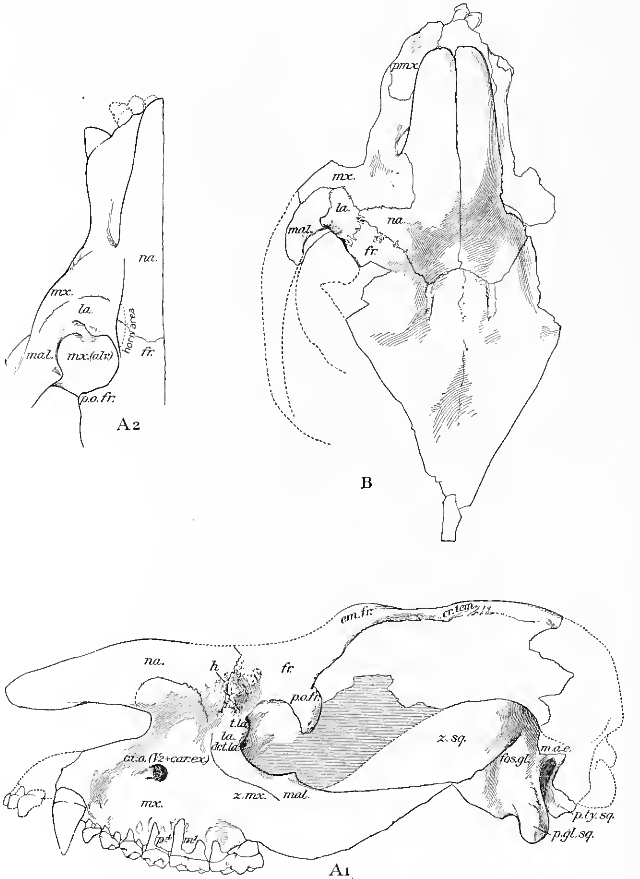

FIGURE 281.—Skulls of *Palaeosyops leidyi* and *P. copei?* (aff. *P. robustus*)

One-fourth natural size. A₁, *P. leidyi*, Am. Mus. 1581; Henrys Fork Hill, Bridger Basin, Wyo.; Bridger formation, level probably upper C or D; old male skull, side view, showing rugose horn swelling (purposely emphasized in the drawing); skull straightened from Am. Mus. 1544. A₂, The same; top view of the region of the horn swelling. B, *P. copei?*, Am Mus. 12205a; Lone Tree, Henrys Fork, Bridger Basin; level Bridger D 1; top view of skull.

General specific characters of P. robustus.—The horn swellings, as compared with those of three of the skulls described under *P. leidyi*, are here more strongly developed. The upper grinding series averages 6 millimeters longer than that of *P. leidyi*. The depth of the ramus behind m_3 is estimated at 98 millimeters. A metatrophic character is the relatively large size of m^3, measuring 42 millimeters transversely in the type, exhibiting large conules and more distinct external cingula. There seems to be considerable range of variation in the size of m^3, as indicated below, so that its large size in the type may not be truly specific.

P. major	32 by 38 to 33 by 40 millimeters.
P. leidyi	34 by 39 to 36 by 38 millimeters.
P. robustus	33 by 37 to 37 by 42 millimeters (type).
P. grangeri	38 by 43 millimeters.
P. copei	34 by 40 millimeters.

The size of the conules is also variable, as would be expected in a character which was losing its hold in most titanotheres. The forward extension of the anterior part of the masseter and deepening of the malar is a progressive metatrophy, as are also the closing of the diastema (postcanine), the closure of the external auditory meatus, and the large size of the skull. A very constant brachycephalic character is the closing up of the postcanine diastemata, which are either reduced or wanting. The sagittal crest is powerful but is differently formed from that of the type of *P. leidyi*, although not dissimilar to that of other *P. leidyi* skulls.

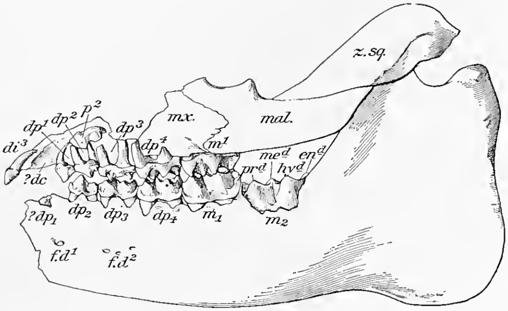

FIGURE 282.—Jaws and deciduous teeth of *Palaeosyops leidyi?*

One-fourth natural size. Am. Mus. 1565; Bridger Basin, Wyo.; upper jaw. Am. Mus. 12197; Henrys Fork Hill, Bridger Basin; Bridger formation, level C 2; lower jaw.

In addition to the specimens which exactly or very closely resemble Marsh's type, there are others which appear to occupy an intermediate position between *P. robustus* and the older form *P. leidyi* of level C.

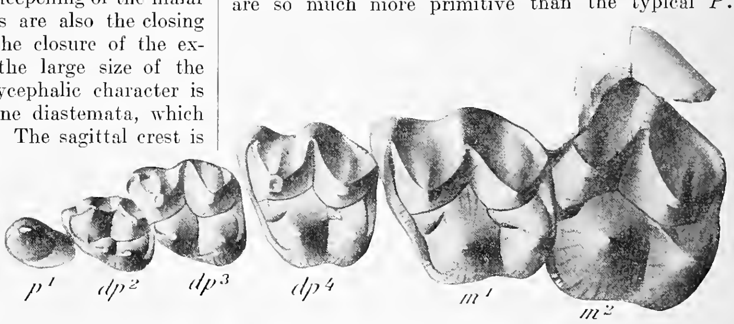

FIGURE 283.—Deciduous cheek teeth of *Palaeosyops leidyi?*

Am. Mus. 1565. Natural size. The identity of m^1, m^2 is positively established by comparison with the adult dentition. The deciduous molars dp^2, dp^3, dp^4, are more molariform than the teeth which succeed them, p^2, p^3, p^4. In this specimen the alveolus for the permanent canine lies closely appressed to p^2, while p^1 has been forced out into association with the milk molars dp^2, dp^3, dp^4. Thus in this middle Eocene titanothere the relations of the milk and permanent teeth are the same as in the Oligocene titanotheres.

Fluctuations.—The mesostyle and other premolar characters (Pls. LVIII, LXII) in these intermediate forms also show considerable fluctuation, but on the whole there is a recognizable metatrophic advance over *P. leidyi*. It appears that at each actual period of geologic time *Palaeosyops* would show a considerable range of variation, partly individual, partly varietal. For example, large size appears as an exceptional variation in a B level *P. major* (Am. Mus. 13116) and in the *P. grangeri* of Bridger C 1, while small size of grinding series appears as an exceptional character in the high level (Bridger D 3) *P. copei* and in the species of *Palaeosyops* from the Washakie Basin.

Mutations.—There seems to be considerable evidence for the view that these "transitional" dentitions and skulls bridge over the structural gap between *P. leidyi* and *P. robustus;* indeed, it would appear that this is clear. This view contradicts the idea expressed elsewhere that *P. leidyi* "stands apart and does not appear to form a connecting link between *P. major* and *P. robustus";* but that statement applies only to the broadened occiput of the type of *P. leidyi*, and since other skulls with narrow crests make up the bulk of the species *P. leidyi*, too much should not be made of the exceptional condition in the type. It may well be that in one or two trifling characters *P. robustus* may be shown ultimately to be descended not from the true race of *P. leidyi* which lived at Henrys Fork Hill during Bridger C 3 time but from some other race of *P. leidyi* living to the north and perhaps during Bridger C 1 to 3 time. However, by such hairsplitting we obscure the grand evolution lesson that *P. major, leidyi*, and *robustus* form successive mutations which are very nearly if not quite in a direct line, which might perhaps have been designated by trinomial names such as *P. paludosus paludosus, P. paludosus major, P. paludosus leidyi*, and *P. paludosus robustus.*

Less progressive mutations, transitional from the P. leidyi stage.—Some of the less progressive forms are so much more primitive than the typical *P. robustus* that they might be placed with equal exactness in *P. leidyi*. They are especially interesting biologically in demonstrating the gradual inception of such specific characters as are seen in *Palaeosyops robustus* rather than the sudden saltation of this species out of its predecessors. In comparing the following four mutations we note especially the very gradual evolution of the rectigradations—namely, of the premolar mesostyles—also the gradual atrophy of the conules.

First mutation: Of these the least progressive is Am. Mus. 1586, consisting of a palate with full dentition. There is a short diastema behind the canine; p^1 is of small size. The following measurements are much inferior to those of the type of *P. robustus:* P^4 23 millimeters, transverse; width of last molar 39, as in *P. leidyi;* small conules on the molars; a faint "shadow" rudiment of the mesostyle on p^3.

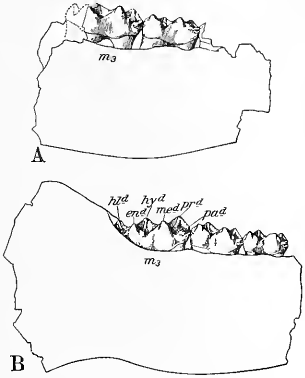

FIGURE 284.—Fragments of jaws of *Palaeosyops*

One-fourth natural size. A, *P. grangeri*, Am. Mus. 12189 (type); Twin Buttes, Bridger Basin Bridger formation, level C 1. B, *P. robustus*, Am. Mus. 1590; Bridger Basin, Wyo.; inner view.

Second mutation: Am. Mus. 1558 also exhibits a faint "shadow" mesostyle rudiment on p^3; a very strong mesostyle on p^4. The following measurements are similar to those of *P. leidyi:* Width of p^4 26 millimeters; width of m^3 39. Small conules on the molars. P^1 is unusually large.

Third mutation: Am. Mus. 1552 is the palate of a small female individual. Premolars and molars exhibit strong external cingula; mesostyle is rudimentary but distinct on p^3, very strong on p^4. The measurements are, however, the same as in *P. leidyi*, namely, p^4, transverse, 23 millimeters; m^3, transverse, 39.

Fourth mutation: Am. Mus. 1584 exhibits an advanced mesostyle on p^3 and p^4. The diastemata are closed up, as in the type of *P. robustus*, and p^4 shows a slightly increased width (27 mm.) transversely. The molars exhibit very small conules and faint cingula.

Detailed characters of the type and other progressive forms.—The dentition of the type specimen is fully described above and figured on Plates LVI, LVIII. In this specimen p^4 attains a width of 26 millimeters, and m^3 a width of 41; the measurement of m^3 as seen in its oblique diameter, measured from the parastyle to the hypocone, is 52 as compared with 48 in *P. leidyi* and 56 in the type of *P. grangeri*. This diagonal expansion of m^3 is characteristic of the species. The mesostyles of p^3 and p^4 are worn off or possibly were not present in the type. The cingulum nearly closes in around the inner sides of the premolars. Both proto- and metaconules on the molars are large.

Stages similar to the type: Very close to the stage represented by the type is the dental series Am. Mus. 11683 (level Bridger D 3), measuring, p^2–m^3, 167 millimeters; width of m^3, 42; width of p^4, 27. The cingula are progressive on the inner side of p^4; as in the type the postcanine diastema is very narrow, and, as observed above, the parastyle expansion is very marked. The masseteric ridge of the malar is very deep below the orbit.

In a similarly advanced stage is Princeton Mus. 10282b, with heavy cingula and a large mesostyle on p^4.

Cope's type of *Palaeosyops diaconus*, Am. Mus. 5106 (Henrys Fork, Bridger Basin, Wyo., level Bridger D?), is also very progressive, with "shadow" mesostyle on p^3 (nearly worn off) and p^4. The internal premolar cingula are nearly in contact on the inner sides of the deuterocones; similarly the cingula nearly embrace the protocones of the molars internally. The transverse measurement of p^4 is 26 millimeters.

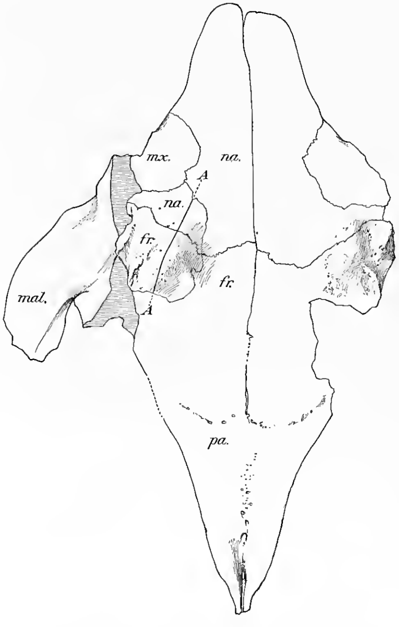

FIGURE 285.—Skull of *Palaeosyops robustus*

Top view. One-fourth natural size. Am. Mus. 1554; Henrys Fork, Bridger Basin, Wyo.; Bridger formation, probably level D. A-A, Section line across horn swelling (cf. fig. 210).

A peculiar feature is the expanded metaconule of m^3, which is unfortunately broken away in the posterior half. Cope believed that this metaconule represented a second internal cusp or hypocone, as in *Limnohyops;*

but by comparison with other specimens this cuspule is seen to be certainly a metaconule and not a true hypocone.

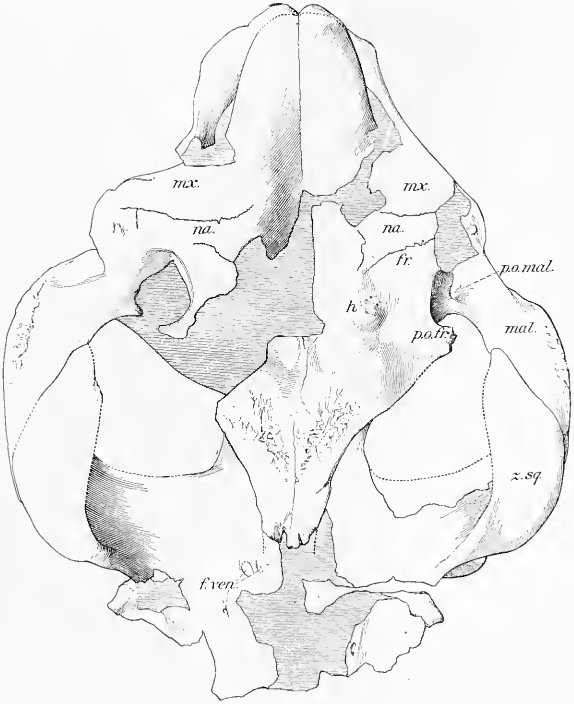

FIGURE 286.—Hyperbrachycephalic old male skull of *Palaeosyops robustus*

One-fourth natural size. Am. Mus. 1580; Henrys Fork, Bridger Basin, Wyo.; Bridger formation, probably level D. Skull crushed downward. Shows horn swelling (*h*) and extreme rugosity.

A similar "pseudo-hypocone" condition of the metaconule on m^3 is also observed in a skull from Henrys Fork (Am. Mus. 11678), level Bridger D 4; this tooth, like that in Cope's type of *P. diaconus*, entirely lacks the true hypocone. Although this skull is a male its molar-premolar series is relatively short, the three true molars measuring only 94 millimeters, as compared with 101 in the type of *P. robustus*. Mesostyles on p^{3-4} if originally present are worn away. Progressive features are the marked external cingula of the molars. This important skull is illustrated in Figure 287.

A skull that exhibits rudimentary horns (Am. Mus. 1554) shows in its detailed measurements (p^4, transverse, 28 mm. (estimated); m^3, transverse, 40; m^3, oblique, 52) close approximation to the type measurements. The mesostyle is absent on p^4, wanting or worn off on p^3. (See fig. 285.)

A more robust skull with horns (Am. Mus. 1580), Henrys Fork, level Bridger D?, exhibits measurements (p^4, 28 mm.; m^3, transverse, 41; m^3, oblique, 52) which are very close to those of the type; also large conules, prominent parastyles, little or no postcanine diastema. (See fig. 286.)

The close concurrence of measurements and progressive and retrogressive characters in the above-mentioned specimens with those of the type of *P. robustus* fully establishes this species as a distinct stage of evolution.

Jaws.—The jaws of this species are not yet fully known. There are portions of the rami of the young adult (Am. Mus. 1590) containing m_{1-3}, which measure 119 millimeters (estimated), as compared with 107 in *P. leidyi*. In these molars the cingulum is progressive and the paraconids are large. These teeth appear to correspond with the *P. robustus* stage.

Skull of P. robustus.—Three skulls are attributed to this species in the American Museum collection, namely, Nos. 11678, 1554, and 1580.

Horns.—The matter of chief interest is the structure of the osseous horn knobs. Rudimentary frontal horns are seen on Am. Mus. 1554 (fig. 285), which are even more prominent than in the transitional skull Am. Mus. 1581 attributed to *P. leidyi*. The position of the protuberances is on the frontals behind the nasal sutures; they are a little more posterior in position than the rugosities observed in *P. leidyi*, the center of the protuberances being 18 millimeters behind the suture and 59 millimeters from the median or internasal suture. The convexity of the horn is a complete oval, approximately 29 millimeters in diameter in transverse and longitudinal sections (Pl. XVI). The frontal bones are thickened and more cancellous beneath the horn.

In a very aged and robust skull, Am. Mus. 1580 (fig. 286), which is covered with exostoses the horn knobs are more prominent and rugose and still more posterior in position than in the specimen above described, the center being 23 millimeters back of the frontonasal suture.

FIGURE 287.—Basicranial region of *Palaeosyops robustus*

One-fourth natural size. Am. Mus. 11678; Henrys Fork, Lone Tree, Bridger Basin, Wyo.; Bridger formation, level D 4.

Cranial evolution.—The breadth of the skull, even in the earlier stages (*P. major*), is the most conspicuous feature of the quantitative and differential evolution. The comparative measurements in the three successive stages are as follows:

Measurements of skull in species of Palaeosyops, in millimeters

	Longitudinal	Transverse	Cranial index
P. major (Am. Mus. 12182)	390	[a] 290	74
P. major (Am. Mus. 13116)	435	335	77
P. leidyi (Am. Mus. 1544)	415	310	74
P. robustus (Am. Mus. 11678)	[a] 440	[a] 340	77

[a] Estimated.

Assuming that these measurements are fairly representative, between *P. major* and *P. robustus* we note little if any rise in the cranial index—that is, relative increase in breadth over length of skull.

In the same period the grinding series (p^2–m^3) has increased in length from 10 to 15 per cent over that of *P. major*, or about as rapidly as the cranial length.

Prominent features of the aged skull (Am. Mus. 1580) are (1) the width and power of the zygomatic arch, including the deepening of the forward extension of the masseteric insertion, which now has a depth of 62 millimeters below the orbits; (2) pterygoid wings of the alisphenoid are very heavy, for the insertion of the external pterygoid muscles opposing the temporals and masseters; (3) sagittal crest, while largely broken away, apparently broadened, as seen in the aged skull; in the younger skull (Am. Mus. 1554) still narrow (11 mm.); (4) occiput apparently broad and low, not confluent superiorly with the vertex of the cranium, as in the type of *P. leidyi*, resembling rather that of *P. major*, with the broadly flaring pillars above the condyles; (5) similarly paroccipital and post-tympanic processes suturally separate, as in *P. major*, and not closely conjoined, as in *P. leidyi*. Viewed from below the basioccipitals are sharply keeled, the keel bifurcating posteriorly into the occipital condyles, as in *P. major*, and dissimilar from the same region in the type of *P. leidyi*. While these advances upon *P. leidyi* are bridged over by several other skulls, yet they are all metatrophic and thus significant.

These characters (assuming them to be specific and not merely individual) would seem at first to indicate that *P. robustus* is to be regarded as a successor of *P. major* rather than of *P. leidyi*, and that in the intermediate levels (Bridger C) we should look for the species contemporaneous with *P. leidyi* but directly intermediate between *P. major* and *P. robustus*. In this connection, however, we should bear in mind the apparent variability in metatrophic characters which is displayed in the skulls referred to *P. leidyi* (see also remarks under "Mutations," above).

Nasals.—Skull Am. Mus. 1510 exhibits the nasals (fig. 288) robust and tapering anteriorly, strongly arching from side to side and anteriorly, extremely solid in section.

Palaeosyops grangeri Osborn

Plates LIX, LXII; text figures 119, 284 B

[For original description and type references see p. 181]

Type locality and geologic horizon.—Bridger formation, *Uintatherium-Manteoceras-Mesatirhinus* zone, level Bridger C 1, is recorded as the geologic horizon of this species. The type is from Twin Buttes, Bridger Basin, Wyo., 200 feet below the "red stratum."

Specific characters.—Exceeding *P. robustus* in certain dental proportions; p^2–m^3, 165 millimeters; fourth superior premolar enlarged; molars with extremely prominent parastyles and oblique ectolophs.

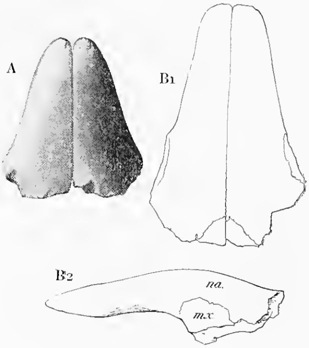

FIGURE 288.—Nasals of *Palaeosyops robustus*

One-fourth natural size. A, Yale Mus. 11122 (type); Bridger Basin, Wyo.; upper (?) part of Bridger formation. B_1, Am. Mus. 1510; Bridger Basin; top view. B_2, The same, side view.

This species was named in honor of Walter Granger, associate curator of fossil mammals in the American Museum of Natural History, whose explorations have done so much to advance our knowledge of the Bridger titanotheres and of Bridger stratigraphy. The animal seems to be a collateral rather than a main-line form, distinguished by several peculiarities of its grinding teeth.

Materials.—The only specimen known is the type, consisting of a palate and grinding teeth, with portions of the jaw and skull (Am. Mus. 12189).

General specific characters.—The species appears to be collateral to the stage represented by *P. robustus*. It comes from Bridger C and was found 200 feet below the "red stratum"; there is no exposure of Bridger D at Twin Buttes. It is more progressive than *P. robustus*, chiefly in its enormous size, for the premolars (p^{2-3}) are quite backward in development, in both the ectoloph and internal border.

P. grangeri may be a descendant of some large strain of *P. major*, such as Am. Mus. 13116; in fact, very projecting parastyles are seen in Am. Mus. 12185, transitional between the *P. leidyi* and the *P. major* stage, and also in Am. Mus. 12680, from B 5, referred provisionally to *P. paludosus*.

The species is especially distinguished by the extremely prominent parastyles of the molar teeth, which result in the very oblique direction of the ectoloph. The principal measurements are, p^1–m^3 180 millimeters, breadth of p^4 31, of m^3 43, oblique or diagonal measurement of m^3 57. The grinding teeth form a continuous series behind the large and laterally compressed canines. The single incisor preserved exhibits a subcaniform crown, 20 millimeters in height; the mesostyles are not observable on p^3 or p^4 but were possibly present (though small) in the unworn condition. The molars exhibit sharply defined median ridges in the valleys of the ectolophs. Strong development of the cingulum, which surrounds the entire crown excepting only the inner sides of the protocones, is a very characteristic feature. The conules are also well developed but relatively less than in typical specimens of *P. robustus*. In p^3 the internal cingulum is complete though faint.

The fragment of the lower jaw which has been preserved (fig. 284) indicates that the thickening of the lower border which we have traced in successive stages from *P. major* is now carried back below m_3. The ramus measures 86 millimeters below m_3; m_{1-3} estimated at 126 millimeters. The anterior lobe of m_3 measures 31 millimeters transversely. This tooth has strongly striated sides, festooned external cingula, and strong entoconules.

Palaeosyops copei Osborn

Plate LX; text figures 120, 266, 267, 281, 484, 511–514, 519, 543, 547–550, 724

For original description and type references see p. 181. For skeletal characters see p. 629]

Type locality and geologic horizon.—Henrys Fork, Lone Tree, Bridger Basin, Wyo.; Bridger formation, *Uintatherium-Manteoceras-Mesatirhinus* zone, level Bridger D 3. Probably also from level A of Washakie Basin, Wyo.

Specific characters.—Tooth row of somewhat smaller size. The most progressive species of *Palaeosyops* known in superior premolar and molar evolution. Heavy cingula embracing the inner sides of the crowns. P^4, p^3, p^2 very advanced, with subquadrate contours and subequal protocones and tritocones, incipient tetartocones on p^4, and distinct tetartocone constriction on p^2 (rectigradations).

This little-known animal represents a most advanced stage. It is, so far as known, the terminal stage of *Palaeosyops* evolution. In view of its progressive character this species is appropriately named in honor of Edward D. Cope, one of the founders of American vertebrate paleontology and the describer of *Lambdotherium*, "*Palaeosyops*" *borealis*, and other species of Eocene titanotheres.

Materials.—This species is positively known only from the American Museum series of superior grinding teeth (No. 11708) from Lone Tree, Henrys Fork, Bridger level D 3, including the premolars and molars of opposite sides (Pl. LX; fig. 120). Detailed measurements are given above. As shown in Plate LX this is by far the most specialized or advanced of the species of *Palaeosyops* in respect to the molarization of the premolars. It shows the following features: (1) The cingula are carried broadly around the inner sides of p^{1-4}, a character approached but not so fully attained in any of the previous stages of the evolution of the premolar teeth of this genus; (2) a rudimentary tetartocone is present on p^2, as indicated by a constriction of the deuterocone to form this cusp, very apparent on the outer side of the deuterocone and less strongly marked on the inner side; (3) the decided convexity of the protocone and tritocone ridges of the ectoloph approaches that of some of the uppermost Eocene titanotheres and is quite different from that in *P. robustus* or *P. leidyi;* (4) p^1 is a very progressive elongate tooth (17 mm. as compared with 12 in *P. leidyi*), with rudimentary deuterocone; (5) the molar cingula are very broad and heavy, continuous around the inner side of the protocone in m^3; (6) the inner side of all the premolars is more filled out, more subquadrate.

P. copei is also very probably represented in Washakie A by Am. Mus. 13177, a very aged skull, in which the teeth, so far as preserved, closely resemble those of the type but are a little larger. Portions of the skull indicate an animal about the size of the *P. leidyi* type, resembling the *leidyi-robustus* group in its very convex forehead, nasals, and basicranial region. The nasofrontal horn swelling was if anything more pronounced than in *P. robustus*. The nasal sinus beneath the horn, so prominently developed in Oligocene titanotheres, was present.

A specimen doubtfully referred to *P. copei?* is the young jaw (Am. Mus. 12205a, level Bridger D 1) that belongs with the cranium and skeleton described on page 629. The associated top of the cranium (fig. 281) is almost certainly that of a *Palaeosyops*, but the specific reference is uncertain. In the jaw of this specimen (fig. 266, B) the measurement from the angle to the incisive border is 340 millimeters; p_2–m_3, 172. The second and third incisors are approximately equal in size. The canine is comparatively small and probably indicates that this animal is a female. Close behind it is p_1, followed by a narrow diastema (5 mm.). P_2 and p_3 are very narrow, simple teeth, but slightly more progressive than in *Limnohyops priscus*, the metaconid being quite distinctly formed on the inner side of p_3. P_4 is decidedly more progressive than that of *L. priscus*, the posterior crest being well defined and the entoconid ridge being somewhat more decided.

A larger and more progressive jaw, also of doubtful specific reference, is Am. Mus. 12201 (fig. 266, C), from Bridger level C 4. In this the measurement from the condyle to the incisive border is 365 millimeters; p_2–m_3, 171. The paraconids are distinctly defined on p_2 and p_3. The teeth are otherwise very simple, although the posterior crescent (hypolophid) is deepened and slightly broadened. In p_4 a distinct entoconid is seen. The true molars measure 111 millimeters; the ramus behind m_3, 94 millimeters.

A jaw (Am. Mus. 12198) from Henrys Fork (level D 2) is in a slightly more advanced stage of evolution on the evidence presented in its inferior premolar teeth.

Palaeosyops copei is the last known species of this palaeosyopine race. Its specialized condition and its reduction in size may indicate that it was declining and on the point of extinction. On the other hand, it may have migrated from this region.

SUBFAMILY TELMATHERIINAE OSBORN

Middle and upper Eocene titanotheres of larger size. Skull with elongated cranial and abbreviated facial region, mesaticephalic (*Telmatherium*) or sub-brachycephalic (*Sthenodectes*). Basicranium abbreviated. Nasofrontal horns retarded in development. Dentition of macrodont type; large cingula; incisors heavy, sublanceolate; premolars progressively molariform; molars large, progressively subhypsodont.

Geologic horizon and geographic distribution.—The genera are *Telmatherium*, mesaticephalic, of levels Bridger C 3 to Uinta C 1, and *Sthenodectes*, mesaticephalic to brachycephalic, of level Uinta B 2.

These are the least known of the middle and upper Eocene titanotheres. Remains are infrequently found, and the parts preserved are incomplete. The Bridger region was probably beyond the center of their favorite habitat. The telmatheres appear to have been the most elegant and graceful as well as the most progressive and active of the middle Eocene titanotheres; in this respect they correspond with the Menodontinae of the lower Oligocene. As shown in Figure 257 they appear suddenly in the upper Bridger (levels C and D) and extend up into Uinta C 1, which probably represents the end of upper Eocene time. No known telmathere is directly related to the Oligocene *Menodus*, yet certain telmatherines may have given rise to the Oligocene offshoots known as the Menodontinae. The resemblances and differences between *Telmatherium* and *Menodus* are set forth below.

Resemblances to contemporary titanotheres.—The telmatheres may be regarded as intermediate in anatomy between the *Limnohyops-Palaeosyops* type and the *Manteoceras* type. The earliest species known, *T. cultridens*, exhibits certain resemblances to *Manteoceras*, others to *Limnohyops*. The skull as a whole is long; the basicranial region is short; the zygomata are moderately arched. A distinctive feature of the face is that the frontonasal horn swelling is feeble or wanting, perhaps because the horns were compensated for by the large, powerful canine tusks.

These relatively dolichocephalic, subhypsodont, supposedly subdolichopodal, and subcursorial characters doubtless indicate that the telmatheres frequented firmer ground and made longer excursions for harder kinds of food than did members of the *Palaeosyops* phylum. They were also probably more intelligent and alert. Since the rise of *Telmatherium*, *Manteoceras*, and other phyla possessing relatively long-crowned molars occurred simultaneously with the decline of the earlier group of *Palaeosyops* and *Limnohyops*, the general replacement of the latter by the former may be attributed to the mechanical superiority of their grinding teeth as well as to physiographic changes from forests and lakes to more open flood-plain country.

Compensation for small horns by large tusks.—The pronounced development of the canine tusks in the telmatheres indicates that they were probably combative and vigorous fighters; another respect in which they resemble the Oligocene menodonts. This development of the tusks may have compensated for the absence or retarded development of the osseous nasofrontal horns. In the earliest known species, *T. cultridens*, this horn rudiment was evidently represented by a slight nasofrontal convexity. The condition of the horns in *T. validum* is unknown, but even in a male of *T. ultimum* the horn rudiment is only slightly developed (Pl. XVI), while the canine tusks and lateral incisors are both enlarged and tusklike (Pl. LV).

Two subphyla.—There is evidence of an early division of the *Telmatherium* phylum into *Telmatherium* (mesaticephalic to dolichocephalic, index 60, incisors moderately large) and *Sthenodectes* (mesaticephalic, index 63–65, incisors greatly enlarged).

Geologic succession.—The telmatheres appear in Bridger C 3 and extend into Uinta C 1, through a vertical thickness of over 1,500 feet. Their span of life thus covers a very long period of geologic time.

History of discovery.—As stated above, the *Telmatherium* phylum is comparatively little known, probably because the known areas of deposition did not present a habitat favorable to these animals; they are very rare in the upper Bridger deposits; they are as yet unknown in the deposits of Washakie Basin; and only a few specimens have been found in the deposits of the Uinta Basin.

The first remains of a member of the group to be discovered were the maxilla and superior teeth that Marsh described as *Telmatherium validum* in 1872. His type description was brief and was published without illustration; the geologic entry is simply the

Bridger formation, but the type specimen may have been found in Bridger D. A maxilla discovered by the Princeton expedition of 1877 in Bridger C or D was considered by Scott and Osborn to represent a new genus of animals, to which they gave the name *Leurocephalus*, the type being the species *L. cultridens*; but in 1891 Earle pointed out that *Leurocephalus* is generically identical with *Telmatherium*. All the exploration of many subsequent years in the Bridger Basin has not revealed anything certainly similar to these types. In the upper deposits of the Uinta Basin (Uinta C or true Uinta formation) Peterson, of the American Museum expedition of 1894, secured a fine skull of a female specimen to which the name *Telmatherium ultimum* has been given; and in the same deposits was found the anterior portion of a male skull of the same species (fig. 297). These skulls fortunately throw a flood of light on the cranial structure of these animals, which were previously known only by upper and lower jaws.

These animals reappear (Riggs, 1912.1) in the uppermost levels of horizon B 1 of the Uinta Basin (in the "*Metarhinus* sandstones"), and in the middle of horizon Uinta B 2 Douglass discovered in 1908 the type of *T. incisivum* to which Gregory (1912.1) gave the name *Sthenodectes*, a telmathere with very large incisor teeth.

Finally a large jaw was found by Peterson in Uinta C which apparently represents the latest known member of this series, to which the name *T. altidens* has been given by Osborn.

Irregular geologic distribution.—It is important to note that these animals appear simultaneously with the first species of *Mesatirhinus* and *Manteoceras* in the upper Bridger levels; that they have not been recorded thus far in the Washakie Basin levels nor in the lower levels of the Uinta Basin; and, finally, that they are sparsely found in the upper or true Uinta levels. As above intimated, this rarity of geologic distribution appears to prove that they dwelt apart or in another food region and rarely invaded the region inhabited by *Manteoceras* and *Mesatirhinus*.

General structure and habits.—Little can be said regarding the general proportions of these animals until the skeleton has been discovered. The known individuals of *T. cultridens* somewhat exceed in size the largest tapirs, *T. validum* is somewhat larger, and *T. ultimum* of Uinta C is still larger, having a skull about 20 inches long. In divergent adaptation the telmatheres were probably swifter and of more graceful build than *Palaeosyops* and *Limnohyops*. The incisor, canine, and grinding teeth are much more elevated, sharp, and trenchant (hence the specific name *T. cultridens*) than in *Palaeosyops* and were reinforced with distinctly defined cingula.

Phyletic affinities of the telmatheres.—The first question that arises is, Are these animals more closely related to *Limnohyops*, to *Palaeosyops*, or to *Manteoceras?* The answer in brief is that although they are somewhat intermediate in position they are related by most of their ancestral or hereditary characters to *Limnohyops* and *Palaeosyops*. This real ancestral affinity was long obscured by the general mesaticephalic character and correlations of the different parts of the skull, jaws, and teeth in *Telmatherium*, which are the dominant distinguishing features of this animal.

Affinities to the Palaeosyopinae.—The ancestral affinities of the telmatheres to the Palaeosyopinae are indicated (1) in the transversely subconvex contour above and in front of the orbit, correlated with the very retarded development of the frontonasal horns (*T. ultimum*); (2) in the subrectangular, rounded rather than shelf-like section of the malars below the orbits; (3) in the deep, laterally compressed form of the zygomatic arches and the progressive development of a vertical flange (*T. ultimum*); (4) in the tusklike enlargement of the third or outer superior incisors; (5) in the rounded rather than angular posterior borders of the temporal fossae (*T. ultimum*); (6) in the elevated and rounded superior contours of the occiput (*T. ultimum*); (7) in the absence of distinct lateral occipital pillars above and on either side of the foramen magnum (*T. ultimum*); (8) in the presence of two facets for the atlas just above the foramen magnum (*T. ultimum*); (9) in the shape of the base of the skull, which is sub-brachycephalic or mesaticephalic, perhaps the strongest indication of affinity with the Palaeosyopinae. The concurrence of these resemblances in so many different parts of the skull is strong evidence of a community of descent; moreover, the species *Limnohyops monoconus* exhibits several characters that are seen also in *Telmatherium*—(1) the very high, rounded occiput, with thin sagittal crest; (2) a deep superior flange on the squamosal portion of the zygoma; (3) a similar, though less quadrate infraorbital portion of the malar.

Comparative indices in telmatheres and related species

	Cephalic	Faciocephalic	Molar
Telmatherium ultimum	60	[a] 49	26
Sthenodectes incisivus	63–65	[a] 48	[a] 27
Manteoceras manteoceras	60–66	49	20–23
Palaeosyops leidyi	70	46	24–28
Palaeosyops major	74–75		

[a] Estimated.

Influence of dolichocephaly.—It appears that the *Telmatherium* cranium is a partly elongate or drawn out *Limnohyops* type of cranium, and that correlated with this incipient dolichocephaly are the beginnings of numerous familiar dolichocephalic characters; but this incipient dolichocephaly affects chiefly the facial and midcranial regions, while the base of the cranium proper remains relatively short. In the teeth the incipient dolichocephaly appears in the following characters: (1) Incisors somewhat compressed, opposite pairs ranged in convergent series; (2) canines laterally compressed, or lanceolate, rather than rounded; (3) premolars and molars generally with elevated crowns somewhat compressed transversely, and with decidedly compressed crescents and sharply pointed cones; (4) conules reduced or vestigial; (5) first inferior premolars laterally compressed, with diastemata on either side; (6) molars laterally compressed.

In the skull we first observe the elongate, deep, and narrow premaxillary symphysis and the corresponding form of the "median suture." This is the generic character originally pointed out by Marsh and emphasized by Earle, in contrast with the shallow, rounded symphysis and median suture of *Palaeosyops*. The anterior aspect (fig. 295) of the symphysis is very characteristic of the species of this genus as compared with *Palaeosyops* and *Mesatirhinus* but is not greatly different from the *Manteoceras* type. The zygomata bend outward widely but not so much as in *Palaeosyops;* they are deeply extended vertically into flanges. The external auditory meatus remains widely open below.

Distinctions from Manteoceras.—The distinctions from *Manteoceras* are seen in a number of prominent characters in the *Telmatherium* series: (1) The horn rudiments are less prominent and the facial concavities less pronounced (*T. ultimum*); (2) the malar section below the orbits in *T. cultridens* is roundly angulate and in *T. ultimum* it is more rounded, approaching that in *Palaeosyops*, whereas in *Manteoceras* it is sharply angulate externally, foreshadowing the shelf-like flattening and rudiment of the infraorbital shelf which is so prominent a feature in *Mesatirhinus* and *Dolichorhinus;* (3) the canines are elongate, laterally compressed, and lanceolate, while in *Manteoceras* they are suboval and incurved rather than vertical; (4) the lateral superior incisors of *Telmatherium* (Pls. LV, LXIV) rapidly increase in size, progressively becoming caniniform (*T. validum, T. ultimum*), but in *Manteoceras* the lateral incisors are moderately large and increase in size progressively, though the disparity between i^3 and i^2 is less marked than in *T. cultridens;* in *Dolichorhinus* they progressively diminish in size, but the lateral incisor, while the largest of the three, is both relatively and absolutely smaller than in *Telmatherium* and *Manteoceras;* (5) in *Telmatherium ultimum* the ectolophs of the superior premolars (Pl. LXV) exhibit a very pronounced development of the cingulum, which rises in a festoon upon the protocone, producing an asymmetry of the outer face (a highly progressive character), whereas in *Manteoceras* the cingula are less pronounced and the protocones and tritocones are less subequal on the ectoloph; (6) in *Telmatherium* the deuterocones of the premolars are longitudinally compressed (Pls. LXIII, LXIV, LXV, fig. 291), with a tendency to a ridged apex, which becomes more marked in *T. validum* and very decided in *T. ultimum,* whereas in *Manteoceras* the deuterocones of the premolars are more oval or conical; (7) in *Telmatherium* the mesostyles of the superior molars are sharply compressed (Pls. LXIV, LXV, fig. 292), the buttress rising into a horizontal ridge, which becomes a very decided character in *T. validum* and *T. ultimum,* while in *Manteoceras* the mesostyles are more robust and rounded; (8) in the members of both genera the conules tend rapidly to disappear owing to the lateral compression of the crown and the elongation of the ectoloph, but the ectolophs in *Telmatherium* seem to be even more elongate, progressive, and trenchant than in *Manteoceras.*

There are, however, some peculiar features which distinguish the incipient dolichocephaly of this phylum from the more pronounced dolichocephaly seen in the genera *Mesatirhinus* and *Dolichorhinus*—namely, the free nasals are relatively short; the sagittal crest is elongate and relatively persistent; the basicranial region is relatively abbreviate. These differences are consistent with the general law that dolichocephaly is a process of differential growth of different parts of the cranium, not all parts being elongated equally.

Affinity to Manteoceras.—There are important features in which *T. cultridens,* from the upper Bridger, the earliest known member of this series, resembles the contemporary representatives of *Manteoceras,* as shown in a comparison of Figures 290 and 308. There appears to be a similar development of the nasofrontal horn rudiment and a somewhat similar concavity in front of the orbits, though unfortunately this region of the type of *T. cultridens* is fragmentary (fig. 290). A decided resemblance to *Manteoceras* and *Limnohyops* and distinction from *Palaeosyops* are seen in the form of the nasal bones, which in *T. ultimum* are elongate but with a short free portion which is laterally decurved and truncate instead of pointed distally (contrast *Palaeosyops*).

With these exceptions the progressive affinities of *Telmatherium* to *Manteoceras* and *Mesatirhinus* appear to be adaptive and convergent characters rather than ancestral or genetic characters.

It thus appears that the distinctions from *Manteoceras* outweigh the resemblances and that the resemblances to *Manteoceras* and *Mesatirhinus* are in part attributable to parallel or convergent adaptation, in part to similarity of origin.[25]

Progressive and conservative or stationary characters.—It appears at present that the horn rudiments are not progressive in the telmatheres; they are found to be even less prominent in the Uinta *T. ultimum* than in the Bridger *T. cultridens*—a feature possibly com-

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[25] W. K. Gregory regards the species *T. cultridens* as linked by intermediate stages (Am. Mus. 12193, 12194) with *M. manteoceras* and as very closely related in all characters, a resemblance not due to convergence. *T. cultridens,* according to this view, is intermediate between the manteoceratine and the palaeosyopine divisions.

pensated for, as above noted, by the development of the tusks. As a second conservative character it is important to note that the first and the second lower premolar teeth exhibit in *T. cultridens* a distinctively high, laterally compressed, and secant character, and that vestiges of this character are conserved in the species *T. altidens* of Uinta C. The free or projecting portion of the nasals remains relatively short (*T. ultimum*).

All the other distinctive incipient dolichocephalic characters of *Telmatherium* appear to be progressive: (1) the lateral superior incisors are decidedly progressive, becoming elongate and tusklike; (2) the hypsodonty in the superior grinding teeth becomes more marked; (3) the posterior superior premolars (p^{3-4}) acquire similar internal ridges longitudinally placed, which in *T. ultimum* tend to develop tetartocones; (4) there is a decided elongation of the postcanine diastema, culminating in the very long diastema of *T. altidens;* (5) there is a marked elongation of the third inferior molar (m_3); (6) while the canines of *T. ultimum* are not relatively larger than those of *T. cultridens*, the canines of *T. altidens* of Uinta C are exceptionally large and show progressive development of this character; (7) the ectolophs of the superior premolars as seen in *T. ultimum* of Uinta C tend to develop symmetrical convexities of protocones and tritocones such as are characteristic of all Oligocene titanotheres.

Sex characters.—Differences in sex are indicated very markedly in the male and female specimens of *T. ultimum* in the inferior size of the canines in the female, and apparently also in the absence or faint development of the horn rudiments. Contrary to an earlier opinion of the author it now appears that even in their first development the horn swellings are less prominent and rugose in the female than in the male Eocene titanotheres.

Resemblances to the Oligocene Menodus.—There are many resemblances in *Telmatherium ultimum* to the characters of the Oligocene genus *Menodus*, as follows: (1) Middle region of the skull between the orbits and the postglenoid processes lengthened; (2) molar series enlarged absolutely and proportionally both in length and in breadth; (3) canines of sublanceolate form; (4) grinding teeth sharp and hypsodont; (5) posttemporal and occipital regions similar in their rounded and elevated form, also in the absence of the separate condylar pillars at the back of the occiput and in the presence of accessory articular facets above the foramen magnum; (6) zygoma deep in section in both *Telmatherium* and *Menodus*, with a vertical flange; (7) coronoid process high and slender.

Contrast with Menodus.—On the other hand, *Telmatherium* appears to be excluded from the ancestry of *Menodus* by the wholly different trend of development of certain parts: (1) the elongation of the postcanine diastema seems to be a progressive feature culminating in *T. ultimum*, whereas in *Menodus* this diastema is much reduced; (2) the progressive increase in size of the incisors contrasts with the extremely vestigial condition of the incisors in *Menodus;* (3) all the Uinta Basin species of *Telmatherium* and *Dolichorhinus* are characterized by the great prominence of the incisor series and by sharp constriction of the face back of the enlarged canines, probably indicating grazing habits, and no species seems to fulfill all the ancestral conditions of any of the Oligocene titanotheres.

It therefore can not be said that we now know any species of *Telmatherium* that would fill the ancestral characters of the Oligocene *Menodus*.

Telmatherium Marsh

(*Leurocephalus* Osborn, Scott, and Speir)

Plates XVI, XLVI, LI, LV, LXIII–LXV; text figures 126, 127, 210, 219, 220, 223–226, 255, 256, 289–300, 508, 516, 588, 592, 593, 647, 717, 733, 735, 745

Generic characters.—Skull as a whole long, basicranial region short, zygomata spreading, with deep malar flanges; frontonasal horn swellings rudimentary or wanting. Incisors large, with heavy posterior cingulum; i^3 very large and pointed; canines large, compressed, pointed, with sharp anterior and posterior borders; upper premolars relatively advanced, with complete internal cingulum; upper molars subhypsodont, relatively large, with rudimentary conules and slender parastyles and mesostyles, m^3 without hypocone. These animals are without difficulty distinguished from the species of *Mesatirhinus* and *Dolichorhinus*, but the earlier stages show certain resemblances to *Manteoceras manteoceras*.

The known specific stages are as follows:

T. cultridens, from Bridger ?C or D. The premolar-molar series measures 180 millimeters. The premolars are somewhat simpler in structure than in *T. validum*. The animal is inferior in size to *T. validum* and is of the same size as the smaller members of *M. manteoceras*.

T. validum, Bridger D. The premolar-molar series measures 195 millimeters. This animal is represented by part of a male skull, the only specimen known. The lateral superior incisor is more distinctly caniniform than in *T. cultridens*, and the premolars and molars are somewhat more progressive.

T. ultimum, from Uinta C. The premolar-molar series measures 217 millimeters. The lateral superior incisors are greatly enlarged and caniniform; the superior premolars are progressive and have more symmetrically convex protocones and tritocones and well-defined external cingula. The second superior premolar is simpler than the third and fourth.

T. altidens, from Uinta C (? lower levels). The inferior premolar-molar series measures 330 millimeters. The anterior premolars are primitive and laterally compressed. The canines are exceptionally prominent, hence the name *T. altidens*.

Measurements of skull and teeth of species of telmatheres, in millimeters

	Telmatherium cultridens, Princeton Mus. 10027 (type); upper Bridger	T. validum, Yale Mus. 11120 (type); upper Bridger	Sthenodectes incisivus, Carnegie Mus. 2398 (type); Uinta Basin, level B 2	Telmatherium ultimum, Am. Mus. 2060 (type); Uinta C (true Uinta)	T. ultimum, Am. Mus. 2004 (paratype); Uinta C
Basal length of skull	------	------	490	500	------
Zygomatic breadth of skull	------	------	330	300+	------
Length of dental series i^1–m^3	255	270	295	305	------
P^1–m^3	180	------	207	218	229
P^1–p^4	80	79	82	89	95
M^1–m^3	103	113	128	130	137
I^1, ap. by tr	9 × 8	11 × 9	22 × 21	14 × 14	14 × 14
I^3, ap. by tr	14 × 13	------	25 × 22	19 × 18	22 × 20
C, ap. by tr	20 × ?	------	27 × 24	------	25 × 22
P^4, ap. by tr	21 × 26	22 × 30	22 × 36	25 × 35	27 × 35
M^1, ap. by tr	29 × 29	30 × 30	38 × 38	38 × 40	40 × 37
M^3, ap. by tr	36 × 39	39 × 38	38 × 43	46 × 52	49 × 48

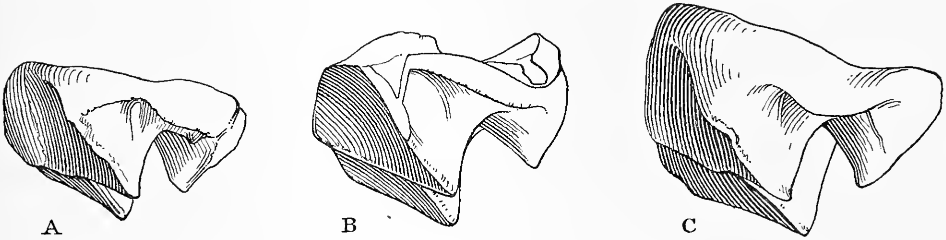

FIGURE 289.—Progressive hypsodonty of the molars in *Telmatherium*

Natural size. Posterior view of third left upper molar. A, *T. cultridens*, upper Bridger (C or D); B, *T. validum*, Bridger D; C, *T. ultimum*, Uinta C (true Uinta).

The table illustrates (1) the marked increase in the size of the skull and dentition as we pass from *T. cultridens* of the upper Bridger to *T. ultimum* of Uinta C; (2) the relatively larger size, in the later stages, of the true molars as compared with the premolars; (3) the increase in both the length and the breadth of the molars.

Telmatherium cultridens (Osborn, Scott, and Speir)

(*?Leurocephalus cultridens*)

Plates LV, LXIII, LXV; text figures 101, 223-226, 289-293, 735

[For original description and type references see p. 168]

Type locality and geologic horizon.—Henrys Fork Hill, Bridger Basin, Wyo.; Bridger formation, level C or D. Also recorded from Bridger C 2 and probably other horizons, as described below.

Specific characters.—P^1–m^3, 180 millimeters. In males superior canines elongate (46 mm.), laterally compressed; premolars less progressive than in *T. validum.*

The history of this species has already been given. (See pp. 167–168.)

Materials.—As noted above, the type (Princeton Mus. 10027) is from the Bridger Basin, Henrys Fork Hill, level C or D. It represents a smaller and considerably more primitive animal than *T. validum*, especially in the more incisiform character of the superior lateral incisor. Another specimen from Bridger C 2 referable to this species (Am. Mus. 12209) consists of p^4, m^1, and m^3. Another specimen that is certainly referable to this species is a young lower jaw (Am. Mus. 1560), with m_3 not yet entirely exposed, recorded from Twin Buttes, level Bridger C or D. Another well-preserved lower jaw (Am. Mus. 12193), from Henrys Fork, level Bridger C 3, agrees closely with the type in the dentition. Am. Mus. 12685, which includes m^1, with a deciduous molar, and an unerupted p^2, from Sage Creek Spring, level Bridger C 3, may represent a primitive phase of this species. A lower jaw (Am. Mus. 12687) from Henrys Fork Hill, level Bridger D 3, is somewhat more progressive than the type in p_2 and p_3. Another specimen from the Bridger Basin (Am. Mus. 1546a), consists of p^4–m^3, right and left, and the lower border of the orbit. It differs from the type in the more complete external cingulum on p^4, but the malar closely resembles that of the type. This specimen also approaches *M. manteoceras* in some respects. A young lower jaw from the Washakie Basin (Am. Mus. 2356), with the milk molars in place, is more advanced than the type in the characters of the permanent p_2.

Type of T. cultridens.—So little is preserved of the cranium of this type (Princeton Mus. 10027) that it can only be partially characterized. As shown in Figure 290 there is a slight concavity at the side of the face and distinct evidence of the existence of a nasofrontal horn rudiment. The premaxillary in side view approaches the *Manteoceras* type but is distinguished by the greater depth and by the emphasis of the dorsal symphyseal keel. It is more elongate and more angulate superiorly than the short, rounded premaxillary of *Palaeosyops* and is vertically deeper than in *Mesatirhinus*, *Metarhinus*, and *Dolichorhinus*. Its dimensions are, depth from symphyseal crest to internal alveolar border 38 millimeters, length from anterior border to the anterior edge of the canine 45, extreme length 96. Behind the canine convexity the sides of the maxillaries are somewhat flat. The infraorbital foramen is well exposed on the side of the face, the distance from the antorbital border of the malar being 36 millimeters. Only the anterior portion of the malar is preserved, but the relations of the malar and maxillary are shown by close examination and comparison to have been about as they were in *Manteoceras* and *Limnohyops*—that is, the maxillary contributed an antorbital process and a long internal inferior sliver; there is no infraorbital shelf; immediately below the orbits the malars are gently convex on the outer surface and broadly flattened on the inferior surface, the vertical extent of the outer face being 27 millimeters, and the transverse extent of the slightly concave inferior face opposite m^3 23.

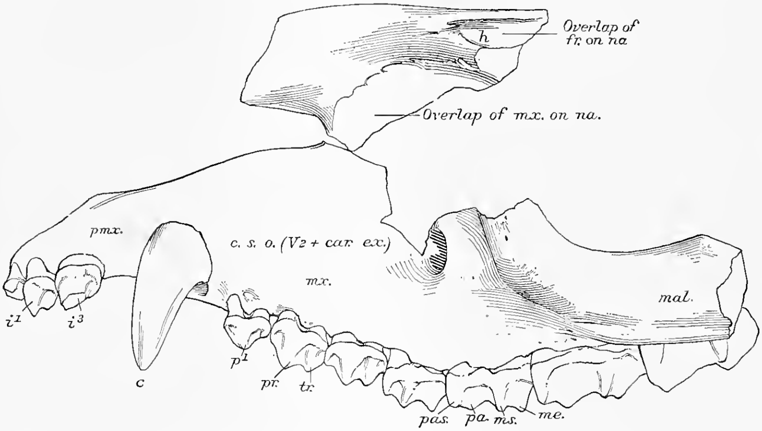

FIGURE 290.—Upper jaw of *Telmatherium cultridens*

One-half natural size. Princeton Mus. 10027 (type), reversed, showing the region of the horn swelling (*h*) and the overlap of the maxilla on the nasal. The fragment of the nasofrontal region here figured is said to be associated with this type. Upper part of Bridger formation, Bridger Basin, Wyo.

The teeth in general are distinguished by the sharply defined, finely sculptured character of all their elements.

Incisors.—In the type (Princeton Mus. 10027) the superior incisors have the typical generic character of the opposite sets, forming acutely convergent or V-shaped rather than gently convergent series; the incisors increase rapidly in size from i^1 to i^3, the fangs measuring 8, 10, and 14 millimeters, respectively. The antero-external faces of the crowns are readily distinguished from those of *Mesatirhinus megarhinus* by a sharp anterior ridge, which divides the crown into a flattened external portion, feebly convex and cingulate, and a narrow anterior portion, feebly concave. Similarly the postero-internal face is flattened, with a median basal ridge and a very prominent postero-internal cingulum, especially upon i^2. I^3, which is less perfectly preserved, is a large subcaniniform tooth, with a sloping and less prominent internal cingulum. The single inferior incisor preserved (i_3, Am. Mus. 1560) is, in contrast to its mate above, typically incisiform, with a more uniformly convex antero-external face, feebly cingulate, and a nearly plane postero-internal face, with a median ridge and sessile postero-internal cingulum; the long axis of this tooth is oblique, the diameters being 14 by 11 millimeters.

Canines.—In the type the superior canines have not fully emerged, the crown measuring 49 millimeters vertical, 24 anteroposterior, 22 transverse (estimated); the tusk has the true generic lanceolate or laterally compressed character, the anterior and posterior ridges being sharply defined and terminating in the piercing apex; the outer face is broadly convex; the inner is more nearly plane, with a convex median swelling. The inferior canines belonging to an animal of the same size (fig. 293; Am. Mus. 1560) are somewhat smaller (vertical 30 millimeters, anteroposterior 17, transverse 15), distinctly lanceolate, with a sharply defined anterior ridge, which becomes especially prominent and inflected near the base of the crown; the posterior ridge is much less sharply defined.

Premolars.—The superior molar-premolar teeth in the type specimen (see Pl. LXIII, fig. 291) have the laterally compressed, sharp-cusped, secant, and piercing form so characteristic of *T. validum*, the type of this genus; they are distinctly smaller—180 millimeters, as against 195 millimeters in *T. validum*.

The superior premolars (81 mm.) exhibit nearly complete internal cingula, excepting p^1, also an external cingula except directly opposite the protocone swelling. P^1 is a narrow tooth (ap. 15 mm., tr. 9), with sharply compressed ridges extending forward and backward from the protocone, a rudimentary tritocone, and well-defined but low anterior style. P^2 is a subtriangular tooth; the deuterocone in this tooth is double, extending backward to the postero-internal portion of the crown. As seen externally (fig. 292) the protocones and tritocones of p^{2-4} are of equal height, but the convexity of the protocone broadens characteristically at the base into an anterior and posterior cingulum; the tritocones present narrow vertical external ridges, which enable us to distinguish these teeth from the typically more flattened tritocones of *Mesatirhinus megarhinus* and *Manteoceras manteoceras*. In p^3 the ectoloph exhibits the same characters and the same length as in p^2, but p^3 is relatively much broader, the length of the ectoloph being 21 millimeters and the breadth across the crown 22; the deuterocone is more median in position, elongate, and flattened internally, as in *T. ultimum*; this tooth also exhibits a low antero-external style. In p^4 this style is still more prominent, the protocone and tritocone convexities of the ectoloph are more symmetrical, and the crown seen from above is more quadrangular, the deuterocone being sharp and slightly flattened internally.

Of the inferior premolars p$_1$ (preserved in Am. Mus. 1560) is spaced, lying 13 millimeters behind the canine and 3 millimeters in front of p$_2$; it is laterally compressed (12 by 7 mm.), sharply pointed, and simply plano-convex in section, with a noticeable paraconid, or anterior style. P$_2$ is elongate, laterally compressed, 22 by 10 millimeters (in Am. Mus. 1560), with an elevated protocone, rudimentary antero-internal cusp (=metaconid) and well-developed postero-external cusp (=hypoconid), slightly concave internally. P$_3$ exhibits more symmetry; the protoconid still being more elevated than the postero-external cusp (=hypoconid), the proportions of the crown being a shade larger in the type than in Am. Mus. 1560 (ap. 22 mm., tr. 14); the form is thus feebly molariform. In Am. Mus. 1560 the posterior half of p$_3$, p$_4$ is widely expanded transversely. P$_4$ is submolariform (ap. 23 mm., tr. 15 in the type), with cusps analogous to the paraconid, entoconid, and metastylid of the molars, and a very prominent cusp analogous to the metaconid; the anterior lobe (=trigonid) is much higher, however (15 mm.), than the posterior (12 mm.).

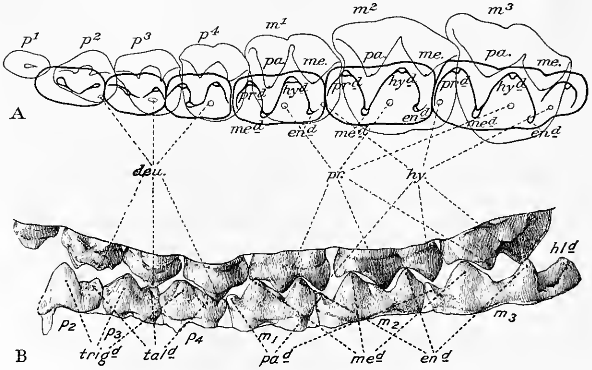

FIGURE 291.—Upper and lower teeth of *Telmatherium cultridens*, showing their mechanical relations

One-half natural size. Princeton Mus. 10027 (type). A, Crown view; upper teeth (light line), with pattern of lower teeth (heavy line) projected upon them. B, Internal view of the same, showing the crushing action of the cones and conids.

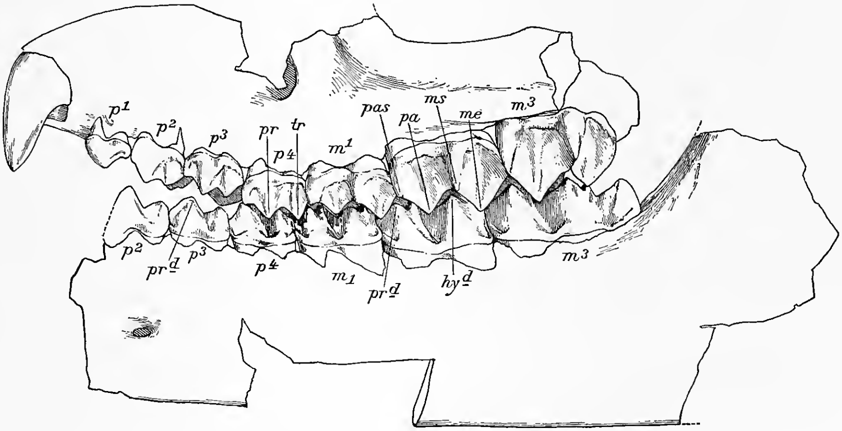

FIGURE 292.—Upper and lower teeth of *Telmatherium cultridens*, interlocked

Outer side view. One-half natural size. Princeton Mus. 10027 (type), reversed; upper part of Bridger formation (level C or D), Bridger Basin, Wyo. This view shows the shearing or cutting action of the grinders by the interaction of the superior and inferior crescents

Molars.—The superior molars (103 mm. in type) exhibit prominent external cingula feebly continuous around the styles in m^1, m^2, and internal cingula nearly continuous on the inner sides of m^2, m^3. The conules are represented merely by a vestige in m^1. The internal cones (protocones and hypocones) are sharply pointed and slightly more flattened internally than externally. In m^3 the unworn protocone and ectoloph measure in height 18 and 31 millimeters, respectively, exhibiting incipient hypsodonty. They are sharply pointed and closely approximated, the apices being only 12 millimeters apart. M^3 exhibits a rudimentary hypocone, also a rudimentary swelling of the anterior cingulum corresponding with the protostyle of *T. ultimum* and *Menodus.* The inferior molars constitute a long, narrow series (122 mm.) in the type specimen and exhibit distinctly defined paraconids as well as rudimentary metastylids and entostylids. In the elongate m_3 (54 by 22 mm.) the apex of the hypoconulid is placed nearly in line with the outer wall, and this cone is deeply crescentic within.

Mechanical correlation of upper and lower teeth.—The significance of these accessory cuspules as well as the mechanical relations of the upper and lower cusps is well demonstrated in the accompanying drawings (figs. 291, 292), which show that the metastylid below serves to press the food against the protocones and their ascending internal cingula above. The adaptive significance of these minute features in the comminution of the harder food which was probably selected by this species is thus clearly brought out.

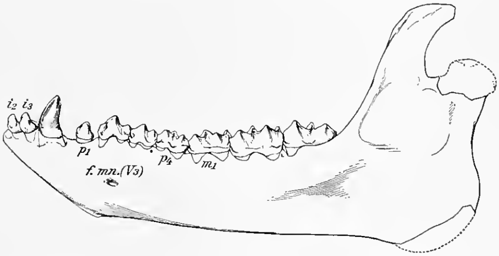

FIGURE 293.—Lower jaw of *Telmatherium cultridens*

One-fourth natural size. Am. Mus. 1560. Twin Buttes, Bridger Basin, Wyo.; upper part of Bridger formation (Bridger C or D).

It is seen also that the entoconid and paraconid below press the food against the hypocones above, that the tip of the hypocone fits squarely into the antero-internal part of the basin of the trigonid, that the single deuterocones of the superior premolars fit into the posterior internal valleys (=talonids) of the inferior premolars, and that the elongate p^2 above is effectively correlated with the elongate and secant p_2 below.

Milk dentition of ?T. validum.—A pair of young jaws from the Washakie Basin (Am. Mus. 2356) exhibit dp_2, dp_3, dp_4, m^1, m^2 in place, with the true premolars as well as m_3 still deeply buried in the jaw. Each of the deciduous premolars is fully molariform, with sharply defined double crescents; precocious molarization is, in fact, characteristic of milk premolars of titanotheres in general. Dp_3 measures (ap. by tr.) 19 by 11 millimeters, dp_4 24 by 14. The enamel is vertically crenulate on the outer surface. An important fact is that this jaw is in a more advanced stage of evolution than the type of *T. cultridens,* since the second permanent premolar (p_2) has the talonid V much better developed, and it may therefore belong to *T. validum.*

Lower jaw of Telmatherium cultridens.—The partially preserved type jaw (fig. 292) exhibits (1) two mental foramina, the second indistinctly shown, the larger and more anterior being below p_2; (2) a gradual increase in depth from 58 millimeters behind p_2 to 65 behind m_2 and 76 behind m_3, with a thickness of 20 millimeters below m_2.

A more perfectly preserved young jaw (Am. Mus. 1560, fig. 293) in which m_3 is not fully emerged exhibits a long (91 mm.) and rather shallow (26 mm.) symphysis and laterally compressed chin (47 mm.); the ramus exhibits two mental foramina and gradually increases in depth from 51 millimeters behind p_2 to 58 behind m_2 (inside), the thickness being 19 millimeters below m_2. All these measurements would naturally increase with advancing age. The depth of the angle below the condyle is 134 millimeters; the coronoid attains a free height of 49 millimeters and is regularly hooked or recurved from base to tip. The angle is thin but extended downward and backward very decidedly, as in *Manteoceras manteoceras.* Comparison with Am. Mus. 12193 (Bridger C 3), which probably belongs with this species, brings out the differences due to age. In the younger jaw (Am. Mus. 1560) the chin and ramus are shallower, the whole ascending ramus narrower, the angle less depressed, the coronoid shorter, more delicate and recurved, less truncate at top, and with the lateral flange much less pronounced.

Measurements of Am. Mus. 12193 are as follows: P_1–m_3, 194 millimeters; p_{1-4}, 68; m_{1-3}, 125.

Telmatherium validum Marsh

Plate LXIV; text figures 93, 289

[For original description and type references see p. 160]

Type locality and geologic horizon.—Bridger Basin, Wyo.; Bridger formation, *Uintatherium-Manteoceras-Mesatirhinus* zone, level Bridger D.

Specific characters.—P^1–m^3, 195 millimeters. In males, superior canines large, elongate (55 mm.), lateral superior incisors subcaniniform; ectolophs of superior premolars with sharply cingulate ridges; premolars more progressive than in *T. cultridens;* transverse measurements of p^3–m^1 greater than in *T. cultridens.* Frontonasal region unknown.

The only teeth definitely known are those of the type in the Yale Museum (No. 11120), a male individual first characterized by Marsh in 1872 and fully discussed later by Earle. The animal is young, since the crown of the last molar is entirely unworn, and all the distinctive characters of the surfaces of the teeth are still sharply defined. As noted above in the description of *Palaeosyops* these surface characters disappear rapidly by the wearing action of the food.

The type specimen represents a comparatively large and powerful animal. The canines, relatively more prominent than in *T. ultimum,* suggest a possible affinity to *T. altidens* of Uinta C. The lateral superior incisors are almost as distinctly caniniform as in *T. ultimum.* As compared with *T. cultridens,* distinctive characters are the more progressive rectigradations, seen principally in the premolar teeth, as enumerated below, also the greater width of the premolars. From *M. manteoceras* this animal is readily distinguished by its very long and less curved canines.

A comparison of the detailed measurements of the teeth is given in the following table:

Measurements of teeth in Telmatherium validum and T. cultridens, in millimeters

	T. validum, Yale Mus. 11120 (type)		T. cultridens, Am. Mus. 1560	
	Antero-posterior	Transverse	Antero-posterior	Transverse
Canine	26	23	24	--------
P^1	18	11	15	9
P^2	24	20	21	19
P^3	18	26	18	22
P^4	23	32	21	26
M^1	34	34	30	29
M^2	39	41	37	38
M^3	42	40	36	40
I^1	13	12	--------	9
I^2	15	15	13	12
I^3	17	16	16	15

In *T. validum* the opposite superior incisor series converge slightly. I^1 has an angulate antero-external face and sharply defined postero-internal cingulum; i^2 is a larger tooth, with a broad and sharply defined cingulum; while in i^3 we have a subcaniniform crown of very large size, with compressed anterior and posterior edges and somewhat less prominent internal cingulum, sloping downward and backward. The inferior incisors are not known.

The superior canine (55 mm.) is a powerful lance-shaped tooth, larger but of the same form as in *T. cultridens,* with a very convex antero-external and more plane postero-internal face, bounded by the sharply defined anterior and posterior ridges.

The superior grinding series, including the spaced p^1, extends 195 millimeters anteroposteriorly, as compared with 180 in *T. cultridens* (both males). In general, the teeth are similar to those of *T. cultridens,* but besides the larger size we note the following progressive features: (1) On p^1 the internal cingulum is well defined, with the rudimentary posterior cusp larger; (2) p^2 is slightly broader and shorter (ap. 24 mm., tr. 20); (3) there are protoconules on p^{2-4}. The protoconules on the true molars are the only variable or reversional characters.

P^1 is much larger than in *T. cultridens.* It is separated by narrow intervals both from the canine (9 mm.) and from the second premolar. In p^2 besides the greater breadth we note the somewhat more anterior position of the deuterocone and the more subequal convexities of the protocone and tritocone on the ectoloph, although the base of the protocone is still much broader than that of the tritocone; p^2 has a rudimentary protoconule but no suggestion of a tetartocone. In p^3 we have a more quadrangular crown with a more elevated ectoloph than in *T. cultridens,* and a more symmetrical development of the deuterocone and tritocone, although the former is still widely expanded at the base. In both p^3 and p^4 the internal cingulum is slightly less complete than in *T. cultridens.* On p^4 there is a very striking elevation of the ectoloph accompanied by greater prominence of the antero-external style and greater symmetry of the deuterocone and tritocone convexities.

The molars represent a progression upon those of *T. cultridens,* with sharp prominent styles, serrate external cingula, elevated anterior cingula, pointed protocones and hypocones, which are somewhat flattened and vertically striated on their inner faces; m^3 has a prominent and serrate posterior cingulum but no trace of a hypocone.

Telmatherium ultimum Osborn

Plates XVI, XLVI, LI, LV, LXV; text figures 126, 219, 223, 255, 256, 289, 294–298, 300, 508, 516, 592, 593, 647, 717, 745

[For original description and type references, see pp. 177, 184. For skeletal characters see p. 653]

Type locality and geologic horizon.—White River, Uinta Basin, Utah; Uinta formation (*Diplacodon-Protitanotherium-Epihippus* zone, Uinta C 1).

Specific characters.—Skull very large (basal length 510 mm.), zygomata arching (zygomatic breadth 300 mm., estimated). Incisors and canines large, i^3 very large, subcaniniform. P^1–m^3, 218 millimeters (type); premolars progressive; p^3, p^4 with the two outer cusps subequal and externally convex; well-developed internal and nearly complete external cingula; very rudimentary tetartocone swellings; molars large (m^1–m^3, 129 mm.) and progressive.

The discovery in Uinta C, by O. A. Peterson, of a female skull and jaw (Am. Mus. 2060) and the anterior half of a male skull with well-preserved dentition (Am. Mus. 2004) representing this species was a most important one. The animal was at first supposed by Osborn to be a terminal member of the *Palaeosyops* series. Subsequently it was compared point by point with Marsh's type of *Telmatherium validum* and was found to exhibit the most striking resemblances in the dentition and those parts of the skull in which comparison could be made in both. Highly distinctive is the premaxillary symphysis, more deep and elongate than in *Metarhinus,* deeper than in the type and paratype of *Manteoceras manteoceras,* more abbreviate than in *Dolichorhinus.* The region of the malars below the orbits is also characteristic and similar to that of *T. cultridens* but shows a more decided depression for the anterior portion of the masseter, and the posterior end of the malar has a deep vertical flange. In dentition, as enumerated above, *T. ultimum* is directly progressive from *T. validum.*

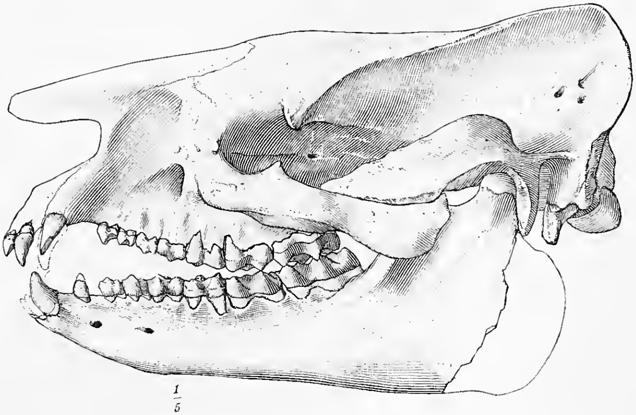

FIGURE 294.—Type skull and lower jaw of *Telmatherium ultimum*

One-fifth natural size. Am. Mus. 2060, from Uinta C (true Uinta); White River, Uinta Basin, Utah.

Measurements of Telmatherium ultimum, in millimeters

	Am. Mus. 2060 (type); Uinta C	Am. Mus. 2004 (paratype); Uinta C	Carnegie Mus. 2339
Skull, basal length	510	--------	[a] 568
Skull, breadth across zygomata	[a] 300	--------	--------
Face, length	270	--------	--------
Cranium proper, length	[a] 250	--------	323
Free nasals	85	[b] 66	80
Dental series, total length i^1–m^3	303	320	--------
P^1–m^3	218	229	243
P^1–p^4	90	95	89
M^1–m^3	129	137	148
I^1, ap. by tr	14×14	15×14	--------
I^2, ap. by tr	15×15	15×17	--------
I^3, ap. by tr	19×18	22×20	--------
C, ap. by tr	--------	25×22	--------
C, vertical	--------	44	--------
P^1, ap. by tr	19×12	19×12	--------
P^2, ap. by tr	20×19	20×22	--------
P^3, ap. by tr	21×28	23×28	--------
P^4, ap. by tr	26×35	27×35	--------
M^1, ap. by tr	38×40	40×37	--------
M^2, ap. by tr	46×49	49×44	--------
M^3, ap. by tr	46×51	50×48	--------

[a] Estimated. [b] Crushed.

In general comparison with *Manteoceras* the skull of this species of *Telmatherium* presents very pronounced differences: (1) the occiput differs widely in its height and rounded summit and in the presence of two large facets above the foramen magnum; (2) in front of this, on the vertex of the skull, is a relatively long, delicate sagittal crest without the characteristic pit of *Manteoceras* and lacking the overhanging supratemporal ridges; (3) the nasals are laterally recurved and distally truncate, as in *Manteoceras,* but the free portion is relatively shorter; (4) the zygoma resembles that of the *Palaeosyops* or *Limnohyops* type—that is, it is without the infraorbital shelf—and especially parallels that of *Palaeosyops* in the development of a deep flange on the lower surface of the malars, which is an advance on the *M. manteoceras* condition.

The above table shows rather marked differences in proportions of the teeth between the type and paratype; the cheek teeth in the paratype are all relatively longer and narrower.

As a whole the skull is mesaticephalic. Comparison of the outline dorsal and palatal views of *Telmatherium ultimum* and *Manteoceras* (figs. 296, 303) brings out a large number of very distinctive characters.

The horn rudiments are so inconspicuous in both the male and female skulls that they were not observed by the author for a long time. In the female they may be said hardly to exist, and in the male (Pl. XVI) they can be seen only by very close scrutiny. As above noted, it is difficult to say whether they are in a retrogressive or stationary condition. They are certainly far less progressive than in *Manteoceras.*

Skull of T. ultimum.—The cranium of this species is represented by the type, a superbly preserved female skull (Am. Mus. 2060), and by the anterior portion of the paratype, a male skull (Am. Mus. 2004), in which the youthful age is such that many of the sutures can be made out. The skull of the type is laterally crushed in the anterior half, but the width across the zygomata has probably not been greatly lessened. The general proportions are mesaticephalic, the cranium being very much longer than that of *P. leidyi* but much less elongate and deeper vertically than that of *D. hyognathus.* The measurements are, length 510 millimeters, breadth 300 (estimated). It is readily distinguished from all other crania by the combination of the following principal characters: (1) Nasals relatively short (free length 78 mm.), the lateral downward extensions being wholly covered by the maxillaries; (2) prominent narrow sagittal crest; (3) greatly elevated occiput; (4) deeply extended malar and squamosal flanges of the zygomatic arch; (5) premaxillary symphysis vertically extended; (6) frontals with horn swellings rudimentary—that is, consisting of convexities so slight (paratype) that they are with difficulty observable.

In palatal aspect the brachycranial proportions decidedly predominate over the dolichocranial in the basicranial region of the skull as shown in the following characters: (1) The shortness of the anteroposterior measurements (as from glenoid facet to mastoid process, from foramen ovale to condyle 100 mm.), as compared with the transverse measurements (across zygomata, 300 mm., estimated; across postglenoid processes, 195; across mastoid processes, 180); (2) the upward slant of the basisphenoid; (3) the shortness of the distance (140 mm.) between the pterygo-alisphenoid wing and the condyle; (4) the postglenoid and paroccipital processes greatly flattened or extended transversely with very moderate anteroposterior diameter.

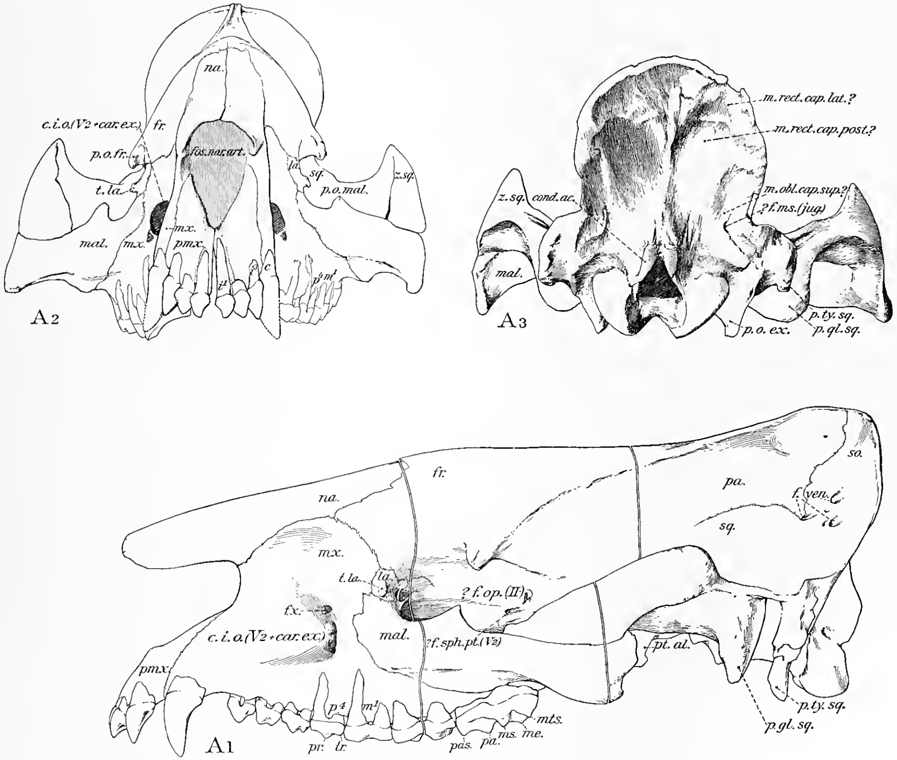

FIGURE 295.—Type skull of *Telamatherium ultimum*

One-fourth natural size. Am. Mus. 2060. White River, Uinta Basin, Utah; base of Uinta C, true Uinta formation. A$_1$, Side view. The depth of the skull in the middle region and immediately in front of the orbit has been increased by lateral crushing. The double lines mark the plane of the sections in Figure 255, B$_1$, B$_2$. A$_2$, Front view. A$_3$, Occipital view.

More in detail: The posterior nares open immediately between m^2 and m^3, whereas in *P. leidyi* they open opposite the posterior half of m^2, and in Oligocene titanotheres they often open opposite the posterior half of m^3. The postnarial space is relatively deep, or vertically extended, and short anteroposteriorly; the line of junction between the pterygoid wings of the alisphenoids and the palatines can not be clearly made out. Unlike those of *M. megarhinus* or *P. major* the pterygoids and lateral wings of the alisphenoids descend abruptly. The foramen ovale is separated from the foramen lacerum medium by a bridge, 24 millimeters as compared with 38 in *D. hyognathus*. Between the foramen lacerum medium and foramen lacerum posterius the basioccipital forms a prominent, laterally compressed keel. The occipital condyles are comparatively slender and widely separate below the foramen magnum. This aspect of the skull illustrates admirably (1) the broadly transverse extension of the articular facets for the condyle of the jaw, (2) the broadening of the postglenoid processes, (3) the separation of the postglenoid and post-tympanic, which is much wider than in the brachycephalic *P. major* but very much narrower than in the dolichocephalic *D. hyognathus;* (4) also the sharply produced downward flange of the posterior portion of the malar.

The superior aspect of the skull (fig. 296) fails to give the actual shape of the nasals owing to the marked crushing at this point. The entire length of the nasals is 219 millimeters, as compared with 520, the entire length of the vertex.

Horn rudiments.—In the type female skull there is no evidence of the existence of a horn swelling at the junction of the frontals and nasals. In the paratype male skull (Am. Mus. 2004), however, there is a low swelling (Pl. XVI) at the junction of the nasals, maxillaries, and frontals, at a point above and somewhat in front of the anterior rim of the orbit, which betokens the presence of a horn rudiment in an even more incipient stage than that of *M. manteoceras* or *D. hyognathus*.

The uncrushed skull was evidently rather broad between the orbits. The supratemporal crests are moderately defined anteriorly, but as they enter the parietals they become more sharply defined, leaving a shallow groove between the summits of the short sagittal crest. The superior border of the lateral occipital crest is rather delicate; in fact, the entire skull is slender rather than broad and massive.

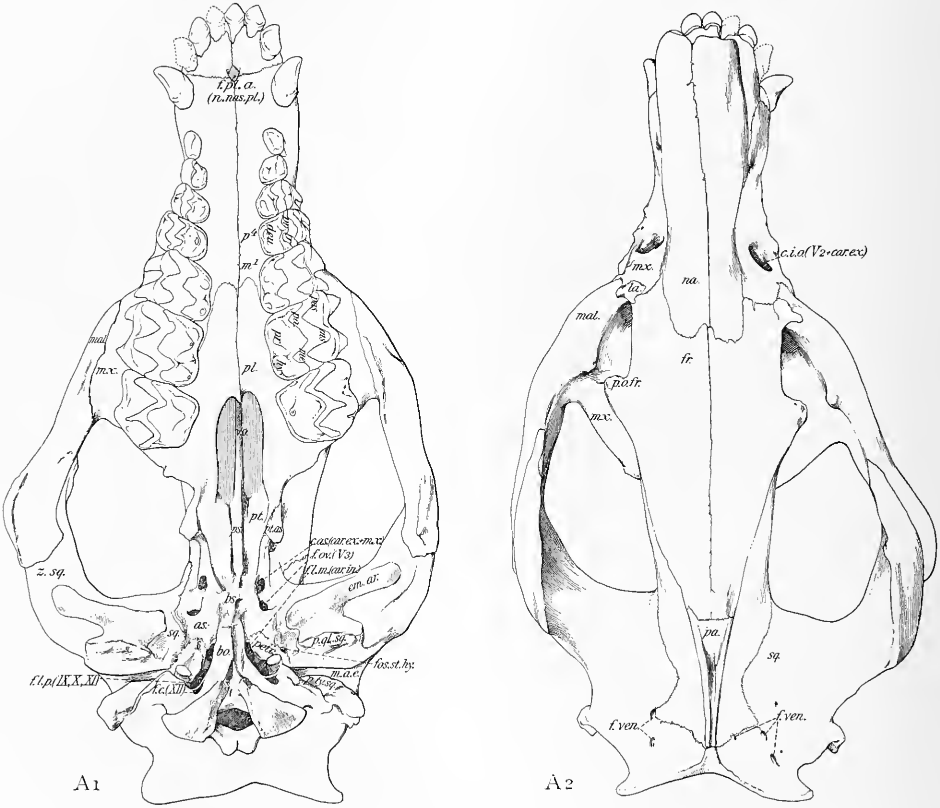

FIGURE 296.—Type skull of *Telamatherium ultimum*

One-fourth natural size. Am. Mus. 2060. White River, Uinta Basin, Utah; base of Uinta C, true Uinta formation. A_1, Palatal view; A_2, top view. Lateral crushing has narrowed the frontal region and distorted the zygomata.

The lateral aspect of the skull is distinguished by the following characters: (1) The relatively short (85 mm.) free portion of the nasals; (2) the elevation of the maxillaries on the sides of the face, somewhat as in *M. megarhinus* and *D. hyognathus*, and the covering over of the downward lateral extension of the nasals; (3) the wide interval (109 mm.) between the antorbital border and the narial notch; (4) the anterior extension of the malars below the orbit; (5) the clear definition of the lacrimals, partly external to and partly within the orbit; (6) the prominence of the postorbital processes of the frontals and malars respectively; (7) the gently rounded conformation of the malar below the orbit, which most nearly resembles that in *T. cultridens;* (8) the sharp downward or inferior flange of the malars beneath their junction with the squamosals; (9) the moderate upward extension of the zygomatic squamosal bar; (10) the presence of a cranial depression at the point of junction between the parietals and the frontals, or above the mid-cranial region, the skull being gently arched upward in front of this point.

The anterior aspect of the skull (fig. 295) exhibits the relatively deep premaxillary symphysis as compared with that of *P. leidyi*, and the absence of the extremely long and deep maxillary union so characteristic of *D. hyognathus.* The nasals are much less thickened and decurved at the sides than in *D. hyognathus.* This aspect of the skull also exhibits the depth of the zygoma, including the malar and squamosal portion, compared with the extreme shallowness of this arch in *D. hyognathus.*

The occipital view of the skull is still more characteristic, owing to its great height (194 mm.) as compared with its breadth (137 mm.), also to the presence of a pair of oval prominences on either side of the superior portion of the foramen magnum, as in *Menodus giganteus.* This view also illustrates the breadth of the paroccipital and postglenoid processes.

The dentition is finely represented in the complete type skull (Am. Mus. 2060) and in a somewhat more progressive stage in the paratype, consisting of the anterior portion of a skull (Am. Mus. 2004).

The incisors are superbly shown in Am. Mus. 2004 and 2060 (Pl. LV; figs. 294–297). The superior incisors in the type are pointed, decidedly cingulate or cupped posteriorly, and sharply convex anteriorly, and increase in size rapidly from i^1 to i^3; the lateral incisor (i^3) is more caniniform than incisiform; the crown of i^1 measures 15 millimeters vertically, and a slight ridge extends down the posterior face to the apex of the basal cingulum which branches on either side to form lateral depressions; the crown of i^2 (measuring 19 mm. vertically) is slightly larger and of exactly similar form; in i^3 the caniniform crown (measuring 28 mm. vertically) is distinguished on its postero-internal surface by a lanceolate face with sharply defined antero-internal and postero-external ridges, which sweep at the base into the low, broad cingulum, exactly as in the canine. In Am. Mus. 2004 the superior incisors are even larger and the posterior cingulum is more strongly accented. All the cutting teeth, both incisors and canines, bear a striking similarity to those of *T. cultridens* and *T. validum*—in fact, they are almost directly progressive upon them, the only difference being that the posterior angles and cingula are a little less sharply accented. The inferior incisors are not known.

The superior tusks, which are completely preserved only in the paratype (Am. Mus. 2004), are much more decidedly of the lanceolate, typical *Telmatherium* type than those of *M. manteoceras*, although the anterior and posterior ridges are not quite so prominent and sharply defined as in *T. cultridens*, *T. validum*, or *D. hyognathus;* the tusks are none the less long (43 mm.) and transversely narrower (22 mm.) at the base of the crown than those of *M. manteoceras* (25 mm.); the ridges pass inferiorly into a strong postero-internal cingulum, which also clearly distinguishes these tusks from those of other species so far as observed. The superior molar-premolar series as a whole is not only larger (229 mm. in Am. Mus. 2004) but has a very marked individuality throughout, so that every tooth in the series can be distinguished by careful observation from those of either *M. manteoceras* or *D. hyognathus.* The type is distinctly telmatherioid, exhibiting peculiar progressive modifications upon the dental type of *T. cultridens* and *T. validum* which partly anticipate those seen in *Menodus.* The series in the type (Am. Mus. 2060) is of somewhat smaller size and in an earlier or less progressive stage than that in Am. Mus. 2004. In both specimens the breadth of the molars equals or slightly exceeds the length, whereas in the more dolichocephalic *D. hyognathus* molars the length decidedly exceeds the breadth. The dental proportions are therefore mesaticephalic.

Premolars.—The superior premolars of the type are so much worn as to obliterate certain of their rudimentary progressive characters. The following description of these parts is accordingly based upon the unworn premolars of the paratype specimen, which appears to be in a somewhat more progressive stage of evolution. A narrow diastema, 12 to 16 millimeters, separates the canine from p^1. The premolar series, measuring 90 (type) and 95 (paratype) millimeters, as compared with 82 in *M. manteoceras*, exhibits not only increase in size but marked progression in pattern, as seen in the following characters: (1) Slightly increased complication of p^1 (ap. 19 mm., tr. 12) in the rudimentary internal cingulum and more decided elevation of the tritocene; (2) in p^2 to p^4 of the paratype (No. 2004) the deuterocones consist of antero-posteriorly elongate ridges, much more pronounced than in *T. cultridens*, convex on the lingual and flattened on the buccal surfaces, totally different from the smooth-sided deuterocones of *M. manteoceras* and from the apically compressed cones with faint lateral ridges in *D. hyognathus;* this feature, it should be added, is much more distinctly exhibited in the little worn series of Am. Mus. 2004 than in the much worn series of the type, Am. Mus. 2060; (3) this deuterocone ridge is destined to give rise to the tetartocones by constriction, and in p^3, p^4 a faint rudiment of the postero-internal cingulum can be observed in the unworn crown; (4) the internal cingulum is faintly defined around the entire lingual surface of the deutero-

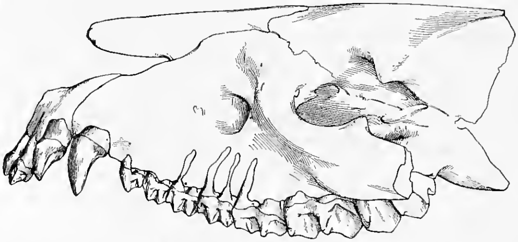

FIGURE 297.—Paratype skull of *Telmatherium ultimum*

One-fourth natural size. Am. Mus. 2004, reversed; White River, Uinta Basin, Utah; Uinta C, true Uinta formation.

cones; (5) the ectolophs are greatly elevated and consist of the two well-defined subequal protocone and tritocone convexities with a rudimentary external cingulum and pronounced antero-external style; (6) in p^2 the progressive broadening tendency is illustrated by the fact that the breadth (22 mm.) equals the length on the ectoloph, a marked advance upon what is observed in either *M. manteoceras* or *D. hyognathus*—in fact, this tooth now resembles p^3 in general pattern, although retaining a more elongate contour; (7) in p^3 the breadth considerably exceeds the length and the crown is broadened internally by the expansion of the deuterocone; (8) in p^4 we have a still more quadrangular and molariform tooth, the length being 27 millimeters and the breadth 35, but in this tooth the deuterocone is not quite so sharply defined.

The superior premolars of the type (Am. Mus. 2060) are distinguished from the premolars of the paratype (Am. Mus. 2004) by the following characters: (1) The premolar series is somewhat shorter (90 mm. as compared with 95 in Am. Mus. 2004); (2) p^2 in the type is less advanced, in that the deuterocone is smaller and placed farther back and the tritocone is less subequal with the protocone; (3) in p^3 also the deuterocone and tritocone are somewhat less progressive and the tetartocone ridge is barely suggested; the cingulum also is slightly less developed; (4) in p^4 the tetartocone is indicated by a low, obtuse swelling, whereas in Am. Mus. 2004 it forms the distal spur of a very prominent deuterocone ridge. These differences in the tetartocones can hardly be due entirely to differences in degree of wear (the type being much the older of the two), because in the paratype the ridges in question are so strong that they would probably show even in the worn stage. These differences seem to indicate that the paratype is somewhat more advanced than the type in its premolar evolution.

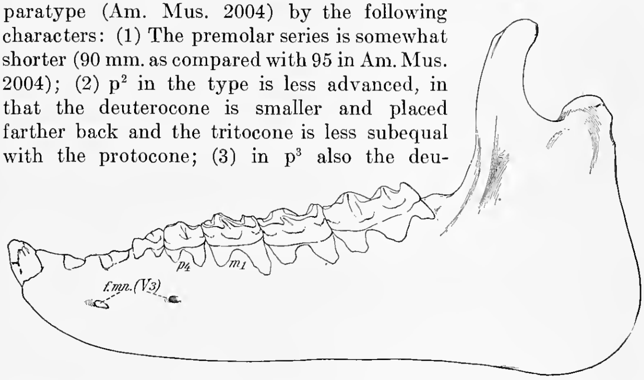

FIGURE 298.—Lower jaw of *Telmatherium ultimum*

One-fourth natural size. Am. Mus. 2060 (type). White River, Uinta Basin, Utah; base of Uinta C, true Uinta formation.

The inferior premolars, as observed in the lower jaw of the type (Am. Mus. 2060), exhibit the following characters: The postcanine diastema is about 20 millimeters in length; behind p_1 is a shorter diastema of 11 millimeters in length; p_1 and p_2 are represented only by the alveoli; p_3 is much damaged but was incompletely molariform.

P_4 (ap. 27 mm., tr. 19) is submolariform, lacking only the prominence of the postero-internal cusp, which is analogous to the entoconid of the molars. The trigonid is higher than the talonid, and its V less sharply defined. A weak external cingulum appears opposite the outer midvalley and festoons the external slope of the hypoconid.

Molars.—The superior molars are a powerful series of teeth measuring 129 (type) to 137 (paratype) millimeters, with extremely elevated or subhypselodont cusps, the ectoloph of the least worn m^3 reaching a height of 35 millimeters and the protocone of the same tooth 24. The external cingulum is more pronounced, especially in the type, Am. Mus. 2060, in which it prominently guards the outer valleys and begins to encircle the styles, reminding us of the cingulum development in *Menodus giganteus;* the internal cingulum is similarly prominent, embracing the entire inner side of the crown in m^3 of the same specimen. A marked peculiarity which is an advance on both *M. manteoceras* and *T. cultridens* is the prominence of the anterior cingulum in m^1 to m^3, which swells into a large median cingule, comparable to the protostyle of most species of *Menodus*. The posterior cingulum is less prominent except in m^3, in which it is free and exceptionally high (type); in the paratype it is connected with an incipient hypocone swelling. The elevated ectoloph is accented by the sharp development of the parastyles, mesostyles, and metastyles. The hypocones of m^1, m^2 of both type and paratype are very large and prominent, an advance upon the conditions in *T. cultridens* and *T. validum.* A further peculiarity is that in the unworn paratype the buccal surfaces of the internal cones (protocone and hypocone)—that is, the surfaces facing the ectoloph—are somewhat flattened and vertically striate, instead of rounded and smooth, as in *M. manteoceras* and *D. hyognathus*, which is faintly prophesied in *T. validum*. The only retrogressive elements are the conules, which have disappeared. The conules are largest in brachyodont titanotheres; with advancing hypsodonty the base of the paracones and metacones extends linguad and either absorbs or crowds out the conules.

The inferior molar series represented in the jaw associated with the type (Am. Mus. 2060) is of large size (155 mm.). A smaller jaw (Am. Mus. 2033), formerly referred to this species but now referred provisionally to *Manteoceras uintensis*, is somewhat shorter (147 mm.). Although this specimen probably represents another genus and species, the molar characters are somewhat similar to those of the type, including as progressive features (1) the prominence and the backward extension of the paraconid into a parastylid; (2) the variable but distinct metastylid ridge; (3) the external position of the hypoconulid on m_3 and the prominent internal ridge on it, which gives it a concave form internally; (4) the external cingulum slightly more progressive than in *M. manteoceras* and dipping somewhat into the valleys but not so deeply as in *D. hyognathus.*

Lower jaw of T. ultimum.—The jaw of this specimen is represented by that of the type (Am. Mus. 2060). The type jaw retains the characters of *T. cultridens* in the rather slender recurved coronoid process but departs from them by its rapidly increasing depth posteriorly—in fact, the whole jaw is relatively deeper than in the ancestral species. The distance from the condyle to the incisive border is estimated at 435 millimeters in the type. The chin is strongly compressed laterally (54 mm.), and behind it the jaw gradually broadens and deepens, the lower border being more nearly straight than in *M. manteoceras* and terminating in the slightly depressed and backwardly produced angle; the condyle exhibits two marked peculiarities: the outer half of the rotular facet extends broadly forward, whereas the inner half has a straight anterior border and unites posteriorly by a much broader union than in *M. manteoceras* with the broad facet for the postglenoid process. The coronoid process, perfect in the type, is rather narrow and uniformly recurved. The striking resemblance to *T. cultridens* observed in the dentition of this species is therefore not seen in the jaws, which are relatively shorter, more massive, and deeper posteriorly (below m_3) than in *T. cultridens*, all of which are progressive characters.

A second jaw (Am. Mus. 2033) was at first doubtfully referred to the same species. In this jaw the second premolar is spaced as in the type. In other features, as in p_2, in the coronoid process, and in the proportions of m_3, this jaw resembles those of members of the *Manteoceras* phylum, to which this one is now provisionally referred. (See *Manteoceras uintensis*, below.)

A skull in the Carnegie Museum (No. 2339) differs from the type and paratype in having a longer tooth row but shows generic agreement with *T. ultimum* in the general form of the skull, especially of the zygomata, occiput, and nasals.

Telmatherium altidens Osborn

Plate LXV; text figures 127, 299, 300

[For original description and type references see p. 184]

Type locality and geologic horizon.—Uinta Basin, Utah; Uinta formation, *Diplacodon-Protitanotherium-Epihippus* zone (Uinta C).

Specific characters.—P_1–m_3, 313 millimeters; a wide diastema (55 mm., estimated) behind the inferior canines; canines in males elevated (76 mm., estimated) and pointed; p_{1-2} laterally compressed, nonmolariform; p_{3-4} submolariform. Subdolichocephalic, upper postcanine diastema elongate.

Materials.—As described in Chapter III, this animal is known only from a single lower jaw (Am. Mus. 2025) with no parts of the skull or skeleton associated.

Comparison.—The reference of this specimen to the genus *Telmatherium* depends chiefly upon (1) the large size and vertical elongation of the canines, as in *T. validum;* (2) the very large size of the lower incisors; (3) the exceptional elongation of the lower postcanine diastema, which is incipient in *T. ultimum* but was evidently carried to a much greater extreme in *T. altidens;* (4) p_2 much less molariform than in *Protitanotherium* and hence more like the simple, laterally compressed p_2 of *T. ultimum;* (5) the very large size of the lower molars (m_{1-3}), the form of which indicates large, broad upper molars, as in *T. ultimum.*

The skull when discovered may well prove that this animal represents a well-marked new generic stage. On the other hand, the very large incisors and lofty canines, the pronounced diastema, the characters of p_1, p_2, and the large, broad molars, as noted above, appear to indicate generic kinship with *T. ultimum.*

Chief characters.—The exceptionally long mandibular symphysis and wide postcanine diastema, as foreshadowed in *T. ultimum*, distinguish this titanothere as possessing a relatively elongated facial region. This character, as well as the long, relatively shallow jaws, the elongation of m_3, and the wide space behind m_3, is evidence that the skull as a whole was subdolichocephalic, although far less so than that of *Dolichorhinus.* In common with *T. ultimum*, "*T. incisivum,*" *Protitanotherium*, and all other upper Eocene and Oligocene forms, *T. altidens* had undergone a differential elongation of the middle part of the skull, which allowed the molars to become extremely large, both absolutely and as compared with the premolars. The elevated, piercing canines are also exceptional among titanotheres; they exceed those of the ancestral species. Thus the animal is very readily distinguished from any of the known species of the contemporary *Diplacodon* and *Protitanotherium.* A fourth feature is the simple, nonprogressive, elevated, and somewhat laterally compressed form of p_2, which is decidedly more primitive than the corresponding tooth in *Protitanotherium.*

The cracked and much weathered teeth of this male individual (Am. Mus. 2025) fortunately include the median incisors (i_1) of the opposite sides, the left canine, and the entire grinding series of the right side in sufficient preservation to define the species sharply. In detail the median incisors are much larger, with more pointed tips than those of *Protitanotherium emarginatum*, measuring 19 millimeters on the anterior face, 20 anteroposteriorly, and 15 transversely. These teeth distinctly suggest the upper median incisors of *T. ultimum.* The laterally compressed or convex anterior faces, the smoothly sloping posterior faces, the U-shaped posterior cingula also suggest the *Palaeosyops* type of tooth, although this dolichocephalic animal does not appear to present any affinity to that genus. It is difficult to determine the precise form and proportions of the canines, the fang measurements (vert. 76 mm., estimated; ap. 31; tr. 26) indicating a more laterally compressed or dolichocephalic type of canine than in *Protitanotherium emarginatum.* The height of this tall and slender canine exceeds 76 millimeters (estimated), as compared with 53 in the male *P. emarginatum* and 56 (estimated) in the male *P. superbum.* The name *T. altidens* refers to this feature, as the tusk is the most elevated and piercing among all the known titanotheres, not excepting the giant *Menodus giganteus* of the Oligocene. Faint anterior and posterior ridges can be detected on the anterior and posterior faces of the crown, distinguishing this tooth readily from the canine of *Palaeosyops major,* in which the posterior ridge is on the internal face of the crown. The very wide total diastema between the canine and p_2 measures 70 millimeters, as compared with 40 in *Protitanotherium superbum* and 45 in *Telmatherium ultimum,* which is approached only by the wide diastema (51 mm.) in *Dolichorhinus hyognathus.* The grinding series as a whole measures 313 millimeters, as compared with 304 in *P. emarginatum* and 318 in *P. superbum,* the lower grinding series being, therefore, slightly smaller than in *P. superbum.*

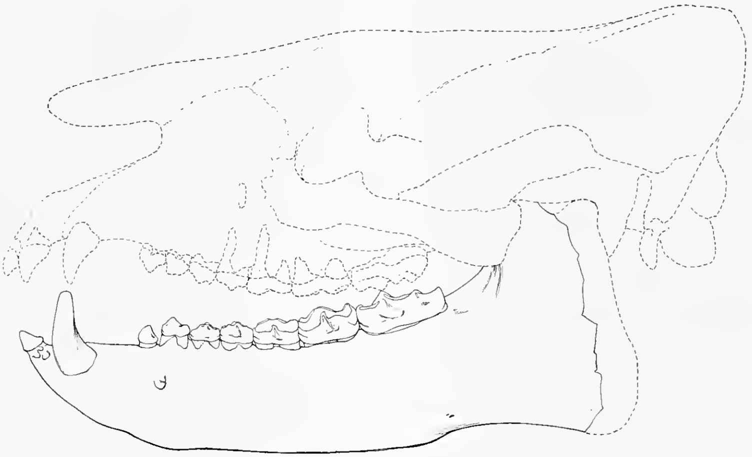

FIGURE 299.—Hypothetical reconstruction of the skull of *Telmatherium altidens*

One-sixth natural size. Designed to show especially the long postcanine diastema, the elongated face, and the supposed generic resemblance to *T. ultimum.* The lower jaw is Am. Mus. 2025 (type of *T. altidens*). The skull is restored from Am. Mus. 2060 (type of *T. ultimum*).

Premolars.—P_1 and p_2 are not so much compressed as in *Telmatherium cultridens* but are somewhat swollen transversely. P_1 (ap. 19 mm., tr. 12) is a simple, gently compressed cone, with a small posterobasal cusp rising from the posterior ridge. This cusp is less advanced than in *Protitanotherium superbum* or *P. emarginatum.* P_2 (ap. 27 mm., tr. 15) is also less advanced than in those species, its posterior lobe being smaller, lower, and much less crescentic superiorly. It has a faint paraconid, no metaconid, and very faint anterior and posterior internal valleys. It is thus much like p_2 of *Manteoceras manteoceras, T. cultridens,* and (so far as known) *T. ultimum.*

In striking contrast with this is the progressive structure of p_3 (ap. 30 mm., tr. 18), especially its extremely prominent median cusp (=protoconid); the anterior and posterior crescents are correspondingly more defined than in p_2; the rudiments of the metastylid and cusps appear, corresponding to the paraconid and entoconid in the molars. P_4 is a decidedly larger tooth (ap. 35 mm., tr. 23) with prominent internal cusps (= paraconid, metaconid, metastylid, entoconid).

Molars.—The true molars measure 195 millimeters in length, as compared with 214 in *Protitanotherium superbum.* The measurements (ap. by tr.) are, m_1, 45 by 29 millimeters; m_2, 59 by 32; m_3, 89 by 35. The very large size of the molars as in *P. superbum* and other Uinta C titanotheres is thus noteworthy. The much worn grinders give an imperfect picture of the distinctive characters of these teeth, but it would appear that the external cingulum and the metastylid are faintly indicated and that in m_3 the hypoconulid is placed more on the internal or lingual side of the crown, as in *Palaeosyops paludosus.* The grinding series, therefore, presents two resemblances to that of *P. paludosus*—namely, the prominent internal cusp on p_3 and the more internal position of the hypoconulid on m_3—yet neither of these characters is believed to indicate genetic affinity. The closest resemblances are to the inferior dentition of *T. ultimum,* from which this jaw differs, however, in its greater size, its relatively larger canines, and the more internal position of the hypoconulid. This last condition may be partly due to crushing.

Jaw.—The jaw of *T. altidens* is readily distinguished from the jaw of *Protitanotherium emarginatum* and that of *P. superbum* by its dolichopic characters, the wide diastema between the canine (55 mm., estimated) and p_1, and that between m_3 (54 mm.) and the anterior border of the coronoid process. The symphysis is extremely long (200 mm.); it is both actually and relatively longer than in *P. emarginatum* (155) or *P. superbum* (158, estimated). The jaws are decidedly deep, measuring 107 millimeters below p_2, 124 behind m_2. The coronoid was probably elevated, tapering, and recurved toward the summit. The thickness of the rami in the type jaw has been reduced by crushing; below m_1 it is 40 millimeters. This jaw therefore represents a large but fairly slender and active animal, which in some respects is suggestive of relationship with species of the long-jawed genus *Menodus* of the Oligocene but in other respects is very unlike an ancestor of *Menodus*—namely, the excessively large size of the incisors, the retarded condition of p_1 and p_2, and the very long postcanine diastema.

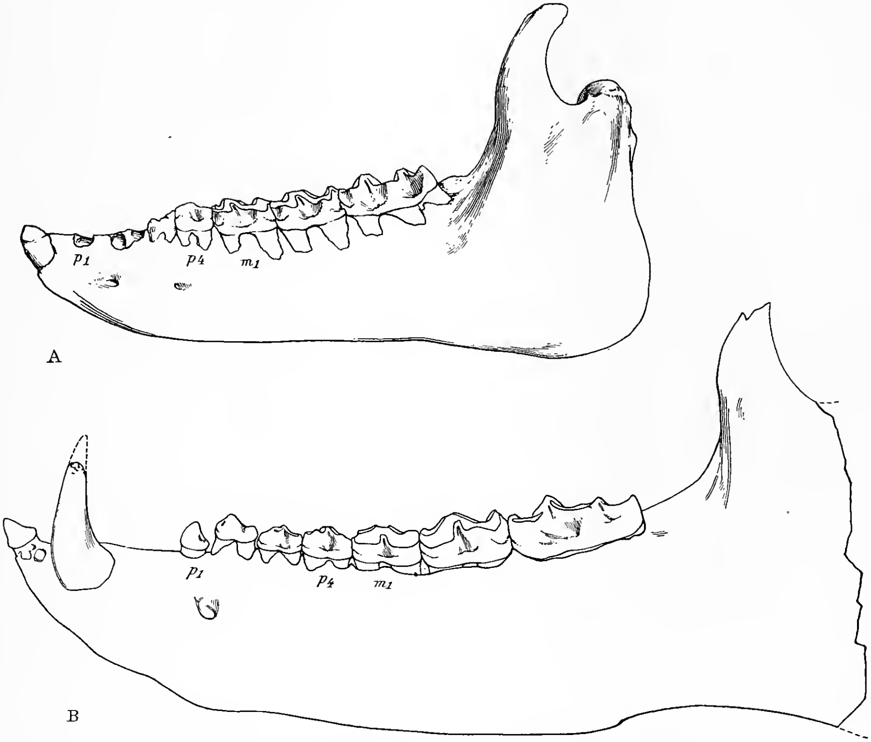

FIGURE 300.—Lower jaws of *Telmatherium ultimum* and *T. altidens*

One-fourth natural size. A, *T. ultimum*, Am. Mus. 2060 (type), reversed; White River, Uinta Basin, Utah; base of Uinta C, true Uinta formation. B, *T. altidens*, Am. Mus. 2025 (type); White River, Utah; Uinta C.

Sthenodectes Gregory

Plates LXV, LXVI; text figures 129, 130, 301

[For original description and type references see p. 190]

Generic characters.—Skull mesaticephalic or subbrachycephalic; cephalic index 62–65; malars without infraorbital shelf or protuberance; nasals apparently short, broad proximally, and tapering distally; face concave in front of orbits; frontonasal "horn swellings" not evident; sagittal crest deep and narrow; occiput low with thin crests; dentition extremely macrodont; incisors relatively larger than in any other known titanothere.

Historical notes.—In describing the type species (*Sthenodectes incisivus*) of this genus the author, Earl Douglass (1909.1, p. 305), said: "I think that this skull represents a different genus from *Telmatherium*, but I prefer to place it provisionally here rather than establish another genus." Through the courtesy of Douglass, Gregory (1912.1) was enabled to compare this type with the extensive material in the American and Yale Museums and reached the conclusion that *T. incisivum* represents a different genus or subgenus, to which he gave the name *Sthenodectes*, in allusion to the great power and development of the incisors and canines. The following characters were assigned by Gregory in the original description of the genus as compared with *Telmatherium*: (1) The incisors are much larger and more advanced in evolution; (2) the postcanine diastema is reduced or absent; (3) the superior premolars p^2, p^3, p^4 are more progressive than in *T. ultimum*, having very heavy internal cingula and pronounced external cingula; (4) the basicranial region differs in many details.

The type skull of the species (Carnegie Mus. 2398) is vertically crushed, a condition that led to some errors in the original description of the species which a second skull in the Field Museum (No. 12168) enabled Gregory to correct and to reach the following conclusion as to the affinities of this animal:

Relation to Telmatherium.—*Sthenodectes* is sharply separated from the Dolichorhininae and at the same time allied with *Telmatherium* by the following characters: (1) General contour of the skull in basal view, wholly unlike *Metarhinus* and resembling *Manteoceras* or *Telmatherium*; (2) complete absence of infraorbital protuberance, the infraorbital portion of the malar more like that of either *Manteoceras* or *Telmatherium*; (3) midportion of malar with deep vertical flange as in *Telmatherium* (contrast *Metarhinus*); (4) incisors and canines readily derivable from the *Telmatherium* type (compare figures of side view, crown view; compare premaxillaries); (5) dentition extremely macrodont (microdont in *Metarhinus*, macrodont in *Telmatherium*); (6) premolars more advanced than in *T. ultimum* but derivable from the *Telmatherium* type (cf. *T. validum*) by enlargement of internal cingulum, filling out the internal contour of p^2; (7) referred lower jaw (Field Mus. 12168) decidedly nearer to *Telmatherium ultimum* than to *Metarhinus*, macrodont, especially molars, ramus massive and deep; (8) basis cranii with postglenoid, posttympanic, meatus, and basioccipital nearer the subbrachy-mesaticephalic type of *Telmatherium* than to the subdolichocephalic type of *Metarhinus*.

Through parallel evolution there are some marked resemblances to the Dolichorhininae, as follows: (1) Premolars (p^{2-4}) with very heavy internal cingula and crowns well filled out on the inner side; (2) incisors cupped by upgrowths of heavy cingulum; (3) subhypsodont or elongate character of the molars of the type specimen.

Effects of crushing.—To the vertical crushing of the type skull is possibly due the wide displacement of the lacrimal bones on both sides of the face, resulting in the false appearance of "lacrimal pits." To the crushing is also due the union of the postglenoid and post-tympanic processes, the depression of the occiput, and the abbreviation of the nasals.

Sthenodectes incisivus (Douglass)

Plates LXV, LXVI; text figures 129, 130, 301

[For original description and type references see p. 185]

Type locality and geologic horizon.—About 3 miles northeast of well 2, Uinta Basin, Utah; upper levels of *Eobasileus-Dolichorhinus* zone (Uinta B 2).

Specific characters.—Skull, length 488 millimeters, zygomatic breadth 305 millimeters, cephalic index 62. Dentition, p^1–m^3 207 millimeters; m^1–m^3 125; p^2 large (ap. 19 mm., tr. 22), very progressive, with advanced tritocone and complete internal cingulum, deuterocones of p^{2-4} relatively elevated, internal cingula heavy, complete, m^3 (ap. by tr.) 42 by 45 millimeters with reduced posterior metacone crescent.

Materials.—Besides the type skull in the Carnegie Museum (No. 2398), on which the above specific characters are based, there is a well-preserved skull in the Field Museum (No. 12168), also a pair of lower jaws (Field Mus. 12166). According to Riggs (1912.1, p. 38) all three specimens are from the same locality and belong to the same species. The skull and lower jaws in the Field Museum were discovered by Abbott in the lenticular sandstones near well 2 at the foot of Coyote Basin. The skull, Field Mus. 12168 (Pl. LXVI), is shorter (460–300 mm., cephalic index 65) than in the type of *S. incisivus* but has the broad-crowned molars and massive incisors of that species. At approximately the same geologic level but half a mile distant was found the lower jaw (Field Mus. 12166) referred to this species (Pl. LXVI), which belongs to an older individual, as is evident from the worn molars and incisors. It is described below.

This short-headed, massive-jawed titanothere exhibits a remarkable combination of characters. It exceeds all other known titanotheres in the size of the incisor teeth, which are correlated with the massive jaws and the relative abbreviation of the skull, the general proportions of which suggest those of *Manteoceras*. The abbreviation of the facial region constitutes a differentiation directly the opposite of that which was occurring in the line which gave rise to *Telmatherium altidens* in Uinta C, in which the face, judging by the wide postcanine diastema, was elongated. The indices are significant.

Indices of Sthenodectes incisivus

	Carnegie Mus. 2398 (type)	Field Mus. 12168 (referred)
Cephalic index	63	65
Faciocephalic index	47	44
Molar-cephalic index	26	28

The grinding teeth are also proportionally very large. The skull is at once separable from that of *Mesatirhinus* and *Dolichorhinus* by the short basicranial region and the stout, wide, spreading zygomata, as well as by the heavy, short premaxillae and the absence of a rounded infraorbital protuberance, or shoulder. It also differs from any of these genera in the proportions of the molar teeth, m^2 and m^3 being wider, or more brachycephalic in type. It parallels the true Dolichorhininae, however, in the advanced condition of the premolars and in the cupping of the incisors. It resembles *Metarhinus*, especially *M. earlei*, in the following characters: (1) Broad forehead; (2) concavity of the face in top view; (3) certain features of the premolars; (4) proportions of the occiput; (5) thin, high sagittal crest.

From the contemporary species of *Manteoceras*, namely, *M. uintensis*, it is distinguished by (1) the characters of the incisors and canines; (2) the much more advanced condition of the premolars; (3) the less elongate m^2; (4) the feebly constricted postcanine region. It parallels *Manteoceras* in the general proportions of the skull and in the form of the zygomatic arches, except that the malar portion of the arch has the deep flange characteristic of *Telmatherium*.

Sthenodectes suggests *Telmatherium ultimum* in certain features of the incisors, canines, and molars, in the detailed characters of the basicranial region and in the spreading zygomata; but it is distinguished from that form by (1) the much larger size and higher development of the incisors, (2) the more advanced condition of the premolars and premolar cingula, (3) the different form of m^3, (4) the lower occiput and sharper sagittal crest, (5) the wider forehead, (6) the more angulate section of the infraorbital portion of the malars, (7) the sharply tapering nasal bones. From the European genus *Brachydiastematherium*, which it resembles in having three large incisors, *Sthenodectes* is distinguished by the markedly lower evolution stage of the premolars (p_2–p_4).

Side and top views.—The top of the type skull has been crushed downward, especially above and in front of the orbits. The premaxillaries, though somewhat flattened by pressure, are of very large size, in correlation with the exceptional dimensions of the incisors. The nasals are imperfectly preserved at the end but appear to be even shorter than in *T. ultimum;* they converge rapidly in front, about as in *Metarhinus*, and proximally they spread rapidly and widely, measuring 125 millimeters transversely at the outer junction with the frontals. The latter were somewhat flattened but were very wide across the orbits (tr. 192 mm.). In front of the orbits there is a prominent vertical facial concavity suggesting the conditions in *Metarhinus fluviatilis*. The infraorbital foramen is large and prominent, apparently more so than in *T. ultimum*. Above this foramen and in front of the orbit is a triangular depression, in the position of the lacrimal bone, occurring on both sides of the skull but much larger in the right, which is referred to by Douglass as a vacuity. It now seems probable that these vacuities resulted from the downward crushing which has squeezed the lacrimals out of place; they lie immediately below the region where the horn swelling usually appears, but the presence of the latter is but vaguely if at all indicated. The forehead, as already stated, is broad and flat, and the depth of the skull appears to be less than in *T. ultimum* The opposite postorbital temporal crests run backward into a long sagittal crest, which is quite high and thin. The occipital crests are thin, but the whole occiput is much lower than in *T. ultimum.*

Palatal view.—In the inferior aspect of the skull we are struck by the great size of the dentition as a whole, the great size and spatulate outline of the incisor region, the prominent pointed canine tusks, the long, straight tooth row, the virtual lack of a postcanine diastema, the wide, very progressive premolars, the relatively large, subhypsodont molars, the widely arching zygomata, and the short basicranial region—all these, with the exception of the prominence of the incisors and canines, being characteristic of Oligocene titanotheres. The infraorbital part of the malar is like that of *Manteoceras* in that it did not flare outward into an infraorbital protuberance; just behind the orbit the malar was very massive, and its broad inferior expansion shows an area for the attachment of the masseter; the postero-inferior portion of the malar is a deep vertical flange, as in *Manteoceras* and *T. ultimum.* The squamosal portion of the zygoma is very stout and broad anteroposteriorly; the postglenoid process is rather small. The prominent external auditory meatus of the type in side view appears to be closed below by the appression of the postglenoid and post-tympanic processes, but this is probably due to crushing, as the Field Museum specimen shows these processes widely separated. The palate is long, and the anterior border of the posterior nares is between m^2 and m^3.

Incisors.—The anterior incisor (i^1) is very large (ap. 22 mm., tr. 20), and closely appressed in the median line to its fellow of the opposite side; its large, blunt tip lies near the median line; back of this is a wide, oval basin, or pit, bounded by the very heavy posterior cingulum and by the external ridge; the front face is vertically deep (26 mm.). The median incisor (i^2) has a low median tip and wide posterior basin. It remotely resembles that of *Dolichorhinus* but is far larger (ap. 25 mm., tr. 26) even than that of *T. ultimum.* The very large canine (ap. 27 mm., tr. 27), as already observed, is long and piercing, with a vertical crown length of 57 millimeters, as compared with 42 in the paratype of *T. ultimum.* Its transverse diameter is 27 millimeters, as compared with 22 in *T. ultimum.* It has similar antero-internal and postero-external edges but is distinguished by its heavier posterior basal cingulum.

Premolars.—The premolars are larger and wider than in *T. ultimum.* There is little if any postcanine diastema, p^1 being crowded in behind the base of the canine. Its crown is not preserved, but it appears probable that this was broader—that is, more advanced—than in *T. ultimum.* In p^2, p^3, p^4 the tritocones are nearly equal to the protocones, and both external and internal cingula are extremely progressive, the external cingula being well defined across the base of the protocones and tritocones, and the internal cingulum forming a wide basal shelf extending around the whole anterior as well as the posterior internal border of the crown. P^2 is thus almost like p^3 (except for its smaller size and relatively smaller transverse diameter), whereas in the type of *T. ultimum* p^2 is much simpler than p^3. P^3 (ap. 23 mm., tr. 32) and p^4 (ap. 23 mm., tr. 39) are correspondingly advanced but unlike *T. ultimum* show no trace of tetartocone ridges and swellings.

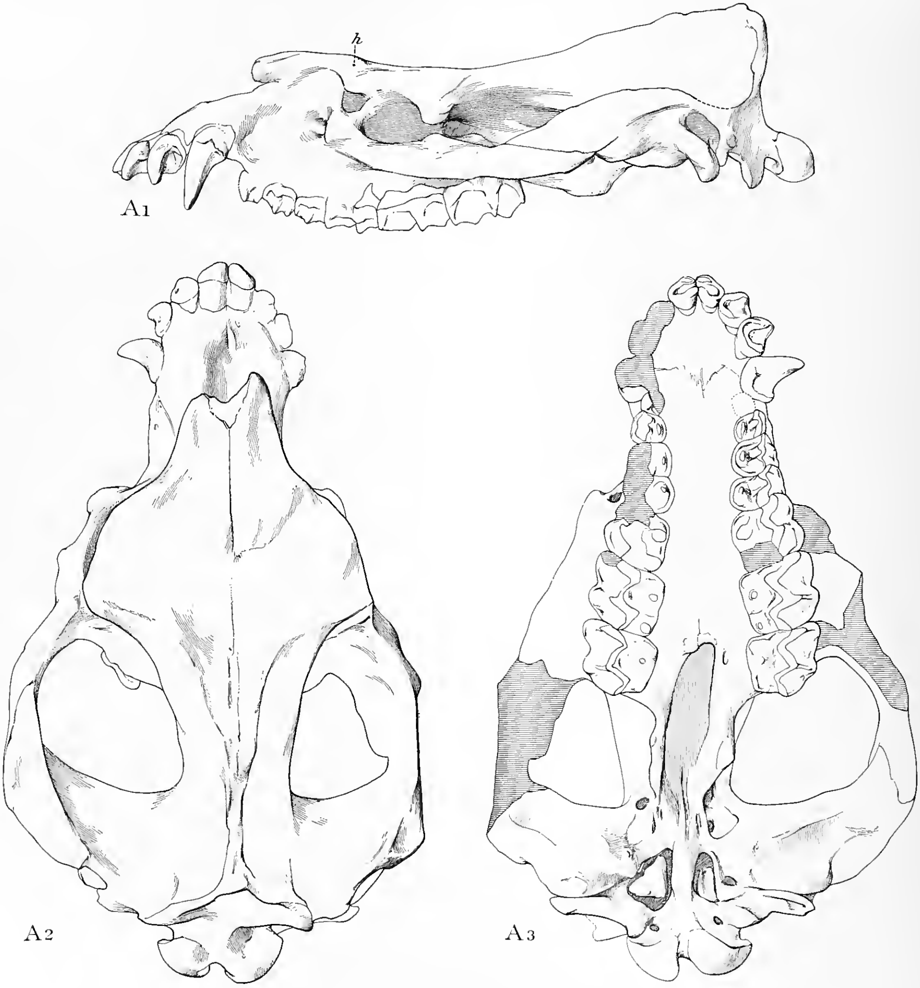

FIGURE 301.—Type skull of *Sthenodectes incisivus*

One-fourth natural size. Carnegie Mus. 2398 (type). About 3 miles northeast of well 2, Uinta Basin, Utah; upper levels of *Eobasileus-Dolichorhinus* zone (Uinta B 2). A_1, side view; A_2, top view; A_3, palatal view.

The premolar series is thus readily distinguished from that of the contemporary *Manteoceras uintensis* by the more advanced condition of the deuterocone of p^2, of the tritocones of p^{2-4}, and of the internal cingula. At the same time the premolars of *S. incisivus* simulate those of *Dolichorhinus longiceps*, especially in their advanced tritocones, but are distinguished from them by their greater breadth and far heavier internal cingula. A still nearer resemblance is with the premolars of *Metarhinus earlei*, in which p^2 is almost as progressive and p^3 and p^4 have heavy internal cingula.

Molars.—The molars of the type are distinguished from those of *T. ultimum* by the greater minimum transverse diameter of m^1, m^2, by the less prominent hypocone on m^2, by the weaker internal cingula on

m^2, m^3, and by the detailed form of m^3. From those of the contemporary *Manteoceras uintensis* they are distinguished by their smaller size, by the greater relative breadth of m^2, more quadrate contour, especially of m^3, relatively smaller parastyles and mesostyles, sharper external cingula. M^3 is wide anteriorly (53 mm.) and narrow posteriorly; the posterior V is relatively small. The molars of *Metarhinus earlei* are relatively longer anteroposteriorly.

Comparative measurements of Telmatherium and Sthenodectes, in millimeters

	T. ultimum, Am. Mus. 2060 (type)	S. incisivus	
		Carnegie Mus. 2398 (type)	Field Mus. 12168
Basal length of skull	500	490	488
Zygomatic breadth of skull	300+	[a] 310	305
Cephalic index	60	63–65	
Length of dental series (i^1–m^3)	305	295	
P^1–m^3	218	207	211
P^1–p^4	89	84	
M^1–m^3	130	125	132
I^1, ap. by tr	14×13	22×21	
I^2, ap. by tr	15×14	25×26	
I^3, ap. by tr	19×17	25×27	
C, ap. by tr	[b] 25×23	27×27	
C, vertical	[b] 42×?	57×?	
P^4, ap. by tr	25×34	23×39	
M^1, ap. by tr	39×36	40×44	
M^2, ap. by tr	45×46	45×49	
M^3, ap. by tr	44×51	41×46	

[a] Estimated. [b] Am. Mus. 2004.

Lower jaw.—A lower jaw (Field Mus. 12166), found on the same geologic level as the skulls but at some distance, belongs to an aged individual. The crowns of the incisors are almost worn away. The following description and measurements are from Riggs (1912.1, pp. 38, 39):

> The mandible is 10 millimeters shorter than would be required to fit the skull, but the dentition matches closely. The molars have the strength necessary to oppose the massive upper series; the canines and incisors, though not so massive as those above, show such wear as would be expected in this form. The canines are worn away diagonally at the point of contact with the third upper incisor, but very little from contact with the upper canines. There is a short diastema between canines and premolars. The mandible as a whole is titanothere-like—deep through the ramus, broad at the angle, concave in the tooth line, and tapering toward the anterior extremity. The coronoid is short and recurved at the tip.

Lower jaw of Field Mus. 12166

	Millimeters
Length, condyles to incisors	360
Height, condyles above angle	168
Length of molar-premolar series	215
Length of molar series	130
Length of crown of canine (estimated)	30
Diameter of crown of canine	19
Depth of ramus from base of p_3	60
Depth of ramus from base of m_3	84

THE MANTEOCERAS-DOLICHORHINUS GROUP (MANTEOCERAS, MESATIRHINUS, DOLICHORHINUS, SPHENOCOELUS, METARHINUS, RHADINORHINUS)

Stages, series, and subfamilies.—This second great group of middle and upper Eocene titanotheres is characterized by precocious horn swellings above the eyes and many other features in common. The single specimen of this group (*Eometarhinus*), discovered in the Huerfano B (=Bridger A) horizon of the Huerfano formation of Colorado, is the sole known forerunner. With this exception, this group is of much later geologic appearance than the first group (*Palaeosyops, Telmatherium*), being found in the upper levels of the Bridger Basin, in the Washakie Basin, and in the lower and middle levels of the Uinta Basin. The group commenced to flourish in the Bridger and Washakie regions during the period of the decline of the *Palaeosyops* phylum and survived it for a very long period, but it was contemporaneous with the *Telmatherium* phylum.

We find that this group radiates into four series, as follows:

Series included in the Manteoceras-Dolichorhinus group

	Progressively large and mesaticephalic to brachycephalic	Progressively large and dolichocephalic	Arrested in size, mesaticephalic to dolichocephalic	
			Nasals wide	Nasals pointed
Later stage	Protitanotherium	Dolichorhinus	Unknown	(?).
Earlier stage	Manteoceras	Mesatirhinus	Metarhinus	Rhadinorhinus.
Earliest stage			Eometarhinus	

Besides the rudimentary horns there are very numerous characters which tie the members of this second group together and distinguish them from the palaeosyopine group. These characters point indisputably to a common ancestor. An underlying unity of descent is at once observed in the accompanying figures (fig. 302) of the four types of skulls included in this group, which are all reduced to the same scale.

The four series are grouped into subfamilies and genera as shown below.

Subdivisions of the Manteoceras-Dolichorhinus group

Manteoceratinae (=Brontopinae)	Dolichorhininae	Rhadinorhininae
Subfamilies		
Horns on frontals. No infraorbital shelves. Mesaticephalic to brachycephalic. Nasals broad.	Horns chiefly on nasals. Large infraorbital shelves. Dolichocephalic to hyperdolichocephalic. Nasals broad.	Horns retarded. Rudimentary infraorbital shelves. Dolichocephalic. Facial region upturned. Nasals pointed.
Genera		
Protitanotherium (Eocene). Manteoceras (Eocene).	Mesatirhinus (Eocene). Dolichorhinus (Eocene). Metarhinus (Eocene). ?Sphenocoelus (Eocene). Eometarhinus (Eocene).	Rhadinorhinus (Eocene).

The phyletic position of the recently discovered *Eometarhinus*, from Huerfano B (=Bridger A), is ancestral either to *Metarhinus* or to *Rhadinorhinus*.

Of these genera *Manteoceras* and *Mesatirhinus* represent phyla which appear contemporaneously in the upper Bridger but which have already diverged from each other toward brachycephaly and dolichocephaly, respectively. As these subphyla diverge more and more the resemblances which are observed between the lower members of each series become fewer, and the differences become greater. Thus *Manteoceras* and *Mesatirhinus* are much nearer each other than the forms to which they respectively gave rise, namely, *Protitanotherium* and *Dolichorhinus*. The *Rhadinorhinus* phylum may prove to be a distinct one, and in some characters it points toward the Oligocene *Megacerops* (*Symborodon*).

SUBFAMILY MANTEOCERATINAE (=BRONTOPINAE) OSBORN, EOCENE ANCESTORS

A branch of the same stock as that of *Mesatirhinus* and *Dolichorhinus*. Precociously horned animals, known from the upper deposits of the Bridger Basin, from the Washakie Basin, and from the Uinta Basin. First referred to *Telmatherium* and subsequently described as *Manteoceras*, or "prophet horn." In all known characters more nearly central or ancestral to the Oligocene titanotheres of the genus *Brontops* than any of the Eocene forms thus far discovered.

Manteoceras

General structure and habits.—The presence of the rudiment of a horn above and in front of the eyes is the most distinctive and interesting feature of the middle Eocene *Manteoceras*, which is the earliest known member of this subfamily. Many more characters both of the skull and the teeth make this a prophetic or ancestral form of great significance and interest, worthy of the most thorough, detailed study. Altogether more than fourteen such prophetic characters have been found in these animals. In point of size the known individuals are intermediate between the largest tapirs and the smaller rhinoceroses, such as *Rhinoceros* (*Dicerorhinus*) *sumatrensis.*

The skull in these animals is moderately elongate, or mesaticephalic. The fluctuations are between mesaticephalic and brachycephalic types. Female skulls tend to be somewhat more long and narrow; aged male skulls tend to be broader and more robust.

The parts of the limbs and feet which signify speed, especially the humerus, femur, and manus, indicate that the quadrupeds belonging to this genus were swifter than *Palaeosyops* but slower than *Mesatirhinus.* They were brachypodal as compared with *Mesatirhinus* but considerably longer footed than *Palaeosyops.* The large tusks of the males and the earlier development of horn rudiments as compared with the palaeosyopine group indicate that these quadrupeds were vigorous fighters. In a large percentage of the adult specimens the teeth are much worn, indicating that the food was somewhat harder and drier than that of *Palaeosyops.* As feeders these animals were better equipped than the members of the *Palaeosyops* and *Limnohyops* series, for their grinding teeth were decidedly more trenchant or cutting, but even in the later members of *Manteoceras* the grinding teeth are somewhat less efficient than those of the contemporary telmatheres, because the molar ectolophs are a little shorter and the premolars are less advanced in evolution.

History of discovery.—The discovery of these animals was one of the turning points in the history of the evolution of the titanotheres. In 1894 the American Museum expedition was working under the direction of Dr. J. L. Wortman in a layer of brown sandstone 3 miles north of the base of Haystack Mounain, in what is now known as the Washakie A level. Here two skulls (Am. Mus. 1569, 1570) were found, and as partly exposed in the field they attracted the attention of Doctor Wortman as seemingly different from any previously discovered. He described them in a letter written to Professor Osborn from the field as exhibiting rudimentary horns at the junction of the frontals and nasals and suggested the generic name *Manteoceras* or "prophet horn." On the arrival of these skulls at the American Museum Professor Cope, the writer, and others who examined them expressed great doubt as to whether the tuberosities (Pl. XVI; figs. 305, 307) above the orbits could really be regarded as incipient horns. These doubts were soon removed by the discovery of similar horns in *Dolichorhinus cornutus* (=*hyognathus*) of the middle Uinta, and Doctor Wortman's observation was thus verified.

As detailed in Chapter III (p. 151) the animal was first identified by Osborn with the imperfect upper cotype teeth of the species *Palaeosyops* (*Telmatherium*) *vallidens* Cope, previously found by Professor Cope in the Washakie Basin; but it was subsequently ascertained that this species, now provisionally referred to the genus *Dolichorhinus*, belongs in a higher level, Washakie B, whereas the types of *Manteoceras manteoceras* were both found in Washakie A.

These animals (*M. manteoceras*) were first supposed to be confined to the lower levels of the Washakie Basin, but subsequent exploration of the upper Bridger by the American Museum expeditions has proved that they were still more numerous in the Bridger Basin; altogether the remains of more than twenty animals of the type species (*M. manteoceras*) have been found by the American Museum parties, including seven skulls in Bridger D and four skulls in Washakie A. In the upper levels of horizon A of the Washakie Basin a more advanced stage has been found, *M. washakiensis*. Thus far these animals have not been found in the Uinta Basin in beds of level B, deposited during a period when they undoubtedly lived; but in the lower part of Uinta C the genus reappears in the important species described by Douglass as *Manteoceras uintensis*. In the lower part of Uinta C an animal nearly related to *Manteoceras*, if not its direct successor, was discovered by the Princeton expedition in 1894 and was subsequently recognized by Hatcher as probably a successor of *Manteoceras*, and named by him *Protitanotherium emarginatum*.

Geologic distribution.—The geologic levels at which the remains of these animals have been found are shown in Figure 334, and as the remains are numerous in the upper Bridger, levels C and D, and in the lower Washakie, level A, they indicate that these deposits are contemporaneous. As observed in the text on *Telmatherium*, the advent of *Manteoceras* appears to have been contemporaneous with the last stage in the development of the *Palaeosyops-Limnohyops* phylum and with the first appearance of the *Mesatirhinus-Dolichorhinus* phylum. The abundance of remains of these animals in the upper Bridger deposits is very striking. It is possible that they are represented also by skeletal remains in the lower Bridger.

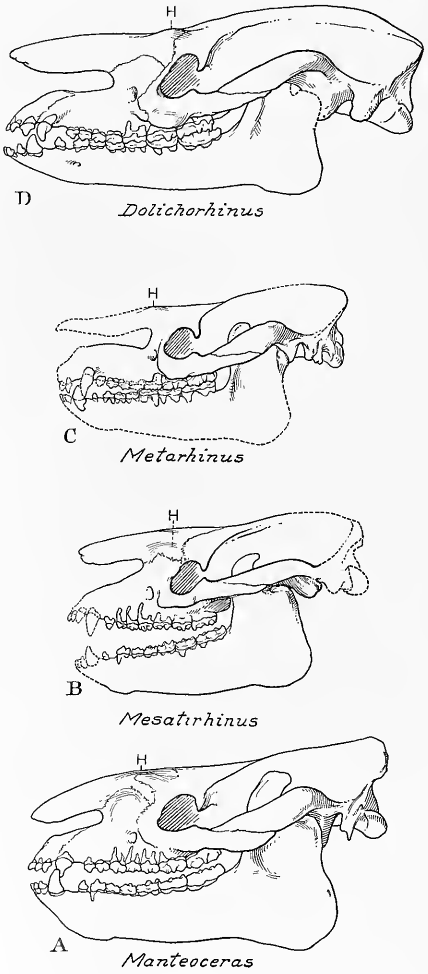

FIGURE 302.—Skulls of titanotheres of the *Manteoceras-Dolichorhinus* group

One-eighth natural size. A, *Manteoceras manteoceras*, middle Eocene of Bridger Basin, Wyo.; upper Bridger. B, *Mesatirhinus petersoni*, middle Eocene of Bridger Basin, Wyo.; upper Bridger. C, *Metarhinus earlei*, middle Eocene of Washakie Basin, Wyo.; summit of Washakie A. D, *Dolichorhinus hyognathus*, middle Eocene of Uinta Basin, Utah; Uinta B 2.

Affinities to other Eocene titanotheres.—The resemblances and contrasts between *Manteoceras* and *Telmatherium* have been pointed out in some detail in the descriptions of *Telmatherium*. They may also be very clearly seen by comparing the crania of the types of these two general (figs. 210, 219). To summarize *Manteoceras* is distinguished from *Telmatherium* by (1) deeper facial concavities; (2) much more prominent and rugose frontonasal horns; (3) progressive anterior flattening of the vertex of the cranium and recession of the sagittal crest; (4) presence of a supraparietal pit and strongly bifid sagittal crest; (5) broad and depressed occiput; (6) oblique shelf-like suborbital part of the malars; (7) widely arched zygomata with descending flange of malar relatively shallow; (8) progressively more round-topped superior incisors, the outer relatively smaller than in *Telmatherium*; (9) shorter, heavier, and rounder superior canines, with very heavy roots; (10) less progressive tritocones, deuterocones, and cingula on superior premolars; (11) somewhat less pronounced hypsodonty of the grinding teeth; (12) broader and more rounded mesostyles; (13) the less deep and finally more elongate premaxillary symphysis.

Comparisons with Mesatirhinus and Dolichorhinus.—The general resemblances of these animals have been enumerated above. A number of resemblances in general conformation are seen by comparison of similar views of the crania of *Manteoceras* and of *Mesatirhinus*. These indicate a closer ancestral affinity to *Mesatirhinus* than to *Telmatherium*. Detailed points of resemblance between *Manteoceras* and *Mesatirhinus* are seen in (1) the tendency to form a suborbital shelf, which is more pronounced in *Mesatirhinus* than in *Manteoceras*; (2) the depth of the facial concavities, giving prominence to the nasofrontal horn rudiments (a distinction must be noted here, however, that the horn rudiments in *Mesatirhinus* and *Dolichorhinus* are borne rather by the nasals than by the frontals, whereas in *Manteoceras* the reverse is the case); (3) pronounced affinities in the foot and limb structure.

The statement may be made very emphatically, therefore, that *Manteoceras* and *Mesatirhinus* have risen from a common stock.

The distinctive characters of *Manteoceras* lie principally in the proportions of the skull, dentition, and feet and in the divergent evolution of the premolar-molar series. *Manteoceras* is mesaticephalic in skull and tooth structure and subbrachypodal in foot structure, while *Mesatirhinus* is progressively both dolichocephalic and dolichopodal.

Incipient horns.—As observed above, a notable characteristic of these animals is the precocious horn development. The horn swellings are borne directly over the frontonasal suture (Pls. XVI, XVII). They involve very slight convexity and are slightly rugose only in the more aged specimens. As they are exhibited in various degrees in all the skulls known, they were certainly present in both sexes, although less prominent in the females. These horn swellings have a different origin in *Dolichorhinus*, as well as in *Mesatirhinus*, for in these genera (Pl. XVII, figs. B, C^1, C^2), although placed about as in *Manteoceras*, they are borne chiefly on the nasals and partly on the frontals—that is, in front of the frontonasal suture.

Facial concavities.—The second distinctive character that is correlated with or lends itself to this precocious development of the horns is the concavity in the side of the face, in front of the orbit, beneath the nasal. This gives a greater prominence to the horn rudiments and in life would permit the warty epidermal swellings that covered these rudiments to be used more effectively in butting. This overhanging frontonasal suture shows a wide contrast to the condition seen in *Palaeosyops*. The concavity of the face in front of the orbit, beneath the horn, is a very prominent feature also in the Oligocene titanotheres and in *Sthenodectes incisivus* of level B of the Uinta Basin, Utah.

The vertex.—In lateral or profile view the skull is convex above the brain region, concave in the midcranial region, and convex again in the nasal region, as in *Mesatirhinus*. The horn rudiments, or hornlets, are thus thrown into considerable prominence both laterally and superiorly. The concave midportion of the skull is again a progression in the direction of the saddle-shaped top of the titanothere cranium. When viewed from above the cranium also exhibits a spreading of the space beneath the supratemporal ridges in such a manner that the sagittal crest proper is limited to the posterior region. In the V-shaped space on top of the skull between these converging temporal ridges (or bifid sagittal crest) it is especially interesting to observe that a deep pit is developed in the more progressive and older forms, because we shall find a vestige or reversion to this pit on top of the large, flattened crania of some of the Oligocene titanotheres (*Brontops*, compare figs. 304, 307, 374).

Dentition.—The superior incisors form a more Λ-shaped series than in *Dolichorhinus*, where they tend to form a ∩, and the inferior incisors are more transverse in position. The grinders are less hypsodont on the ectoloph, and the protocone tips are more blunt than in *Mesatirhinus* and *Dolichorinus*. The premolars are less advanced than in *Mesatirhinus* and *Dolichorhinus*, because the tritocones and deuterocones are relatively smaller, the ectolophs less flat, and the "ribs" on the external face of the outer cusps wider at the base. The relative degree of progression of the premolar ectolophs in *Dolichorhinus* and *Manteoceras* is a very complex matter, but after careful comparison it may be summarized as follows:

Characters of p^2 *in Manteoceras, Mesatirhinus, and Dolichorhinus*

	Manteoceras	Mesatirhinus	Dolichorhinus
Protocone convexity	Very broad at base	Very broad at base, but "rib" appearing.	Often pinched or riblike.
Tritocone convexity	Strong	Flattened	Gently rounded.
Deuterocone	Very posterior	More anterior	Still more anterior.
Inner contour	Very oblique	More rounded	Filling out.
Relative size of protocones and tritocones.	Variable	Tritocone relatively somewhat larger.	Tritocone nearly equal to protocone.

In general p^2 in *Dolichorhinus* is in a much more advanced stage than in *M. manteoceras.* In p^3, p^4 these differences become more pronounced. The premolars were thus evolving along divergent lines in *Manteoceras* on the one hand and in *Mesatirhinus* and *Dolichorhinus* on the other. The general subfamily kinship of *M. manteoceras* with *Mesatirhinus* and *Dolichorhinus* is shown especially in the comparison of p^3, p^4, in *M. washakiensis* and *Mesatirhinus petersoni*, but the generic differences are still evident.

Jaw structure.—The jaws are prophetic of the Oligocene type, especially in the posterior region, with an elevated coronoid, and with the border sharply depressed below the angle (fig. 310); the chin, however, is weaker and the coronoid relatively much larger.

Sex characters.—Differences in sex are indicated by the smaller size of the canines in the females, as observed in *M. manteoceras.* It is difficult to determine positively whether the horns are also less prominent in the females than in the males. One well-preserved, very old *Manteoceras* skull (Am. Mus. 12678) from Bridger C 5 has small canines and appears to be a female. In it the horns are hardly less prominent than in the type male. The type of *M. washakiensis* has very minute horn swellings and might be taken for a female, but its canines are of intermediate size.

Mesaticephalic skull proportions.—The skulls are intermediate in proportion, or decidedly broader than those of *Mesatirhinus* and *Dolichorhinus* and much longer and narrower than those of *Palaeosyops*, the breadth being about three-fifths the length, and they may thus be described as mesaticephalic. In the earlier forms of *M. manteoceras* of the middle Eocene the zygomatic arches are rather stout and well arched. In the much later *M. uintensis* they are more slender than in *Telmatherium ultimum* but diverge widely, forming a decided angle with the glenoid region. There is only a rudiment of the infraorbital shelf that is so characteristic of most species of *Mesatirhinus* and *Dolichorhinus.*

Detailed features.—Characteristic detailed features, some of which trend progressively toward the Oligocene titanotheres, clearly distinguish these animals from *Palaeosyops* and in a less degree from *Mesatirhinus:* (1) The premaxillary symphysis is long and firm as compared with that of *Palaeosyops* but shorter than in *Dolichorhinus;* (2) the nasals are very characteristic, being relatively short and stout, decidedly truncate, distally somewhat spreading and laterally much recurved; (3) in the sagittal line of the skull the suture between the frontals becomes obliterated in adults, as in many other ungulates with large diploë; (4) the occiput is low and broad (fig. 306), very distinct in form from that of *Palaeosyops,* and in the more advanced specimens (*Manteoceras washakiensis*) it exhibits the lateral pillars which are so characteristic of the Oligocene titanotheres.

Summary of progressive characters of Manteoceras toward Brontops and other Oligocene titanotheres.—Hatcher, at the time of the discovery and description of the animal now called *Protitanotherium emarginatum* of Uinta C, pointed out the fact that *Manteoceras* is in or near the main ancestral line of the Oligocene titanotheres rather than *Dolichorhinus,* which Osborn had supposed also in that ancestral line.

The progressive characters of *Manteoceras* toward the Oligocene forms are naturally somewhat more marked in old than in young specimens. The following items relate chiefly to the species *M. manteoceras,* which is the most fully known and seems to lead especially toward the Oligocene *Brontops:* (1) Middle part of the skull elongate, face never very long, elongation becoming very pronounced in the Oligocene titanotheres; (2) rudimentary frontal-nasal horns apparently increasing in size with age and probably more pronounced and more rugose in the males, as in all the Oligocene forms; (3) concavities in front of the orbits, causing the rudimentary horns to overhang the sides of the face (very prominent in the later Oligocene genera); (4) nasals broad distally, shorter than in *Dolichorhinus* and in *M. uintensis,* suggesting the *Brontops* and *Menodus* nasals; (5) premaxillary symphysis deepened and keeled (compare Oligocene genera); (6) middle or frontal portion of the cranium flattened, the flattening being associated with the progressive obliteration of the suture between the frontals and with the abbreviation of the sagittal crest (compare Oligocene genera); (7) middle portion of the skull saddle-shaped in the region between the frontal-nasal horns and occipital crest, showing a tendency that becomes extreme in the Oligocene forms; (8) overhanging supratemporal crests or ridges characteristic of age, a tendency observed also in Oligocene titanotheres; (9) occiput broadened and lateral pillars above the condyles incipient, a feature observed in all Oligocene titanotheres; (10) incipient expansion of the zygomatic portion of the squamosals and flattening out of the squamosal portion of the zygoma, as in later titanotheres; (11) deep backward angulation and depression of the angle of the jaw, a feature observed in certain Oligocene genera; (12) incisors tending to become round-topped (*M. uintensis*), a tendency that becomes very pronounced in the Oligocene genera; (13) crowns of the canine teeth abbreviated, with stumpy recurvature, foreshadowing the Oligocene *Brontops* and *Brontotherium;* (14) ectolophs of the premolar and molar grinding teeth elongated vertically, a character that becomes pronounced in all Oligocene titanotheres; (15) premolar ectolophs, showing incipient double convexities, a character that becomes well marked in all Oligocene genera; (16) fourth premolar showing a faint suggestion of the tetartocones (*M. washakiensis*); (17) premolars retarded in development.

Despite the approaches of *Manteoceras* to the Oligocene *Brontops* in these 17 characters, there are reasons why none of the known species of *Manteoceras*, and especially the best known, *M. manteoceras*, can be considered the direct ancestor of any known Oligocene titanothere. This species differs from the Oligocene titanotheres notably in the sharp postcanine constriction of the face, the shallowness of the malar below the orbit, and the slenderness of the malar behind the orbit; and it is not yet known whether these are progressive tendencies leading away from the Oligocene type or are characters that were lost during the transformation into the early Oligocene types, such as *Brontops brachycephalus*.

Manteoceras Hatcher

Plates XVI, XVII, XXIX, XLVI, LI, LIII, LV, LXIII, LXVII; text figures 27, 29, 33, 87, 113, 121, 131, 132, 210, 215, 219, 220, 255, 302–313, 323, 324, 380, 406, 408, 409, 483, 484, 508, 510, 512–517, 521, 551–557, 566, 641, 646–649, 661, 673, 674, 685, 686, 688, 690, 701, 709, 710, 712, 717, 720, 721, 723, 724, 733, 745

[For original description and type references see p. 177. For skeletal characters see p. 630]

Localities and geologic horizons.—Bridger Basin, Wyo., levels C and, chiefly, D; Washakie Basin, Wyo., level A; Uinta Basin, Utah, lower part of level C (*M. uintensis*).

Generic characters.—Facial concavities pronounced; horn rudiments borne chiefly on the frontals; suborbital portion of malars flattened, with a rudimentary shelf. Superior incisors moderately enlarged; canines robust, pointed, progressively more obtuse. Grinding series subhypsodont; molar conules vestigial or wanting; molars broader than in *Dolichorhinus* or its allies; premolar evolution retarded as to tritocones, deuterocones, and cingula; ectolophs with two convexities in tandem.

As described in detail in the revision of the nomenclature (pp. 177–178) the synonymy of the genus and type species has been confused and complicated, but it has now been definitely cleared up according to modern principles. The honor of discovering this important evolution stage of *M. manteoceras* and of first recognizing its prophetic character belongs to Wortman, who also invented the apt name *Manteoceras* (prophet horn). Osborn in 1895, the first to publish a description of the skull of this animal, refrained from giving it a new name on account of the general resemblance in the teeth to the very imperfect type of Cope's "*Palaeosyops vallidens*." Hatcher, later in the same year, proposed the generic name and correctly defined the genus. Still later Osborn in manuscript referred to this form as *Palaeosyops manteoceras;* but this specific name is technically to be credited to Hay, who (1902.1) first fastened the specific name *manteoceras* to the previous description and figures of the original "prophet horn" skulls, so that the name now stands as *Manteoceras manteoceras* Hay (Osborn MS.).

It is very important to note that seven skulls and upper dentitions from the upper deposits of the Bridger Basin (mostly level D) equal or exceed in measurement and progressive characters three skulls from level A of the Washakie Basin and thus afford corroborative evidence of the simultaneous deposition of those sediments.

Materials.—A somewhat detailed enumeration of materials seems to be important in this case for purposes of geologic correlation.

1. *Manteoceras manteoceras*

Bridger C 2: A fragmentary adult skull (Am. Mus. 12194), from Burnt Fork post office (Henrys Fork). The sagittal crest bifid with deep intermediate pit. This is in an early stage of development.

Bridger D: A male skull (Am. Mus. 12683), from Sage Creek Spring, is important as supplementing the characters of the type. It probably belongs to a somewhat early stage and presents certain resemblances to the type of *Telmatherium cultridens*. The measurement of p^1–m^3 is 176 millimeters, as compared with 181 in the type of *M. manteoceras*. The most striking feature (see figs. 305, 307) is the depth of the preorbital concavities, which throws the frontonasal horn ridges into exceptional prominence. The horn surfaces are slightly pitted or rugose.

Bridger C or D: A fully adult skull (Am. Mus. 1511) found on Henrys Fork. Basilar length, 447 millimeters; p^1–m^3, 184; canines large. Probably a male specimen.

Bridger C or D: Skull of a very old male (Am. Mus.) 1545 found on Henrys Fork. Basilar length, 523 millimeters; p^1–m^3, 197; large fanged, recurved canines. Horn rudiments rugose.

Bridger C or D: Skull, jaw, and parts of skeleton of a male adult, with open sutures (Am. Mus. 1587) from Henrys Fork. Affords characters of the feet.

Bridger D 2: Skull, jaws, and parts of skeleton (Am. Mus. 12204). Basilar length estimated at 490 millimeters. Probably a male, aged. Grinding teeth relatively small. Affords knowledge of the femur and part of the feet.

Bridger C 5: Very old female skull (Am. Mus. 12678). The first superior molar of both sides has dropped out. Canines short, recurved, cingulate posteriorly. Basilar length, 500 millimeters; zygomatic breadth, 294 (estimated); p^1–m^3, 187. Equal in size to palate from the upper portion of Washakie A.

Washakie A: The type skull of the species (Am. Mus. 1569) from the brown sandstones. Probably an aged male. Horn rudiments prominent, slightly rugose. Estimated basilar length 492 millimeters; p^1–m^3, 183.

Washakie A: The type skull (Am. Mus. 1570). Adult male skull, occiput lacking. P^1–m^3, 186 millimeters. Agrees closely in size with Am. Mus. 1511, from Bridger C or D.

Washakie A: Skull with jaws (Am. Mus 2353) lacking premaxillae. Zygomatic breadth, 274 millimeters. The grinding teeth are of relatively small size (p^1–m^3, 178 mm.).

2. *Manteoceras washakiensis* Osborn

Washakie A (upper levels): Crushed but complete skull (Am. Mus. 13165) from the base of Haystack Mountain, summit of the brown sandstone, or upper part of Washakie A. A female with relatively small, obtuse, recurved and posteriorly cingulate canines. Horn rudiments slightly defined. Grinding series, p^1–m^3, 200 millimeters.

3. *Manteoceras* sp.

Washakie B: Of the three specimens or cotypes described by Cope as *Palaeosyops vallidens*, the jaws (Am. Mus. 5098) from Mammoth Buttes appear to belong to *Manteoceras* sp. indet. The other cotype (upper teeth) is referred to *Dolichorhinus* (see below).

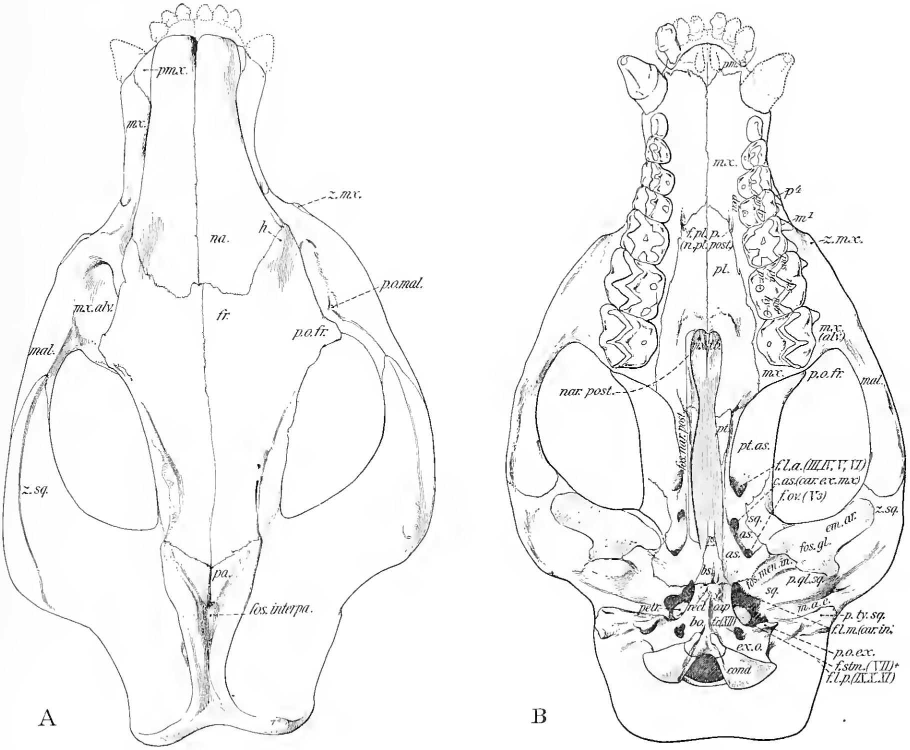

FIGURE 303.—Skulls of *Manteoceras manteoceras*

One-fourth natural size. A, Top view; Am. Mus. 1587, Henrys Fork, Bridger Basin, Wyo., upper (?) levels. B, Palatal view, chiefly from Am. Mus. 2353, south of Haystack Mountain, Washakie Basin, Wyo., lower beds; partly restored from Am. Mus. 1570, La Clede, Washakie Basin; some details and sutures from a specimen now in the National Museum, formerly Am. Mus. 1545, Bridger Basin.

4. *Manteoceras uintensis* Douglass

Uinta C (lower levels): The anterior half of a skull (Carnegie Mus. 2388), "from gray sandstone in red Uinta beds," the type of *M. uintensis*. A large male; grinding series, 240 millimeters (see below).

Synopsis of progressive characters in the three successive species of Manteoceras.—1. *M. manteoceras:* Levels, Bridger C 2 to D and Washakie A. Skull of medium size (basilar length 447–500+mm.). Face relatively short; zygomata stout; horn swelling prominent.

P^1–m^3, 176–186+millimeters; postcanine diastema short; i^3 much larger than i^2; p^2 with deuterocone and tritocone poorly developed; p^4 (ap. by tr.), 19 by 26 to 22 by 29 millimeters; m^1, 28 by 29 to 32 by 33; m^2, 35 by 37 to 41 by 40; m^3, 36 by 39 to 39 by 43.

2. *M. washakiensis:* Level, Washakie A, upper part. Skull somewhat larger (basilar length in supposed female 490 mm., estimated). Face relatively short; zygomata moderate; horn swelling inconspicuous (? ♀). P^1–m^3, 200 millimeters (estimated); p^2 with deuterocone somewhat better developed; p^4 (ap. by tr.), 23 by 29 millimeters; m^1, 35 by 38; m^2, 41 by 43; m^3, 39 by 42.

3. *M. uintensis:* Level, Uinta C, lower part. Skull larger (basilar length not known). Face relatively long; female horn swelling (?) absent; zygomata not stout, in inferior view forming a marked angle in front of the glenoid surface. Postcanine diastema long; disparity of i^3 over i^2 less marked; p^1–m^3, 240 millimeters; p^2 with deuterocone slightly and tritocone markedly more advanced; p^4 (ap. by tr.), 26 by 32 millimeters; m^1, 40 by 38; m^2, 52 by 46; m^3, 45 by 50.

Range in size of Manteoceras manteoceras and two successive stages of increase in size, in millimeters

	Manteoceras manteoceras										M. washakiensis, 13165	M. uintensis, 2388
	12194	12678	12683	1511	12204	2353	1532	1569	1570	1545		
Skull:												
Pmx–condyles		500		447	[a] 490			492		523	490	
Zygomatic breadth		[a] 294						[a] 310		[b] 350		
Length of face		240						[a] 245		[b] 269		[a] 290
Length of cranium		255						305		[b] 320		
Cephalic index		[a] 59						63		[a] 66		
Dentition:												
P^1–m^3		187	176	184		178		183	186	197	[a] 200	240
P^2–m^3			160	168		159		164	165	181	[a] 183	219
P^1–p^4			79	82		77		80	81	83	83	101
M^1–m^3	108		100	104		102		103	107	118	116	138
P^1, ap. by tr			15×8	16×11		17×9					15×9	24×11
P^2, ap. by tr			18×16	22×19		18×18	22×18		21×19		19×17	21×20
P^3, ap. by tr			17×21	19×25		18×23	20×25		19×24		20×25	24×29
P^4, ap. by tr	20×27		20×26	20×28		21×28	23×29		20×28	[a] 22×29	23×29	26×32
M^1, ap. by tr	29×31		28×29	27×[a] 30	29×31	30×31	33×34		31×33	32×33	35×38	40×38
M^2, ap. by tr	38×38		35×37	38×37	33×38	38×39	42×40		38×41	41×40	42×43	52×46
M^3, ap. by tr	40×39		36×39	39×39	36×38	35×38	42×42		38×43	39×43	39×42	45×50

[a] Estimated.

[b] Crushed.

Numbers at heads of columns are those of the American Museum except the last (2388), which is of the Carnegie Museum. The geologic horizon and other facts concerning the specimens are given below:

12194. Intermediate molar proportions. Bridger C 2.
12678. Very old female. Intermediate molar proportions. Bridger C 5.
12683. Young adult male. Smallest molar proportions. Bridger D.
1511. Male. Small molar proportions. Bridger (?).
12204. Very old female. Small molar proportions. Washakie D 2.
2353. Female. Small molar proportions. Washakie A.
1532. Male. Large molar proportions. Washakie A.
1569. Type. Male. Large molar proportions. Washakie A.
1570. Paratype. Large molar proportions. Washakie A.
1545. Old male. Largest molar proportions. Bridger D (?).
13165. Female. Skull medium, cheek teeth large. Washakie A, upper levels.
2388. Type. Male. Skull and molars very large. Uinta C, lower level.

The accompanying table of measurements brings out the following facts:

1. In *M. manteoceras* there is a very considerable range in size: Am. Mus. 1545 is larger in total skull length than the type of *M. washakiensis,* but the first and second molars are smaller.

2. The molars in different specimens of *M. manteoceras* are either microdont (Am. Mus. 12194, 12683, 1511, 12204, 2353) or macrodont (Am. Mus. 1545, 1570), but other measurements, especially the dimensions of the premolars, do not confirm this division; it does not seem to be due to sex, nor, so far as known, to imply specific differences.

3. *M. washakiensis,* from the upper levels of Washakie A, is not much bigger in total skull length, but it is more progressive in the relatively large size of the molars.

4. *M. uintensis,* from Uinta C, is far more advanced than either *M. manteoceras* or *M. washakiensis* in total skull length (inferred), length of face, and all dimensions of the dentition; but the molars are relatively more advanced than the premolars.

Manteoceras manteoceras Hay

[*Telmatotherium manteoceras* (Osborn MS.); *Telmatotherium vallidens* Osborn, not Cope]

Plates XVI, XVII, XXIX, XLVI, LI, LIII, LV, LXIII, LXVII; text figures 27, 29, 33, 87, 113, 215, 219, 255, 302–311, 323, 324, 380, 406, 408, 483, 508, 512–514, 516, 517, 521, 551–554, 556, 557, 566, 646–649, 661, 686, 701, 709, 712, 721, 723, 724, 745

[For original descriptions and type references see p. 177. For skeletal characters see p. 630]

Type locality and geologic horizon.—Washakie Basin, Wyo.; *Uintatherium-Manteoceras-Mesatirhinus* zone (Washakie A). The most abundant material is from the Bridger Basin, Wyo., some from Bridger C but more from Bridger D.

Specific characters.—Skull of medium size, basilar length, 447–500+ millimeters; cephalic indices, 58 to 68, face relatively short; zygomata stout; horn swelling prominent; p^1–m^3, 176–186+ millimeters; postcanine diastema short; i^3 much larger than i^2; p^2 with deuterocone and tritocone poorly developed; p^4 (ap. by tr.), 19 by 26 to 22 by 29 millimeters; m^1, 28 by 29 to 32 by 33; m^2, 35 by 37 to 41 by 40; m^3, 36 by 39 to 39 by 43.

The skeleton.—The skeleton of *Manteoceras* is by no means so fully known as that of *Palaeosyops.* The feet are more slender than those of *Palaeosyops leidyi* but much more robust than those of *Mesatirhinus.* Intermediate proportions are seen throughout between those characteristic of *Palaeosyops,* the extremely broad-headed titanotheres, and of *Dolichorhinus,* the extremely long-headed titanotheres. In *Manteoceras,* therefore, the moderate breadth of the skulls (mesaticephaly, Pl. LIII) is associated with moderate breadth of the feet (mesatipody).

Progressive and specific characters: (1) Several mutations, subspecies, or substages from several different levels may be represented in the 20 or more specimens that have been referred to *M. manteoceras;* (2) as shown above, there is a considerable range in size between the smallest specimen (Am. Mus. 12683) and the largest; (3) some skulls have rather small grinding teeth in transverse measurement and are thus microdont; others have large grinding teeth and are thus macrodont, and this is not a sexual character; (4) in some the canines are more slender (figs. 308, 309), in others more robust, the form typical of the species being represented in Figure 311; but it is certain that the canines in some lines become progressively obtuse and posteriorly cingulate and thus approach the Oligocene types.

From the detailed list of the materials given above it is seen that the known individuals from the upper levels of the Bridger Basin and the lower levels of the Washakie Basin are from a single geologic horizon—the *Uintatherium-Manteoceras-Mesatirhinus* zone. This horizon, however, represents a long period of time, but, owing partly to the slow rate at which the premolars in *Manteoceras* were evolving, the known specimens, although probably representing several different levels, do not present very marked progressive differences, except that Am. Mus. 12683, from Bridger D, is less advanced in the condition of the deuterocone of p^2.

Horns.—As shown in the carefully drawn detailed figures (Pls. XVI, XVII), the rudimentary horn convexity is borne chiefly upon an anterior spur of the frontals; it thus presents exactly the same relations as those observed in *Protitanotherium emarginatum* (figs. 318, 319, 374). In *D. hyognathus* (Pl. XVII) the maximum horn convexity is on the posterior spur of the nasals, and the same is the case in the very much more rudimentary horn of *Mesatirhinus petersoni.* In another *M. manteoceras* skull (Am. Mus. 1545) the swelling and rugosity is shared partly by the nasals. In this stage of evolution, therefore, the osseous horn is, strictly speaking, a frontonasal horn. Some of the more aged specimens (especially Am. Mus. 1569) show a very faintly rugose condition of the surface of the bone on these horn bases.

Proportions.—The width of these skulls (see table of measurements) is increased by the great outward arching of the zygomata posteriorly, the proportions, as presented in Am. Mus. 1569, being, length, condyles to incisive border, 492 millimeters, width 310. In other words, the zygomatic breadth is nearly three-fifths of the skull length, whereas in *Mesatirhinus petersoni* the breadth is a little less than one-half the length, and in *Dolichorhinus hyognathus* the breadth is only a little more than one-third the length.

Additional specific characters.—The other chief features of the cranium are as follows: (1) The rudimentary frontonasal horn swellings above described; (2) the widening of the nasals posteriorly; (3) the posterior spreading of the frontoparietal region; (4) the deep parietofrontal pit between the posterior portion of the supratemporal ridges, which have now almost replaced the sagittal crest; (5) the relatively broad, low occiput.

In many details of structure, enumerated below, this skull unmistakably exhibits subfamily affinity with *Mesatirhinus petersoni,* yet it differs from that species in many important features—namely, (1) the infraorbital ridge is incipient but not prominent, (2) the zygomata are stout and the zygomatic width of the skull is much greater than in *Mesatirhinus,* (3) the basioccipital region is relatively broader and less elongate, and the same is true of the palate.

The skull.—The superior view of the skull (fig. 304) shows several characters which are prophetic of the Oligocene *Brontops:*

1. The nasals are slightly expanded at the anterior extremities, measuring 63 millimeters (Am. Mus. 1569), then contracting slightly to 60 millimeters and again steadily expanding to 112 millimeters at

the junction with the frontals. The midlength of the nasals is 174 millimeters, as compared with 164 in the much smaller *M. megarhinus* skull, showing that while the cranial portion of the skull has greatly increased in length, the nasal bones have not increased in length so fast as they have in *Mesatirhinus;* in other words, a retardation in the progressive lengthening of the nasals is observable and is more strongly expressed in *M. uintensis;* and this points toward the transformation of the *Manteoceras* skull into the Oligocene titanothere type. In the contemporary *D. hyognathus*, on the other hand, which does not lead into an Oligocene titanothere, the nasals attain the extraordinary length of 290 millimeters.

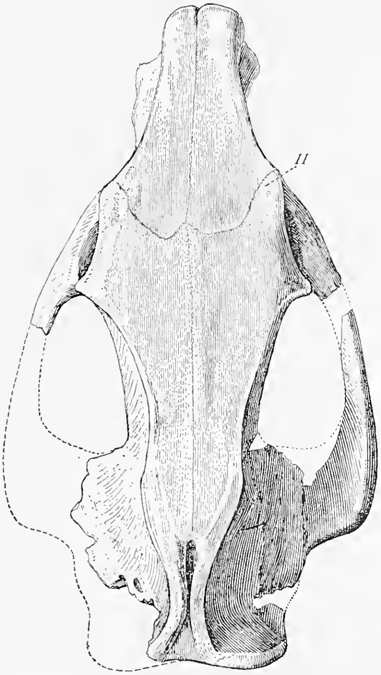

FIGURE 304.—Type skull of *Manteoceras manteoceras*

Top view. About one-fifth natural size. Am. Mus 1569. Washakie Basin, Wyo., level A (*Uintatherium-Manteoceras-Mesatirhinus* zone). After Osborn, Am. Mus. Nat. Hist. Bull., vol. 7, fig. 8, 1895. *H*, horn swelling.

2. The frontal horn caps in the Eocene as in the Oligocene titanotheres overlap the outer sides of the nasals, so that the horn bases present upwardly and outwardly.

3. The orbits (Am. Mus. 1570) are 133 millimeters apart, and from the prominent triangular postorbital processes the narrow but distinctly rugose supratemporal ridges converge backward into a broad, laterally expanded frontoparietal plate which prophetically represents the flattened summit of the Oligocene titanothere cranium. This plate flares laterally over the temporal fossae, as in many other species of titanotheres. Behind this point the supratemporal ridges converge to form a deep midparietal pit, which is apparently homologous with the vestigial pit observed in several species of the Oligocene *Brontops;* the supratemporal ridges again diverge, leaving a narrow groove between the paired sagittal crest, which is from 18 to 29 millimeters in width.

4. A very important feature of the superior view, seen also in *Mesatirhinus*, is the comparatively oval form of the openings left by the zygomatic arches, and the great backward stretch of the floor of the temporal fossa from the junction of the zygomata with the skull of the occiput.

The palatal view of the skull (fig. 303, B), best seen in three specimens in the American Museum, Nos. 1545, 2353, 1570, exhibits the following principal characters: (1) The base of the cranium, the midcranial region (postglenoid to orbit), and the face are all relatively longer than in *Palaeosyops* but shorter than in *Mesatirhinus;* (2) the posterior nares open about the middle of the skull, opposite the interval between m_2, m_3; (3) the hard palate is gently arched; (4) the posterior narial space is elongate and narrowed by the decided median convexities of the palatines; (5) the pterygoids are greatly reduced as thin, elongate plates; (6) the relations of basicranial bones and foramina are as shown in Figure 303, B; (7) there are paired rugosities on the basisphenoid for attachment of the recti capitis muscles; (8) there is an elongate bridge (35 mm.) between the foramen ovale and foramen lacerum medium; (9) the inner portions of the occipital condyles are borne on the basioccipitals; (10) the paroccipital process is delicate.

The anterior view of the cranium (fig. 305, B) clearly illustrates the decurved and thickened margins of the nasals, the prominence of the frontonasal horn, the deep lateral facial concavities, the characteristic structure of the premaxillaries, and the deep premaxillary symphysis.

In the lateral view (figs. 307, 308) the superior profile is incipiently saddle-shaped, as in the Oligocene titanotheres, and we note that the skull descends from the occiput to the midparietal region, then arches gently upward to a point directly above the orbits, and then descends to the tip of the nasals. This facial convexity, combined with the lateral preorbital concavities, contributes to and is correlated with the prominence of the frontonasal horn. The facial concavity profile is similar to that of *Mesatirhinus* and is totally different from the transversely convex preorbital section of *Palaeosyops*. Possible but doubtful evidence of a progressive shortening of the face is observed in the variable position of the infraorbital foramen. In most of the skulls (Am. Mus. 1570, 1511, 1587, 1545) there is a broad bridge of bone over the infraorbital foramen, as in *M. petersoni;* in skull Am. Mus. 2353, on the other hand, in which the face appears exceptionally short (a condition possibly due in part to crushing), this bridge is abbreviated, the foramen issuing directly in front of the malar-lacrimal maxillary bar. The maxillaries contribute the anterior portion of this bar. The projecting infraorbital shelf of *M. petersoni* is absent, being replaced by a prominent, more or less sharply convex longitudinal ridge, quite different from the more rounded suborbital bar of *Palaeosyops* or the broad, gentle convexity of *T. cultridens* and *T. ultimum.* Immediately below the orbit the malars are flat, and behind the orbit they are slightly concave; they give off the prominent postorbital processes and then gently arch outward with a convex exterior and a concave interior surface. The malars thus present two very striking differences from the Oligocene type: first, they are much shallower below the orbit and concave instead of convex externally; second, they are relatively slender and constricted behind the postorbital process. The zygomatic portion of the squamosal exhibits a wide superior as well as a broad lateral expansion, foreshadowing the decided development of this bone in the Oligocene titanotheres.

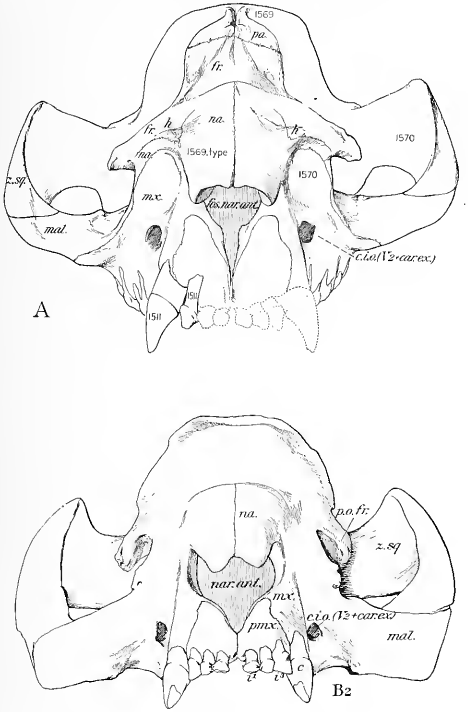

FIGURE 305.—Skulls of *Manteoceras manteoceras* and *Palaeosyops leidyi*

Front view. One-fourth natural size. In *Manteoceras* (A) the horn region projects laterally above the facial concavity. In *Palaeosyops* (B) the horn region does not so project and there is no facial concavity.

Dentition in general.—The dentition as compared with that of *Mesatirhinus* and *Dolichorhinus* agrees in the following characters: (1) The incisors are short-crowned and rounded rather than conical, and the disparity of i^3 over i^2 is less marked than in *Telmatherium;* (2) the sublanceolate canines are broadly obtuse at the base, taper rapidly at the summits, and have faint anterior and posterior ridges; (3) the premolars and molars are identical in general structure

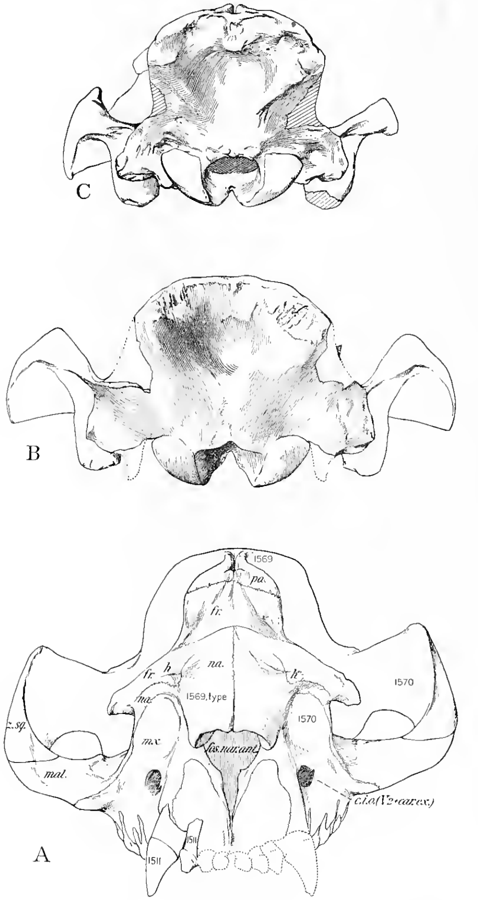

FIGURE 306.—Skulls of *Manteoceras manteoceras* and *M. washakiensis*

Occipital and front views. One-fourth natural size A, *M. manteoceras*, from specimens in the American Museum, chiefly No. 1570, La Clede, Washakie Basin, Wyo., Washakie A. Nasals and occiput restored from No. 1569 (type), Washakie Basin, Washakie A; canines and incisors from No. 1511, Bridger Basin, and No. 12678, Henrys Fork Hill, Bridger Basin, Bridger C 5. B, *M. manteoceras*, Am. Mus. 1587, Henrys Fork, Bridger Basin, level unknown. C, *M. washakiensis*, Am. Mus. 13165 (type), base of Haystack Mountain, east end, Washakie Basin, Washakie A.

but are of the mesaticephalic or subbrachycephalic type. The dentition differs sharply from that of *Mesatirhinus* and *Dolichorhinus* in the relatively short diastema behind the inferior canines and the retarded development of the deuterocones and tritocones of the premolars.

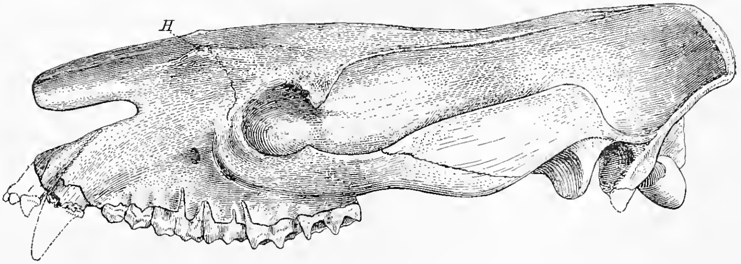

FIGURE 307.—Skull of *Manteoceras manteoceras*

Side view. One-fourth natural size. Am. Mus. 1569 (type) and 1570. Washakie Basin, Wyo., level A. Composite side view (reversed) of the type and paratype skulls. After Osborn, Am. Mus. Nat. Hist. Bull., vol. 7, fig. 7, 1895.

Incisors.—The inferior incisors as seen in Am. Mus. 1566 approach the transverse or slightly arched position observed in *M. petersoni* (Am. Mus. 1567) and in *Dolichorhinus*. The perfectly preserved crown of i_2 indicates that this tooth is slightly larger than i_1 and nearly if not quite as large as i_3; the posterior face is smooth, with a faintly indicated basal cingulum.

Canines.—The canines of the same jaw in the male are estimated as 40 millimeters in height, 21 anteroposterior, 21 transverse; they are implanted by stout fangs which cause the outer face of the ramus to bulge; faint anterior and posterior ridges bound the convex inner face of the canines; the diastema is much shorter than in *Dolichorhinus* (17 mm. in No. 1566). The superior incisors, partly preserved in Am. Mus. 1511, 1545, and fully preserved in Am. Mus. 12683, from Bridger D, are pointed, with a posterior basal cingulum slightly more prominent than in *Dolichorhinus;* in Am. Mus. 12683 they increase regularly in size from i^1 to i^3 and at first sight resemble those of *Telmatherium cultridens*, but, as shown in Figure 309, they are distinguished by their slightly smaller size, weaker posterior cingulum, and less caniniform i^3.

The superior canines are robust, sublanceolate (that is, with anterior and posterior ridges), tapering and recurved; height 39 millimeters, transverse 26, anteroposterior 24; they are provided with very stout fangs. The postcanine diastema is very short, not exceeding 7 millimeters.

Premolars.—The superior molar-premolar series, although entirely broken away in the type specimen, is superbly shown in five almost complete sets of teeth. In general, as compared with the grinders of *Mesatirhinus* and *Dolichorhinus*, we observe the brachycephalic influence, indicated, first, in the relative shortness and breadth of each of the teeth, and second, in the arching or posterior divergence of the series, which is much more marked than in *Mesatirhinus*. The series measures from 176 millimeters in Am. Mus. 12683 to 197 in the old male No. 1545, as compared with 160 in *M. megarhinus*, and is about 20 millimeters greater than in *Dolichorhinus*.

The chief distinctions of the premolars from those of *Mesatirhinus* appear to be as follows (Pls. LXVII, LXXII):

In *M. manteoceras* p^{2-4} are relatively broader, the deuterocones are not so wide anteroposteriorly and lie farther backward, giving a more oblique contour to the crown; the ectoloph is less hypsodont, its anterior convexity is much broader, and its posterior convexity is pronounced. The external cingulum, while variable, is vestigial in Am. Mus. 1511, 2353, and slightly indicated in Am. Mus. 1570, 1532. P^1 is a simple, elongate tooth, bifanged; the tritocone ectoloph is convex, and in certain specimens (Am. Mus. 1511) the tritocone nearly equals the protocone in size; this tooth, nevertheless, still retains the ancestral character of elongation and the marked postero-internal position of the deuterocone. P^3 is slightly broader than long and exhibits various degrees in the prominence and external convexity of the tritocone; the external cingulum in the less worn dentitions is well defined. No rudiment of the postero-internal cusp can be discerned except in one very large individual (Am. Mus. 1532), in which very faint indications of this fourth cusp are seen in p^2 and p^4.

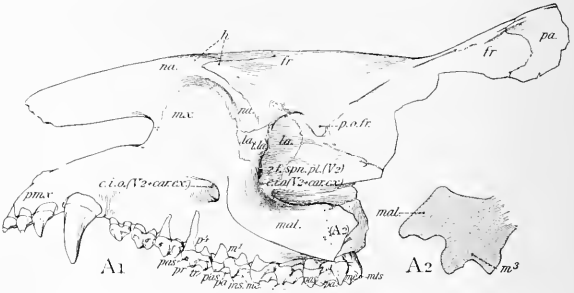

FIGURE 308.—Skull of *Manteoceras manteoceras*

One-fourth natural size. Am. Mus. 12683, Sage Creek Spring, Bridger Basin, Wyo., level D. A_1, Anterior half of skull; A_2, cross section through malar and m^3, showing flattened external face of malar.

In p^4, a larger tooth, we observe a more constant enlargement of the tritocone. The cingulum in all these premolars (except Am. Mus. 1532, the most progressive specimen) fails to encircle completely the inner sides of the obtuse deuterocones. Comparative measurements of the premolars are given below.

The inferior premolars are represented in Am. Mus. 1566, 1563, 2353. Of these, No. 1566 represents the least progressive stage. The premolar measurements here given relate to this specimen. P_1 (ap. 12 mm., tr. 9) is a simple, laterally compressed cone. P_2 (21 by 11) has an elevated protocone, slightly hollowed on its antero-internal border, with a rudimentary cuspule (=paraconid of molars) and a low postero-external cusp (=hypoconid of molars). In p_3 (18 by 12) the cusp analogous to the metaconid in the molars is beginning to be constricted off from the protoconid and is defined by a prominent antero-internal convexity, and the anterior (trigonid) and posterior (talonid) crescents are beginning to be marked, but the entoconid, as in all middle Eocene titanotheres, is not yet developed. In p_4 (20 by 14) we have a submolariform tooth lacking only the cusps analogous to the paraconid and entoconid but with a well-developed cusp analogous to the hypoconid.

Molars.—The subquadrate superior molars, which vary in longitudinal measurement from 100 to 118 millimeters (a wide range of variation), as well displayed in five individuals, exhibit (1) progressive external cingula with internal cingula in the valleys; (2) protoconules vestigial or wanting; (3) a marked angulation of the postero-internal border of m^3, accompanied by a prominent elevation of the cingulum at this point, and in one specimen (Am. Mus. 1511) a small, distinct hypocone, which, however, may represent a metaconule. All the molars in the specimens at hand are too much worn to give the height of the ectoloph, which was undoubtedly elongate in the unworn condition and which slopes strongly inward.

Comparative average measurements (ap. by tr.) of molars of Manteoceras, Mesatirhinus, and Dolichorhinus, in millimeters

	Manteoceras manteoceras (6 skulls)	Mesatirhinus petersoni (4 skulls)	Dolichorhinus hyognathus (4 skulls)
M^1	29×31	25×26	35×35
M^2	38×38	31×32	43×44
M^3	38×40	32×34	45×43

The inferior molars, well preserved in Am. Mus. 1566, 2353, 1563, are uniform in character, measuring from 111 to 118 millimeters, with an incomplete external cingulum which fills the valleys and in No. 1566 rises behind the talonid into a rudimentary entostylid, or reduplication of the entoconid. Beside this reduplication we observe an incipient metastylid or reduplication of the metaconid. The teeth rapidly increase in length as we pass from m_1 to m_3, the measurements in No. 2353 being m_1 28 millimeters, m_2 35, m_3 53. The lower molars show a strong subfamily resemblance to those of *Mesatirhinus* but are distinguished by their somewhat larger size (m_{1-3} 110 mm. in Am. Mus. 1566, as compared with 106 in the type of *M. petersoni*) and especially by their greater breadth (m_3 (tr.) 23 mm.; in *M. petersoni* 18). In *Manteoceras* also the cutting V's, as seen in crown view, form more acute angles than in *Mesatirhinus*. These differences are still more emphasized by comparison with *Dolichorhinus hyognathus*, which has long, narrow molars, wide-angled V's, and a relatively small hypoconulid on m_3.

Jaws.—Many fine jaws belonging to this animal have been collected by the American Museum expeditions in the Bridger and Washakie Basins. Unfortunately only a few are associated with the skulls, namely, Am. Mus. 1545, 1587, 12204, 2353. Another not associated is Am. Mus. 1566 (Bridger D).

As shown in the plates and figures, the jaws, like the skulls, teeth, and feet, show certain characters prophetic of the Oligocene titanotheres. These characters are always most clearly displayed in the aged forms and are (1) the depressed lower border of the angle; (2) the pit in the anterior border of the coronoid behind m_3; (3) the breadth and vertical elevation of the coronoid process and sharp recurvature at the summit; (4) the greater prominence and convexity of the chin.

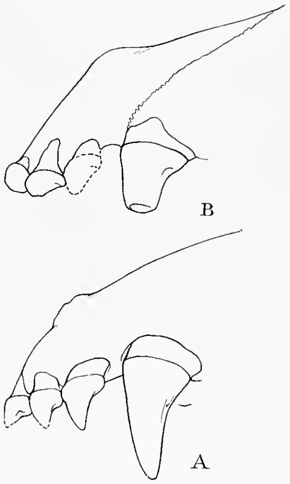

FIGURE 309.—Incisors and canines of *Manteoceras manteoceras*

One-half natural size. A, Am. Mus. 12683, Sage Creek Spring, Bridger Basin, Wyo., level D; supposed male. B, Am. Mus. 12678, Henrys Fork Hill, Bridger Basin, level C 5; aged female.

The coronoid process is more robust and less strongly recurved than in *Telmatherium cultridens*; it is decidedly more elevated and less falciform and recurved than in *Dolichorhinus hyognathus*. It is thus more of the type which we should expect to find as ancestral to the coronoid processes of the Oligocene titanotheres.

The peculiarities of the jaw of *M. manteoceras* (fig. 310, Pl. LI) are as follows:

1. In most of the jaws there is a narrow postcanine diastema (18 mm. in No. 1566).

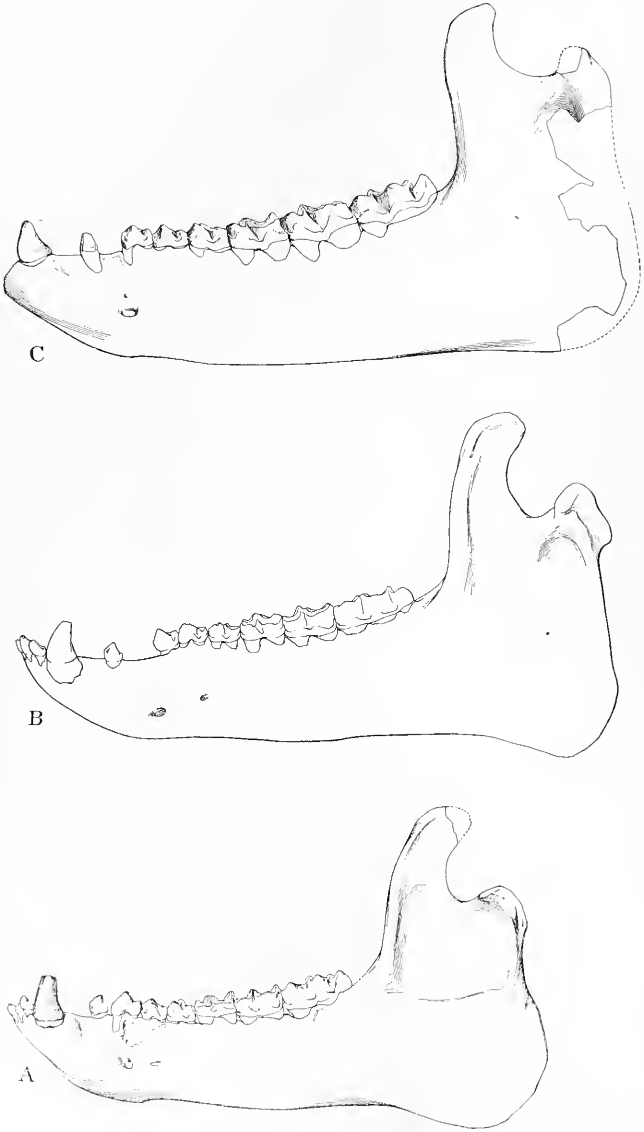

FIGURE 310.—Lower jaw of *Manteoceras*

One-fourth natural size. A, *M. manteoceras*, Am. Mus. 1566, Bridger Basin, Wyo. level probably C or D. B, *M. manteoceras*, Am. Mus. 1563, Bridger Basin, level probably D; very progressive lower jaw (front part corrected from No. 1566). C, *M. uintensis?*, Am. Mus. 2033 (reversed), White River, Uinta Basin, Utah, Uinta C; doubtfully referred lower jaw.

2. The opposite incisor series are placed more transversely than in the premaxillaries above, in which they are more convergent.

3. The powerfully rooted canines involve a sharp convexity of the bone opposite the alveoli, followed by a sharp depression in the outer face just below the postcanine diastema.

4. The chin, as seen from below, is broad and gently convex anteroposteriorly and transversely, but on account of the great variation in both species it is difficult to express exactly the differences in the horizontal rami between *Manteoceras manteoceras* and *Mesatirhinus petersoni*.

5. The principal constant difference is the weaker chin of *Mesatirhinus*, in old jaws of which the lower border of the ramus is straighter than in *Manteoceras;* the ramus also seems stouter and deeper and rapidly increases in depth posteriorly from 54 millimeters behind p_3 to 64 behind m_2 and 87 behind m_3.

6. In adult jaws the coronoid is of an entirely different shape from that of *Palaeosyops*, being elevated and broad at the top with the summit gently recurved, whereas in *Palaeosyops* it is pointed and well recurved at the top. It resembles that of *Mesatirhinus* but lacks the posterosuperior prolongation, and the superior portion of the process is flattened anteriorly with sharply angulate anterior external and internal borders.

7. The angle is produced decidedly downward and backward, and there is a rugose outer border in the old males.

8. The posterior border of the jaw between the angle and the condyle is somewhat incurved in some specimens but nearly straight in others.

Measurements of lower jaws of Manteoceras manteoceras, in millimeters

	Am. Mus. 1566; Bridger C or D	Am. Mus. 2353; Washakie A
P_1–m_3	182	195
P_1–p_4	73	76
M_1–m_3	110	117
Condyle to incisive border	360	----------
Condyle to bottom of angle	165	----------
Depth of ramus below m_3	86	96
Length of symphysis	109	----------

Detailed characters.—Probably as a sexual character the skull itself is not so large as that of the largest Bridger specimens, the estimated basilar length (490 mm.) being less than in the large male *M. manteo-*

ceras (Am. Mus. 1545) from Bridger D, where the length is 423 millimeters. Similarly, from sexual causes the horn rudiments and facial concavities are not pronounced. The posterior sagittal crests are characteristically bifid, or deeply grooved superiorly, terminating anteriorly in the parietal pit which is so distinctive of this species. The occiput is distinguished by the very decided prominence of the occipital pillars.

Dentition.—It is the teeth which afford the most marked distinctions of this species. The canines (ap. 23 mm., tr. 21) are abbreviate, measuring 24 millimeters in length, the tips being worn off. P^1 is a compressed, conical, bifanged tooth, measuring (ap. by tr.) 15 by 9 millimeters. P^2 (19 by 17) exhibits marked external convexities and a weak external cingulum. As there is considerable variation in the strength of the cingulum in *M. manteoceras* it is uncertain whether the weak cingulum is progressive or not. The deuterocone is more advanced in development than in the average *M. manteoceras.* P^3 (ap. 20 mm., tr. 25) exhibits the tetartocone fold somewhat more conspicuously than in the most progressive Bridger D specimens. P^4 (23 by 29) is progressive in transverse measurement and in the development of a low, barely perceptible tetartocone swelling. M^1 (35 by 38) exhibits a prominent internal cingulum, which is almost continuous around the lingual side of the protocone. M^2 (42 by 43) shows a strong development of the cingulum (progressive), a crenulation of the enamel, and an elongate ectoloph. M^3 (39 by 42) is slightly inferior in size to m^2, the cingulum is most pronounced, and there is a well-developed hypocone ridge (progressive) but no distinct hypocone.

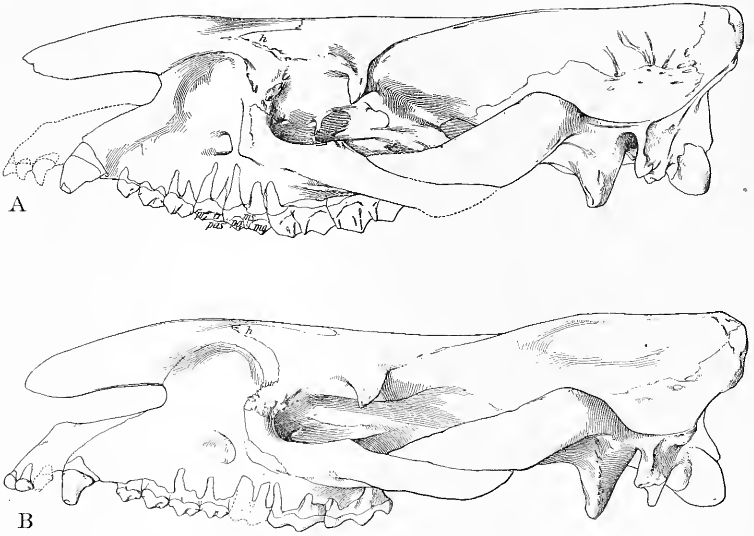

FIGURE 311.—Skulls of *Manteoceras manteoceras* and *M. washakiensis*

Side view. One-fourth natural size. A, *M. washakiensis*, Am. Mus. 13165 (type); base of Haystack Mountain, east end, Washakie Basin, Wyo., upper levels of Washakie A. B, *M. manteoceras*, Am. Mus. 12678; Henrys Fork Hill, Bridger Basin, Wyo., level C 5; supposed female skull; back of skull slightly raised to correct the vertical crushing.

Manteoceras washakiensis Osborn

Plate LXVII; text figures 121, 306, 311, 717

[For original description and type references see p. 182]

Type locality and geologic horizon.—Base of Haystack Mountain, Washakie Basin, Wyo.; summit of *Uintatherium-Manteoceras-Mesatirhinus* zone (Washakie A).

Specific characters.—Skull somewhat larger than in *M. manteoceras* (basilar length in supposed female 490 mm., estimated). Superior molars and premolars greater than in *M. manteoceras* and with complete internal cingula; superior canine in female (?) obtuse, recurved, with heavy posterior cingulum; p^1–m^3 200 millimeters (estimated), p^2 with deuterocone somewhat better developed, p^4 (ap. by tr.) 23 by 29; m^1 35 by 38, m^2 41 by 43, m^3 39 by 42. Face relatively short, zygomata moderate, horn swelling inconspicuous.

The female type skull (Am. Mus. 13165) of this species was found by the American Museum expedition of 1906 at the base of Haystack Mountain, at the summit of the exposures of level Washakie A. Its decidedly progressive characters beyond those of *M. manteoceras*, from Bridger D and Washakie A, perfectly accord with its somewhat higher geologic level. These are displayed chiefly in the canine, premolar, and molar teeth. The horns are inconspicuous, probably because the specimen represents a female, and they are smooth rather than rugose. The small size of the canines is also a sexual character, but the form of the canines is very different from that of the specimens in Bridger D and Washakie A in their approach to the obtuse form characteristic of the Oligocene *Brontops*.

Progressive characters.—(1) Canines short, obtuse, recurved; (2) internal lobes of p^2 and p^3 broadening, with shelf for development of deuterocone; (3) a tetartocone spur observed in p^3, as in most progressive Bridger specimens; (4) very distinct internal cingulum on m^{1-3}; (5) true molar series relatively longer as compared with the premolar series than in *M. manteoceras*, in which an average of six skulls gives the length p^{1-4} as 76 per cent of that of m^{1-3}, but in *M. washakiensis* p^{1-4} is only 71 per cent; in other words, the molar series is relatively longer, which might be expected, as there is a steady general increase in the relative length of the molar series as we pass from the lower Eocene *Eotitanops* to the Oligocene *Brontotherium*.

Jaws of Manteoceras washakiensis? from Washakie A and B.—In the jaw from the base of Washakie A (Am. Mus. 13176) doubtfully referred to *M. washakiensis* the dental measurements are all larger than in the well-preserved jaw of *M. manteoceras* forming Am. Mus. 1566 (p_2–m_3 182 mm. as compared with 168), and the premolars are distinctly more progressive. The large jaw from the Bridger (? level D) (Am. Mus. 1563) referred to *M. manteoceras* agrees nearly in size with Am. Mus. 13176.

It is noteworthy that in all the explorations of the Washakie B and Uinta B levels few or no remains referable to *Manteoceras* have been found. The single exception, and this of doubtful character, is the jaw employed by Cope as the first cotype of his species "*Palaeosyops*" *vallidens*. This specimen (Am. Mus. 5098), consisting of the two incomplete rami, from Mammoth Buttes, Bitter Creek, regarded as an upper Washakie level, apparently represents the Washakie B stage of *Manteoceras*. (1) The measurement of p_2–m_3 (187 mm.) agrees almost precisely with that of a *M. manteoceras* jaw (Am. Mus. 2353) associated with a skull; (2) the measurements of m_3 (ap. 57 mm., tr. 23) indicate a slightly longer tooth than that in Am. Mus. 2353 (54 by 23). The characters of the teeth and jaws are otherwise the same.

Manteoceras uintensis Douglass

Plate LXIII; text figures 131, 132, 310, 312, 313

[For original description and type references see p. 186]

Type locality and geologic horizon.—About 5 miles northeast of well 2, Uinta Basin, Utah; gray sandstone in lower part of Uinta formation (*Diplacodon-Protitanotherium-Epihippus* zone, Uinta C). The persistence of *Manteoceras* in Uinta C is surprising because that level also furnishes the next higher stage in the phylum, namely, *Protitanotherium*. This persistence is partly explainable by the fact that *M. uintensis* is apparently an aberrant side branch with a decided elongation of the muzzle and to some extent of the tooth rows, or grinding series; in other words, it gives certain indications of dolichopy, whereas the main line (*Protitanotherium*) is mesaticephalic.

Specific characters.—Skull larger than in *M. manteoceras* (basilar length not known); muzzle relatively long, horn swelling (?) not larger than in *M. manteoceras;* zygomata not stout, in inferior view forming a marked angle in front of the glenoid surface. Postcanine diastema long (28 mm.), postcanine constriction very marked; superiority in size of i^3 over i^2 appearing less marked than in *M. manteoceras;* p^1–m^3, 240 millimeters; p^2 with deuterocone and tritocone more advanced than in *M. manteoceras;* p^4 (ap. by tr.) 27 by 34; m^1, 37 by 38; m^3, 49 by 52.

That this species should be referred to the genus *Manteoceras* is indicated by the round-topped incisors, the robust, recurved canines, the twin convexities of the premolar ectolophs, the broad, subhypsodont m^3, with large parastyles and mesostyles, and the widely arched zygomata. From the Bridger and Washakie Basin species of *Manteoceras* the present one is distinguished by its larger size, more dolichocephalic appearance, shorter free nasals, slightly more progressive premolars, and more pronounced postcanine constriction. All these characters serve also to distinguish *M. uintensis* from *Sthenodectes incisivus* (Douglass), which has very large, "cupped" incisors, long, lanceolate canines, and very advanced premolars. Affinities with *Protitanotherium emarginatum* and *P. superbum* are indicated by the general form of the incisors and canines, short nasals, and broad molars; but well-marked differences from these forms are seen in the more elongate face, the larger size of the incisors, more pronounced postcanine constriction, and absence or arrested condition of the horn swelling.

A remote analogy to *Dolichorhinus* is seen in the lengthening of the face, of the postcanine diastema, and of m^2, as well as in the broad arching of the incisor series. These dolichocephalic features in a mesaticephalic skull illustrate the subfamily kinship of *Manteoceras* with *Dolichorhinus*.

The skull as a whole must have been large, for the distance from the premaxillaries to the glenoid region of the squamosal is given as 430 millimeters, as compared with 335 for the same measurement in *M. manteoceras*, an increase of nearly 25 per cent. The premaxillaries in correlation with the large size of the incisors are angulate superiorly; the free nasals are short (85 mm.), a progressive feature; the face is long (255 mm., as compared with an average of 184 in *M. manteoceras*). The horn swellings were certainly not larger than in *M. manteoceras*—a surprising fact, because the large canines and incisors indicate male sex. The infraorbital canal is broad; the zygoma is deep in its middle portion, but apparently the buccal swelling was slight or absent. Just back of the orbit the malar was slender but not so slender as in *M. manteoceras;* in inferior view the infraorbital portion of the malar formed a low ridge which was somewhat more pronounced than in *M. manteoceras* but did not form a distinct shoulder as it does in *Mesatirhinus* and *Dolichorhinus*. The posterior nares open opposite the metacone of m^2, whereas in *M. manteoceras* they sometimes open opposite the paracone of m^3.

Passing to the dentition, we note that the incisors are intermediate in form between those of *Manteoceras manteoceras* and of *Protitanotherium emarginatum*, although nearer the former in shape and much larger than in the latter. The anteroposterior and transverse dimensions of the incisors are, i^1, 18 by 14 millimeters; i^2, 19 by 17; i^3, 22 by 20. The incisors in general resemble those of *M. manteoceras* in their rounded front faces and obtusely pointed tips but differ in the form of the posterior cingulum, which is now represented by a very large, obtuse basal rim. The posterior face of i^1, i^2 shows a median vertical ridge. The posterior face of the large i^3 is much worn. The canine is very stout, with widely protruding and divergent fangs; crown measurements (ap. by tr.), 27 by 20 millimeters; it is followed by a large postcanine diastema (26 mm.), which distinguishes this species from *M. manteoceras*, and also by a marked postcanine constriction.

Premolars.—P^1 (ap. 22 mm., tr. 11) seems to be a somewhat more compressed, elongate tooth than in the preceding species, in which the posterobasal cingulum is produced upward along the median line into a very low incipient cusp. In p^2 (25 by 21) the deuterocone is still confined to the postero-internal corner of the tooth but is a little more advanced than in *M. manteoceras;* the tritocone is also slightly more developed but not so much as in either *Sthenodectes incisivus* or *Dolichorhinus.* The external cingulum opposite the tritocone is rounded. In p^3 (24 by 29) the deuterocone has a rather backward appearance as compared with the same cusp in *M. washakiensis*, but the internal cingulum is pronounced, although still incomplete opposite the middle of the deuterocone; the protocone is still much larger than the tritocone; the "parastyle" is pronounced; the ectoloph convexities are marked; the external cingulum is pronounced except where it "festoons" the protocone convexity. In p^4 (28 by 33) the deuterocone seems less robust than in *M. washakiensis;* the cingulum is robust but does not surround the deuterocone; the "parastyle" is prominent, and the protocone convexity broad at the base; the tritocone is at least no bigger than in *M. washakiensis;* the external cingulum is a broad, rounded ridge opposite the tritocone.

Molars.—The molars (m^1–m^3, 138 mm.) are somewhat larger than those of *M. washakiensis* but otherwise agree fairly well. The external cingulum is very pronounced opposite the valleys. The molars show a marked asymmetry of the external V's, the anterior V being more widely open and the posterior having a short posterior limb. The antero-internal cingula are heavy but not complete around the inner sides of the protocones (contrast *M. washakiensis*). In m^3 the postero-internal corner is less angulate than in *M. washakiensis.* The anteroposterior and transverse dimensions are, m^1, 37 by 38 millimeters; m^2, 48 by 48; m^3, 48 by 52.

Other measurements of *M. uintensis* are given in the table above.

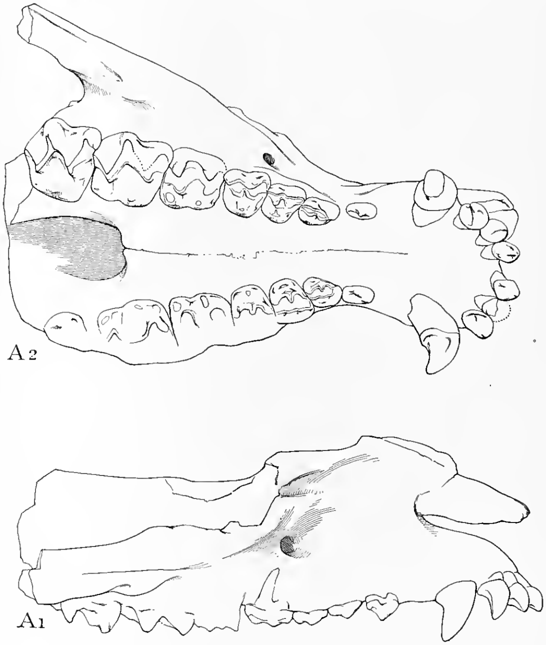

FIGURE 312.—Type skull of *Manteoceras uintensis*

One-fourth natural size. Carnegie Mus. 2388. "About 5 miles northeast of well 2, Uinta Basin; from gray sandstone in red Uinta beds, lower portion of horizon C." A_1, Side view, nasal region crushed; A_2, palatal view, crushed laterally.

Manteoceras uintensis?

From the base of Uinta C in 1895 Peterson obtained a very large skull, apparently female (Am. Mus. 2029), which unfortunately is too aged as well as too much crushed and imperfect to afford distinctive characters for definition. It is somewhat smaller than the type of *M. uintensis.* If more complete it might be found to represent a female of *M. uintensis* (with which it agrees in the retarded evolution of the premolars) or a species transitional between *Manteoceras washakiensis* and a higher stage of evolution. Size or metatrophic characters are truly progressive and undoubtedly correlated with other characters of distinct specific value. Its total length, condyles to incisive border, is about 555 millimeters, as compared with 523 in the largest skull of *M. manteoceras* found in Bridger D. The grinding teeth, p^1–m^3, measure 227 millimeters, as compared with 203 in the largest of the specimens of *M. manteoceras* from Bridger D and 240 in *M. uintensis.* Its progressive zygomatic brachycephaly is indicated by the widely arching zygomata, which attain a transverse width of about 360 millimeters, the relations of width to length thus being width 360, length 555. The reference to *Manteoceras* is confirmed by the obliquely flattened form of the infraorbital portion of the malars, a character by which this animal may readily be distinguished from the contemporary *Telmatherium ultimum*, though there is no infraorbital shelf. The proportions of this part of the skull indicate an elongation of the facial region (as in *M. uintensis*), a feature certainly not charateristic of the line leading to *Protitanotherium*. The animal is undoubtedly a female, as indicated by the relatively small canine teeth.

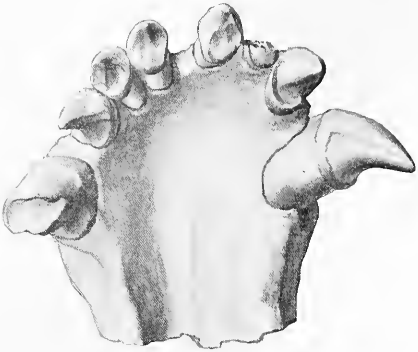

FIGURE 313.—Upper canines and incisors of *Manteoceras uintensis*

One-half natural size. Carnegie Mus. 2388 (type). "About 5 miles northeast of well 2, Uinta Basin; from gray sandstone in red Uinta beds, lower portion of horizon C."

A lower jaw (Am. Mus. 2033, fig. 310, C) found in the same region and at first referred to *Telmatherium ultimum* (cf. above) agrees in size with this specimen. It also belongs to a female animal and is of the mesaticephalic rather than dolichocephalic or brachycephalic type. The canines are relatively small and recurved. M_3 is a relatively short (63 mm.) rather than elongate tooth as in *Telmatherium ultimum* (76 mm.).

Protitanotherium

General characters.—In their phylogeny the animals known as *Protitanotherium* are among the most interesting of the titanotheres that lived in the Uinta Basin, because of their evident relationship to *Manteoceras* on the ancestral side and to *Brontops* and other Oligocene titanotheres on the descendant side. The profile figure of the horn region of *Manteoceras manteoceras*, *P. emarginatum*, two young skulls of the Oligocene *Brontops brachycephalus*, *Allops marshi*, and *Brontops robustus* illustrates the resemblance (fig. 712).

These upper Eocene animals are robust, massive, vigorous, and well protected both by their powerful tusks and by their rapidly developing horns, which are far more prominent than those of any of the earlier Eocene titanotheres. Therefore the suggestion of Hatcher (1895.1, p. 1084) that this animal should be called *Protitanotherium* was eminently appropriate.

Progressive characters.—The phyletic increase in size of the animals of this series is best illustrated by comparison of the adult jaws of *M. manteoceras*, *P emarginatum*, and *P. superbum* (figs. 310, 315, 321). The preservation of the ancestral phyletic character in these jaws is certainly very striking. The change is chiefly proportional, or quantitative. The differential or generic distinctions are to be found especially in the teeth and in the horns.

Specific stages.—These protitanotheres are known to include two stages—(1) *P. emarginatum* Hatcher, originally described as *Diplacodon emarginatus*, found near the base of Uinta C, or the "*Diplacodon* beds" of Marsh, and distinguished from the following stage chiefly by its inferior size and more brachyodont teeth, and (2) *P. superbum* Osborn, a much larger animal, whose remains were probably found at a higher geologic level.

FIGURE 314.—Restoration of *Protitanotherium emarginatum*

By Charles R. Knight. About one-ninth natural size.

Horns.—The bases of the horns preserve the Eocene anteroposterior elongation. This elongate oval form is in marked contrast to the obliquely oval, triangular, or transversely elongate form of adult Oligocene titanotheres. In very young Oligocene titanotheres, however, the resemblance in the elongate oval horn swellings to those of *Protitanotherium* is very noticeable (fig. 374).

Size.—In the species *P. superbum* these animals attain a size considerably surpassing that of many of the smaller forms in the lower Oligocene levels.

Protitanotherium Hatcher

Plates LXVIII, LXIX; text figures 24, 29, 87, 112, 128, 314–321, 371, 374, 375, 408, 409, 594–596, 647–649, 701, 712

[For original description and type references see p. 176. For skeletal characters see p. 655]

Generic characters.—Horns relatively large, elliptical in section, with anteroposterior diameter greatly exceeding the transverse. The incisor series numerically typical, $\frac{3}{3}$; canines relatively large, robust and recurved; p_4 submolariform but without entoconid; p_3, p_2 transitional.

Materials.—These animals are known from three specimens referred to *P. emarginatum* and three referred to *P. superbum.* The lower grinding teeth are fully known, but the upper grinding teeth are only partly known.

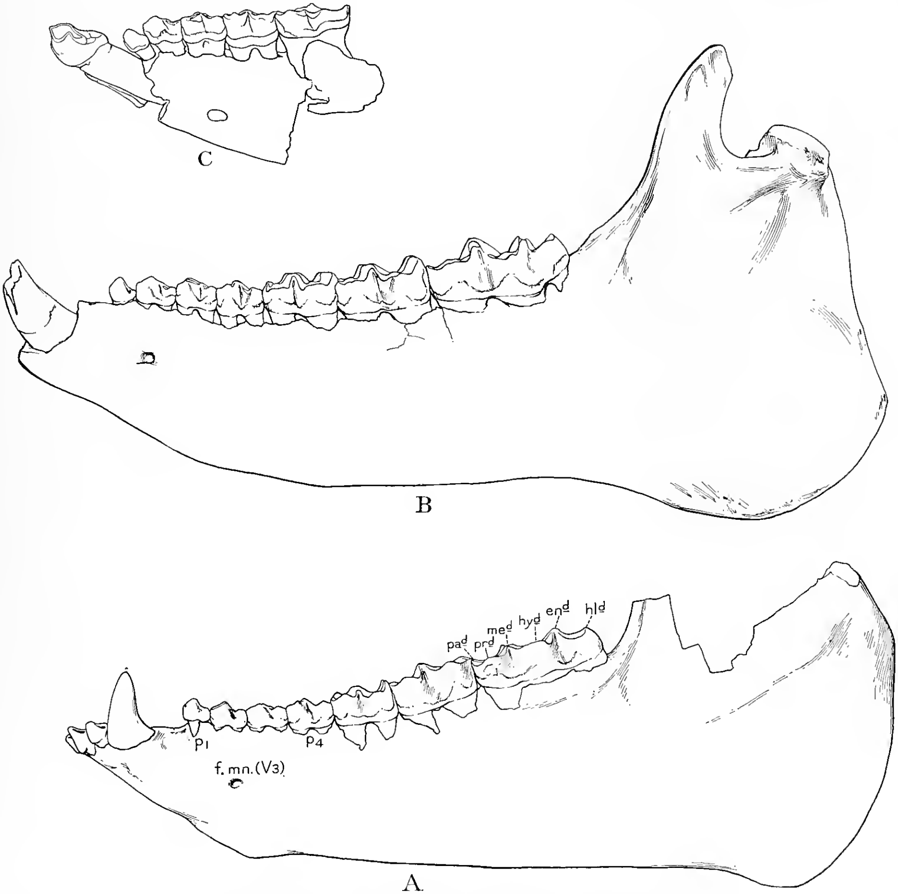

FIGURE 315.—Lower jaws of *Protitanotherium* and *Brachydiastematherium*

One-fourth natural size. A, *P. emarginatum*, Princeton Mus. 11242 (type); Uinta Basin, Utah, Uinta C; region of angle and m_3 supplied from Am. Mus. 2028. B, *P. superbum*, Am. Mus. 2501 (type), reversed; Uinta C. C, *B. transilvanicum*, front type of lower jaw; upper Eocene (?) of Andrásháza, Transylvania.

Comparison.—We at first note the incipient loss of the piercing function of the incisor teeth. The lateral superior incisors are still large, but the median incisors are reduced. This may indicate that these animals were given to browsing and that the tongue and lips were increasingly used for the prehension of food, while the incisors became functionless and gradually aborted.

We observe in comparison with *Manteoceras* that the nasals have taken on the broad, quadrate character which distinguishes the nasals of certain of the lower Oligocene titanotheres, such as *Brontops* and *Menodus.* The horns are intermediate in evolution between those of *Manteoceras* and of *Brontops.* The incisor teeth still retain the proportions observed in *Manteoceras,* but the median upper incisor is acquiring the rounded form characteristic of most Oligocene titanotheres.

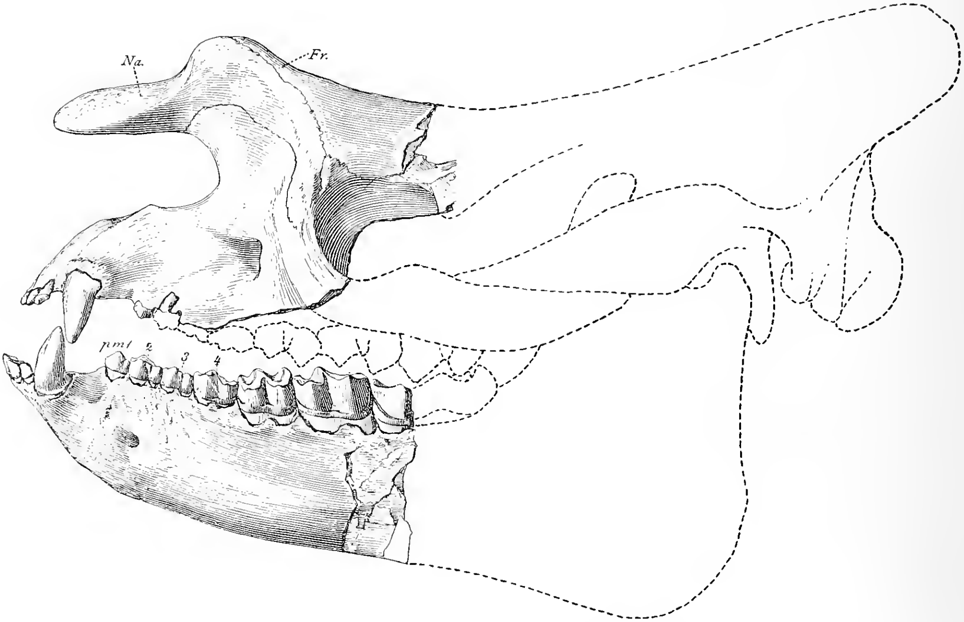

FIGURE 316.—Type skull of *Protitanotherium emarginatum*

Less than one-fourth natural size. Princeton Mus. 11242, Kennedys Hole, 8 miles north of White River and 25 miles east of Ouray Agency, Uinta Basin, Utah; Uinta C. Provisional reconstruction of skull and lower jaw, front part directly from the type.

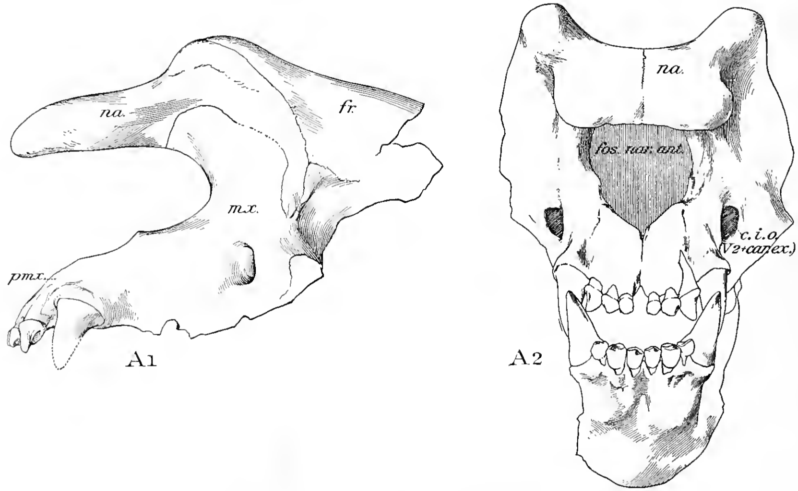

FIGURE 317.—Type skull of *Protitanotherium emarginatum*

One-fourth natural size. Princeton Mus. 11242, Kennedys Hole, 8 miles north of White River and 25 miles east of Ouray Agency, Uinta Basin, Utah; Uinta C. A_1, Side view of front part of skull; A_2, front view of front part of skull and lower jaw.

The canines are intermediate in form between the *Manteoceras* and *Brontops* types, perhaps nearer *Brontops*, and were evidently robust fighting weapons. Unfortunately the form of the superior and posterior parts of the skull is still unknown.

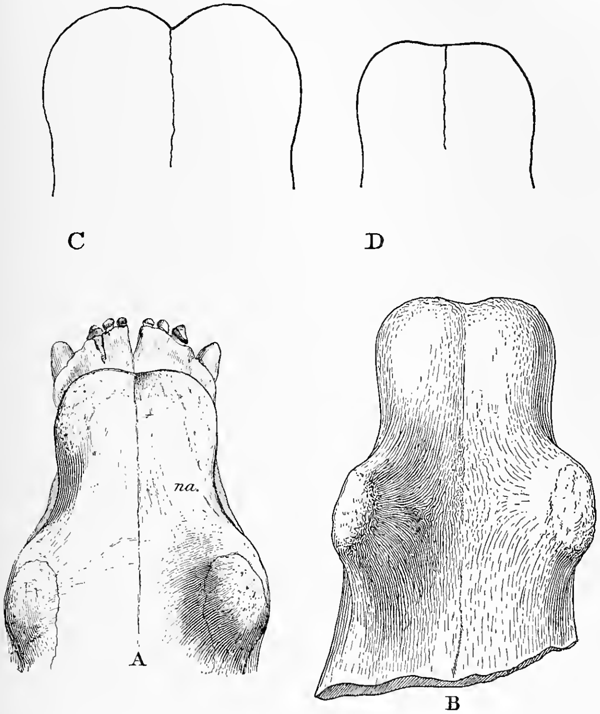

FIGURE 318.—Nasal region in three specimens of *Protitanotherium*

Top view. One-fourth natural size. A, D, *P. emarginatum*, Princeton Mus. 11242 (type); B, *P. superbum?*, Carnegie Mus. 2855; C, *P. superbum?*, Princeton Mus. 11213.

Protitanotherium emarginatum Hatcher

[*Diplacodon emarginatus* Hatcher, p. 177]

Plates LXVIII, LXIX; text figures 24, 29, 87, 112, 314–320, 374, 375, 408, 648, 649, 712

Type locality and geologic horizon.—Kennedys Hole, 8 miles north of White River and 25 miles east of Ouray Agency, Uinta Basin, Utah; Uinta formation (*Diplacodon-Protitanotherium-Epihippus* zone, Uinta C).

Specific characters.—P_1–m_3 294 millimeters (estimated), p_1 with a small talonid; i_1 small, round-topped; i_3 large, bluntly pointed; i_2 much larger than i_3. Lower canine more erect, recurved, and abruptly swelling at the base. Postcanine diastema short (27 mm.) but relatively longer than in *P. superbum.* Lower premolars and molars more brachyodont, with sloping curves.

P. emarginatum appears to be closely allied to *P. superbum* but is apparently a lower stage, distinguished by its smaller size, more brachyodont premolars and molars, and more erect recurved lower canines, which swell more rapidly at the base.

Materials.—This species is represented by the type (see below), by the finely preserved anterior portions of a jaw in the Yale Museum (No. 635 D), and by a fairly well preserved jaw in the American Museum (No. 2028). The jaw in the Yale Museum is especially valuable because it includes, besides the incisors, canines, and portions of the premolars, a complete m_3, a tooth which is imperfect in the type.

Skull.—The type of the present species, discovered by Hatcher himself, is the anterior portion of a skull and lower jaw (Princeton Mus. 11242). Hatcher noted the greater size of this animal than *Diplacodon elatus* as indicated by the length of the grinding teeth (294 mm., as compared with 244). So far as preserved the dorsal surface of the skull is concave anteroposteriorly and suggests the broad, flat frontal region and flattened parietal vertex of the Oligocene forms. The nasal openings are high and deeply incised. The horns are composed of the frontals overlapping the nasals; they are placed longitudinally and directed upward, outward, and forward. The nasals are broad, strong, and rather short, firmly coossified, concave inferiorly; they measure in free length 107 millimeters and in greatest breadth 123. The specific name *P. emarginatum* refers to the fact that the nasals are "emarginate anteriorly," but they are not deeply indented in the midline, as in a larger pair of nasals also described by Hatcher (fig. 318) which may be referred provisionally to *P. superbum.* The premaxillaries are well developed and separated anteriorly by a deep median notch, below which they are firmly coossified. The maxillaries are expanded at the base of the canines and decidedly constricted between these teeth and p^1. The postcanine diastema measures 37 millimeters, and back of this the maxillaries expand rapidly in order to accommodate the large posterior premolars and molars. The infraorbital foramen was probably situated just above p^4, as in *Palaeosyops*, *Limnohyops*, *Telmatherium*, and *Manteoceras*. In *Mesatirhinus* and *Dolichorhinus* it is more nearly above m^1.

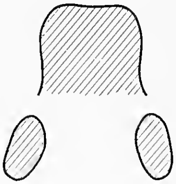

FIGURE 319.—Sections of the nasals and horns of *Protitanotherium emarginatum*

Princeton Mus. 11242 (type). One-seventh natural size.

Dentition.—The statements made below refer to the type specimen unless otherwise indicated. The superior incisors in general are of the *M. manteoceras* type but exhibit several differences, which, on the whole, are progressive toward the Oligocene titanotheres of the genus *Brontops.* The median pair of superior incisors (i^1) are distinctly the smallest of the series and are assuming the degenerate conical form seen in the Oligocene species of *Brontops*,[26] a change that is effected especially by the reduction of the posterior cingulum and the rounding together of the anterior and posterior faces, with the consequent loss of prehensile or cropping function. The inferior series are all still pointed, posteriorly cingulate, and functionally of the cropping type; i$_2$ is the largest of the series and i$_3$ is the most reduced. The superior incisors are nearly in a transverse line, but i^3 is slightly behind i^2. The incisors are separated from the canines at the sides by a narrow diastema (9 mm.) and separated in the median line by a diastema (10 mm.) similar to that observed in *Mesatirhinus megarhinus.* The lateral incisors (i^3) are large pointed teeth (height 21 mm. side, 17 front; ap. 17) with oblique posterolateral basal cingula and rather sharp lateral cutting edges. The second incisors (i^2) are much smaller (height 12 mm., ap. 14) with heavy posterior basal cingula connected with the apex of the tooth by a median ridge which divides the somewhat concave posterior surface. The median incisors (i^1) are still smaller (height 10 mm., ap. 11), with subspherical crowns and posterior median ridges rising to unite with the apex of the crown and obscure the cingulum except on the posterolateral side.

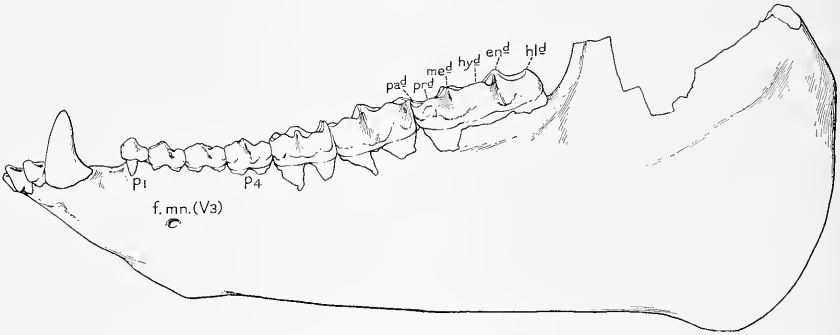

FIGURE 320.—Lower jaw of *Protitanotherium emarginatum*

One-fourth natural size. Partial reconstruction of anterior part of jaw to m$_3$ from Princeton Mus. 11242 (type), Kennedys Hole, 8 miles north of White River and 25 miles east of Ouray Agency, Uinta Basin, Utah, Uinta C; m$_3$ and posterior part of jaw from Am. Mus. 2028, White River, Utah, Uinta C.

The transverse extent of the inferior incisors is 69 millimeters; they all exhibit pointed crowns, with uniformly convex anterior faces, more concave posterior faces, and with low posterior U-shaped basal cingula.

The median incisors (i$_1$) are somewhat compressed laterally (height 15 mm., ap. 14) but exceed in size the lateral pair. The second incisors (i$_2$) are much larger (height 18, ap. 18) and the lateral incisors (i$_3$) are the smallest (height 12, ap. 12, tr. 12) and the simplest, although still incisiform.

The canines are distinguished by robust, rounded fangs, which diminish rapidly into forward-directed, tapering, pointed crowns, again suggesting those of *M. manteoceras,* especially by the posterior swelling at the base and the sublanceolate, internally flattened apex with faint anterior and posterior ridges. In the superior canines the diameters at the base are transverse 26 millimeters, anteroposterior 28; height 49. The inferior canines exhibit much the same form (ap. 32 mm., tr. 28, height 52), the base of the crown sloping backward into a deep, powerfully implanted fang, the crown diminishing rapidly as it rises to a rounded, sublanceolate apex.

The premolar-molar series are separated by a short diastema from the canines in both jaws (27 to 30 mm. above, 23 below). A postcanine diastema of varying length is seen in *Telmatherium ultimum, T. altidens, Manteoceras uintensis, Diplacodon elatus,* and *Protitanotherium superbum,* an indication that it is independently preserved in different phyla. Of the superior teeth unfortunately p^1 only is preserved. This is a bifanged tooth measuring (ap. by tr.) 20 by 11 millimeters, with a simple protocone, a sessile or rudimentary posterior heel, and a postero-internal cingulum and concavity. The alveolus of p^2 shows that it was a broader and much more advanced tooth than that in *Manteoceras manteoceras.* The inferior grinding teeth measure about 294 millimeters in length, as compared with 180 to 192 in *M. manteoceras.*

In the type the lower premolar series measures 103 millimeters on the left side, in which p$_1$ is abnormal

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[26] In the Oligocene genera probably the median pair of superior incisors (i^1) and the lateral pair of inferior incisors (i$_3$) had disappeared, leaving i^2, i^3 and i$_1$, i$_2$ (see p. 448).

There is a marked asymmetry of this tooth on the two sides of the jaw, the right tooth being much smaller than the left and of a form normal in upper Eocene titanotheres. The abnormal p_1 is much swollen, a tendency seen also in the other cheek teeth and even more emphasized in the Oligocene titanotheres. The normal p_1 (ap. 16 mm., tr. 11) is compressed, subconic, with a posteriorbasal lobe that is better developed than in earlier forms. P_2 (ap. 25 mm., tr. 16) is in about the same stage of evolution as in *P. superbum* but is more brachyodont; it exhibits a protoconid relatively much more depressed than in *M. manteoceras,* while the postero-external cusp (hypoconid) is relatively more elevated, and a rudimentary internal cuspule (=paraconid) begins to appear. This is therefore a much more progressive tooth than the p_2 of *M. manteoceras* but is clearly derivable from it. In p_3, though the anterior crescent (=trigonid) remains larger than the posterior crescent (=talonid), the measurements (ap. by tr.) being 27 by 17 millimeters, the antero-internal cusp begins to be well defined; no median internal cusp corresponding to the metaconid of the molars appears, the tooth being less progressive in this respect than in *P. leidyi* but derivable from the conditions observed in p_3 of *M. manteoceras.* P_4 differs from the true molars chiefly in its smaller size (ap. 30 mm., tr. 21), in the somewhat greater elevation of the anterior lobe (=trigonid), and in the absence of a distinct postero-internal cusp (=entoconid). The external cingula are obsolete on p_2, p_3 and much reduced on p_4.

The inferior molars of the type are characterized by shallow internal valleys and an incomplete external cingulum, which is inflected in the valleys, by a well-defined posterior cingulum, by prominent paraconid and metaconid, by a considerable elevation (hypoconid) of the crown (26 mm.) in m_2. Metaconid folds are present as in many other titanotheres. The measurements (ap. by tr.) are m_1, 46 by 26 millimeters; m_2, 57 by 34 (estimated). M_3 is incomplete in the type; in another specimen (Am. Mus. 2028) it measures 78 millimeters, and in a third specimen (Yale Mus. 635 D) 79. In *Protitanotherium superbum* this tooth measures 98 millimeters.

Jaw of Protitanotherium emarginatum.—The type jaw of *P. emarginatum* (Princeton Mus. 11242) exhibits the anterior half of the ramus and symphysis The second jaw (Am. Mus. 2028) preserves the posterior half but lacks the coronoid and condylar processes. The third jaw (Yale Mus. 635 D) includes the symphyseal portion only.

The type jaw exhibits a very massive symphysis, 159 millimeters in length, 80 millimeters across the narrowest portion of the chin below, with the characteristic postcanine constriction seen in *M. manteoceras.* The ramus is thickened (35 mm.) below m_1 and increases very rapidly in depth from 92 millimeters behind p_3 to 126 behind m_2. The progressive increase of the ramus in depth posteriorly is evident in this series as well as in *Telmatherium ultimum, T. altidens, Palaeosyops,* etc. It is more pronounced in forms with relatively large molars. The mental foramen of the type jaw is single and placed directly below the posterior fang of p_2.

In the American Museum jaw of *P. emarginatum* (No. 2028) the depth is 90+ millimeters behind p_3, 108 behind m_2, and 144 behind m_3; the distance from the back of m_3 to the posterior border of the angle is 186 millimeters. The lower border is crushed, the distortion concealing its natural contour, but there appears to be a slight up curve below the coronoid, with a broad downward and backward sweep of the angle, and the posterior border of the angle appears to rise to the condyle with a slight incurvature.

Protitanotherium superbum Osborn

Plate LXIX; text figures 128, 315, 318, 321, 371, 593, 647 701

For original description and type references see p. 185. For skeletal characters see p. 655]

Type locality and geologic horizon.—White River, Uinta Basin, Utah; Uinta formation (*Diplacodon-Protitanotherium-Epihippus* zone, Uinta C, probably higher levels).

Specific characters.—Very large (p_1–m_3, 318 mm.). Lower canines in males very robust, relatively nearer to the midline than in *P. emarginatum;* p_1 distinctly double-fanged; postcanine diastema abbreviated (about 30 mm.); premolars in about the same stage of complication as in *P. emarginatum,* but premolar and molar cusps more steeply sided (that is, more hypsodont), p_4 submolariform, p_3, p_2 transitional; external cingulum on p_3, p_4 a little clearer; true molars very large (m_1–m_3, 210 mm.); m_3 with hypoconulid sharply constricted at base.

Materials.—This species is at present known from the type jaw (Am. Mus. 2501), discovered by Peterson in 1895. There are also two upper molar teeth recorded as belonging to the same individual, as well as a pair of nasals in the Princeton collection (No. 11213). These nasals (fig. 318) are distinguished from those of *P. emarginatum* by their superior size and by a deep incision in the median line anteriorly.

Comparisons.—The relative measurements of *P. superbum, P. emarginatum,* and *Teleodus avus* are shown below.

Measurements of Protitanotherium and Teleodus, in millimeters

	P. emarginatum (upper Eocene)	P. superbum (upper Eocene)	T. avus (lower Oligocene)
P_1–m_3	[a] 294	318	----------
M_1–m_3	[a] 187	210	----------
P_1–p_4	[a] 99	105	(p_2–p_4) 106
Transverse posterior lobe of m_1	27	31	----------
M_3	78	99	99

[a] Estimated.

P. superbum is distinctly of the *Manteoceras* and *Protitanotherium* phylum. It is, however, more progressive toward the *Brontops* stage in that it is larger, that its canines are extremely robust, and that p_{2-4} are a little longer but m_{1-3} much longer than in *P. emarginatum.* We observe that *Teleodus* (*Brontops*) *avus* of the Oligocene has grinding teeth similar in size to those of *P. superbum.*

Inferior dentition.—The canines and grinding teeth are preserved in the type jaw, but the incisor series is wanting. They represent a specific progression upon those of *P. emarginatum* in their greater size; in the abbreviation of the postcanine diastema; in the lengthening and broadening of the true molars, a progressive tendency that may be followed from *Eotitanops* through *Manteoceras* and *Protitanotherium* up into the Oligocene titanotheres; in the arrested length of the premolar series; and in the more pronounced hypsodonty of the cusps of the premolars and molars.

Considered in detail, the inferior canines are seen to be relatively closer together than those of either *M. manteoceras* or *P. emarginatum,* which are presumably near the ancestral types of *P. superbum;* but they retain the characteristically robust fangs and the stout recurved crowns with generally rounded section, faint anterior and posterior cingula. The basal crown measurements of the canines are anteroposterior 32 millimeters, transverse 31. The postcanine diastema is relatively reduced and uneven on the two sides—namely, 30 millimeters on the left, 20 (estimated) on the right.

The premolar series (Pl. LXIX) is closely continuous, measuring 105 millimeters. P_1 of the left side was apparently somewhat smaller than p_1 of the right. Nothing remains of the crown of this tooth except the laterally compressed subsecant talonid. P_2 (ap. 28 mm., tr. 16) is distinguished from that of *M. manteoceras* by the deepening of the crescents and the more decided accent of the internal cusps, which are analogous to the paraconid, metaconid, metastylid, and entoconid on the molars. P_3 (ap. 28 mm., tr. 18) is a slightly longer and decidedly broader tooth than in *P. emarginatum;* it is little if any more progressive in the development of the cusps analogous to the paraconid, metaconid, metastylid, and entoconid of the molars, which, being less worn down than in the type of *P. emarginatum,* produce at first the impression that they mark a higher stage of evolution, but the differences seem to be due largely to difference in wear; however, the entoconid of the right side only is somewhat better developed than in *P. emarginatum.* P_4 (ap. 33 mm., tr. 21) is still more decidedly molariform, the median internal cusp (=metaconid) being much more prominent than in either of the preceding teeth, a feature foreshadowed in *M. manteoceras.*

The true molars are decidedly longer and broader than those of *P. emarginatum.* This progression in size and especially in width points toward brachycephaly. There is a somewhat stronger accent of the paraconids than in *P. emarginatum,* but this may result from the greater wear in the type of that species, which would depress the metaconids and entoconids nearer to the level of the paraconid. The metastylid ridges do not appear very prominent. The external cingulum tends to festoon the sides of the protoconids and hypoconids in a faint line, whereas in *P. emarginatum* the cingulum is straighter and is thus (by comparison with other titanotheres) seemingly more advanced than in *P. superbum.* The outer surface of the ectoloph is entirely smooth on the median portion of the lobes—that is, the cingulum has disappeared. The measurements, in millimeters, are as follows: M_1, ap., 52; tr., 27 through trigonid, 30 through talonid. M_2, ap., 63; tr., 35 through trigonid, 36 through talonid. M_3, ap., 95 (estimated); tr., 40 through trigonid, 38 through talonid.

Superior molars.—The second and third superior molars of the same individual (Pl. LXIX) are almost certainly associated with the type lower jaw; they have the proper dimensions to fit the lower molars, and in this jaw, as in others, they show more dentine than the lower teeth; they are quadrate in form, m^2 measuring 57 by 57 millimeters and m^3 62 by 62. They exhibit imperfectly developed external cingula and an internal cingulum, which faintly festoons the inner cusps of the crown. The features of m^2 are the complete wearing out of the prefossette, the somewhat median position of the protocone, and the somewhat detached and anteroposteriorly compressed hypocone; it is noteworthy that, as in other titanotheres, while the external crescents are extremely worn the internal cones are very slightly worn, the protocone barely exhibiting exposure of the dentine at its apex. M^3 shows the bottom of the prefossette, a very large protocone, and an angulate hypocone region, in which, however, there is a sessile cingulum but no rudiment of the hypocone proper.

Comparison of teeth of Protitanotherium with those of other genera.—*Protitanotherium* is at once distinguished from *Teleodus avus* of the lower Oligocene by the character of the incisors, which in *Protitanotherium* are large and more or less flat-topped and in *Teleodus* smaller, with ovoid or hemispherical tops. The canines of *Protitanotherium* are more robust, especially at the base; those of *Teleodus* are more slender, erect, and evenly sloping. The premolars of *Protitanotherium* are in a lower stage of evolution—that is, they are less molariform than those of *Teleodus* and *Brontops.*

The jaw.—The dimensions of the jaw of *P. superbum* (type) considerably surpass those of *Brontops brachycephalus,* from the lower *Titanotherium* zone, the length from condyle to incisive border being 580 millimeters and the depth of the angle below the condyle 270, as against 490 and 220, respectively, in a small *B.*

brachycephalus (Am. Mus. 1495). The general contour of the jaw in these two species, however, is somewhat similar; there is the same long, slightly convex chin; the lower border in profile is convex below the grinders, slightly concave below the coronoid, and is produced downward and backward into the angle, a concave border rising from the angle to the condyle; and the stout, somewhat recurved coronoid processes have a heavy anterior and gently convex anterior border.

This jaw, as compared with earlier forms, certainly resembles in its main features and proportions those of *P. emarginatum*, *Manteoceras manteoceras*, and *Mesatirhinus megarhinus.*

The symphysis is very massive, extending 158 millimeters anteroposteriorly, with 100 millimeters as the least transverse measurement of the chin; it is gently convex anteroposteriorly and somewhat more decidedly convex transversely; the postcanine constriction is relatively less decided than in *M. manteoceras;* the jaw increases rapidly in depth from 109 millimeters behind p_3 to 124 behind m_2 and 163 behind m_3. In view of the relatively short diastema behind the canine and the rather rapid rise of the coronoid border behind m_3, it appears that this jaw is progressively shortening and deepening. The coronoid is stout, gently recurved, and relatively less elevated above the postcoronoid border than in *M. manteoceras* or *Brontops brachycephalus.*

The condyle is greatly extended transversely (106 mm.) and narrow anteroposteriorly (24 mm.), therefore exhibiting a rather sharply convex rotula, except on the inner side, where it exhibits a deep, vertically oval extension for articulation with the postglenoid process. The broadening and downward extension of this postglenoid facet on the inner side of the condyle is a striking progressive feature, which was probably acquired by all late Eocene and lower Oligocene titanotheres. The anterior border of the rotula extends nearly straight across, as in *Manteoceras* and probably also as in other phyla. The posterior border of the jaw arches gently forward below the condyle and then suddenly expands backward into the downward and backward produced angle.

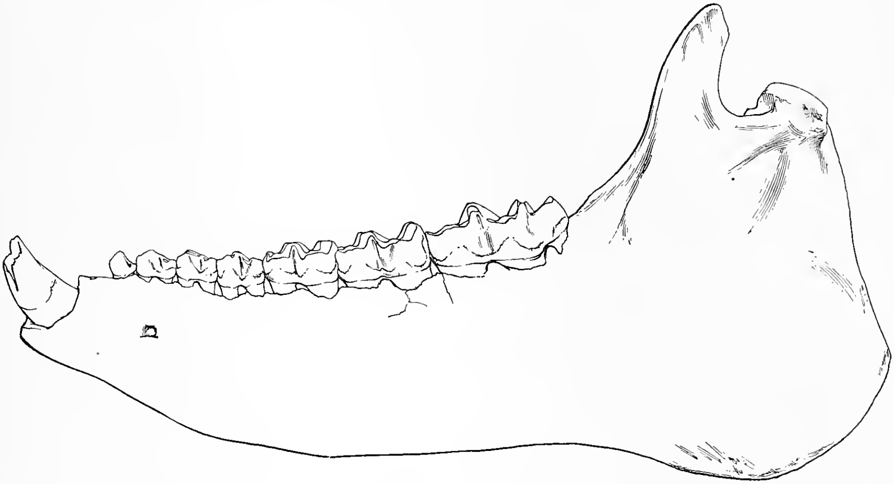

FIGURE 321.—Lower jaw of *Protitanotherium superbum*

One-fourth natural size. Am. Mus. 2501 (type), reversed; White River, Uinta Basin, Utah; Uinta C. The coronoid is somewhat altered by crushing.

Measurements of type lower jaws of Protitanotherium and Brachydiastematherium, in millimeters

	B. transilvanicum	P. emarginatum	P. superbum
I_3, anteroposterior	22	12	--------
I_3, transverse	20	12	--------
C, maximum anteroposterior diameter	38	32	32
C, maximum transverse diameter	31	28	31
C, height of crown	[a] 40	52	--------
Postcanine diastema, maximum	12	35	30
Postcanine diastema, minimum	3+	25	--------
P_1–p_4, anteroposterior	107	[a] 99	105
P_1, anteroposterior	18	16	--------
P_2, anteroposterior	26	25	28
P_2, transverse [b]	[a] 17	16	16
P_3, anteroposterior	31	27	28
P_3, transverse [b]	[a] 22	17	18
P_4, anteroposterior	38	30	33
P_4, transverse [b]	[a] 28	21	21
M_1, anteroposterior	50	46	52
M_1, transverse [b]	[a] 30	26	27

[a] Estimated. [b] Transverse measurements are made through anterior lobe.

TRANSITIONAL TITANOTHERES IN THE EOCENE OF EUROPE

Brachydiastematherium Böckh and Maty

Plate LXX; text figures 100, 315

[For original description and type references see p. 166]

Geologic horizon.—Recorded as lower Eocene, but more probably middle Eocene (Abel), upper Eocene (Osborn), or even lower Oligocene (Stehlin).

Generic and specific characters.—Brachycephalic. Size large, about that of *Protitanotherium superbum.* Dentition: $I_{\overline{3}}$, $C_{\overline{1}}$, $P_{\overline{4}}$, $M_{\overline{3}}$. Lower incisors large, heavily cingulate posteriorly, i_3 larger than i_2; postcanine diastema very short; canines stout, with short, heavily cingulate crowns; p_1 compressed, p_2–p_4 progressive, submolariform; premolar entoconids relatively well developed.

Brachydiastematherium transilvanicum Böckh and Maty

Materials.—The type species, *B. transilvanicum,* from Andrásháza, in Transylvania, Hungary, is represented by a fragmentary lower jaw. As shown by every detail of the dentition this animal was unquestionably a titanothere, much resembling *Protitanotherium,* and not, as its describers supposed, a relative of *Palaeotherium.*

Geologic age.—The age was originally recorded as lower Eocene, but it is probably upper Eocene. The question of the geologic age of this specimen is one of the most important in the chronology of the titanotheres. Pavay, its discoverer, as well as Böckh, its describer, and A. Koch, who studied the strata in which the type was found, assigned a lower Eocene age to the species, and their opinion was accepted by Depéret, who placed the genus among the upper Yprésien fauna, which is correlated by Osborn with the lower part of the middle Eocene Bridger of North America (Bridger B), which contains the relatively primitive *Palaeosyops paludosus.*

This animal was found in the same beds as *Prohyracodon orientale* Koch. In his monograph "Die Säugethiere des schweizerischen Eocäns" Stehlin (1903.1, p. 125, note) remarks: "Ich hege indess einen starken Verdacht, dieser *Prohyracodon* möchte, wie Koch selbst früher annahm, oligocänen und nicht mitteleocänen Alters sein." Schlosser (1901.1, p. 27) points out that *Prohyracodon* is not, as Koch had believed, a forerunner of *Hyracodon* but is closely related to the aceratheres (hornless rhinoceroses). Abel (1910.1, p. 24) appears to be doubtful as to the geologic age of *Prohyracodon* but considers it the most primitive of the European rhinoceroses, more primitive than *Meninatherium,* which is Aquitanian. From Abel's figure of *Prohyracodon* Matthew (letter, 1914) infers that it is of lower Oligocene or at most of upper Eocene age. It is closely allied, as Schlosser and Abel state, to the earlier Oligocene aceratheres, and it is much more progressive than *Hyrachyus* or *Amynodon. Brachydiastematherium* should therefore be considered of lower Oligocene or upper Eocene age.

Characters.—Every detail of the dentition shows that, as compared with the American titanotheres, *B. transilvanicum* is in an upper Eocene stage, closely similar to that of animals found in horizon C of the Uinta Basin. The indications are that titanotheres migrated from some northern center at about the same time into eastern Europe and into North America.

Brachydiastematherium agrees with the upper Eocene *Protitanotherium superbum* in general appearance and in the dimensions of p_1 to m_1. The canines have a peculiar very heavy curved internal posterior cingulum ridge, and the crown seems shorter and more recurved than in *P. superbum.* All the premolars appear to be in a slightly higher stage of evolution, and the pronounced external cingula are horizontal rather than festooned. The postcanine diastema is much shorter, an indication of a higher specialization.

From *P. emarginatum* this species differs not only in the more advanced evolution stage of the premolars and shape of the canine but apparently also in the fact that i_3 is the largest of the series, if Böckh and Maty's identification of this tooth as i_3 is correct. The incisors are also larger and more heavily cingulate posteriorly.

Brachydiastematherium differs from *Telmatherium altidens* especially in the obtuse shape of the canines and in the much more progressive p_1–p_4. The large size of the heavily cingulate incisors suggests, however, the possibility that the genus under consideration may rather be an offshoot of the *Telmatherium* than of the *Manteoceras-Protitanotherium* series. From *Sthenodectes incisivus,* which it resembles in having three very large incisors on each side of the jaw, *Brachydiastematherium* differs in the much more progressive evolution stage of the inferior premolars, p_2–p_4. Derivation from *Sthenodectes* or from a nearly related form is suggested by the general appearance of the incisors, canines, and grinding teeth.

The incisors of *B. transilvanicum,* with their broad posterior cingula, parallel those of the *Brontotherium* type among the American Oligocene phyla.

Brachydiastematherium is completely transitional between the Eocene and Oligocene titanotheres, in so far as it retains six large lower incisors of Eocene type in company with very progressive lower premolars of Oligocene type.

The measurements (estimated from the original illustrations) in comparison with those of the nearest American titanotheres show that the incisors, canines, and p_4 are all very large, the diastema very short, the grinders broad.

On the whole, the evidence indicates that *Brachydiastematherium* represents a distinct European phylum, which closely paralleled certain upper Eocene American titanotheres in many respects but was distinguished by the combination of three large lower incisors; heavy, blunt canines; very short diastema;

very progressive premolars; and broad molars. The skull was probably brachycephalic—that is, it had broad zygomata.

SUBFAMILY DOLICHORHININAE RIGGS

PHYLA AND RELATIONS

These Eocene titanotheres branch from the same ancestral stock as that of *Manteoceras*. Some are dolichocephalic, and some are mesaticephalic. The horn swellings are developed chiefly on the nasals, partly on the frontals. Facial region laterally compressed; elongate symphyseal union of premaxillaries; orbits prominent; infraorbital processes more or less prominent. First occurring (*Mesatirhinus*) on upper levels of the Bridger Basin (C and D) and lower level of the Washakie Basin (A), reaching a dolichocephalic climax (*Dolichorhinus*) in Washakie B and Uinta B 1 or terminating in dwarfed mesaticephalic forms (*Metarhinus*) and other collateral branches.

Following *Eometarhinus* of Bridger A, Huerfano B, the subfamily Dolichorhininae contains the following phyla or separate series:

1. *Mesatirhinus;* probably ancestral to *Dolichorhinus.*
2. *Dolichorhinus;* extremely dolichocephalic, becoming extinct.
3. *Metarhinus;* aberrant, small to dwarfed; broad nasals.
4. *Sphenocoelus;* little known, perhaps a branch of *Mesatirhinus.*

A closely related subfamily, Rhadinorhininae, contains

5. *Rhadinorhinus;* nasals short, pointed; possibly ancestral to Megaceropinae.

In their common ancestral characters these animals exhibit closer affinities to the *Manteoceras* phylum than to either the *Palaeosyops-Limnohyops* phylum or the *Telmatherium* phylum. They possess in common small canine tusks and rudimentary but progressively developing horns and thus do not appear to have been vigorous fighters, their relation to other animals doubtless being defensive rather than aggressive. They possess long and rather straight rows of grinding teeth, usually narrow, and the zygomatic arches are slender and not widely projected. They are thus readily distinguished from their broad-headed contemporaries, such as *Manteoceras.*

The known members of the series geologically are the two species of *Mesatirhinus* of Bridger C and D, each of which gives rise more or less directly to the extraordinarily large, long-headed *Dolichorhinus* of the upper beds of the Washakie Basin and the middle beds of the Uinta Basin. The known species of *Metarhinus* are confined to the sandstone of the fluviatile deposits of the Uinta Basin, a fact which suggests that they may have been small aquatic animals. At the other extreme stand the species of *Rhadinorhinus,* readily distinguished by short, pointed nasals and the absence of infraorbital shelves and exceptionally interesting because of their apparent resemblances to the great *Megacerops* phylum of the Oligocene.

A simple key to the skeletal characters of these middle and upper Eocene animals is as follows:

A. Nasals elongate, spreading laterally, decurved; prominent infraorbital processes (Dolichorhininae); face bent downward:
  1. *Mesatirhinus;* primitive, dolichocephalic, horns rudimentary, feet elongate.
  2. *Dolichorhinus;* progressive, hyperdolichocephalic, horns prominent, feet abbreviate.
  3. *Metarhinus;* mesaticephalic to subdolichocephalic, nasals expanding, dwarfed in size.
  4. *Sphenocoelus;* hyperdolichocephalic, basicranial pits.

B. Nasals abbreviate, pointed, no infraorbital shelves (Rhadinorhininae):
  5. *Rhadinorhinus;* dolichocephalic, facial region upturned.

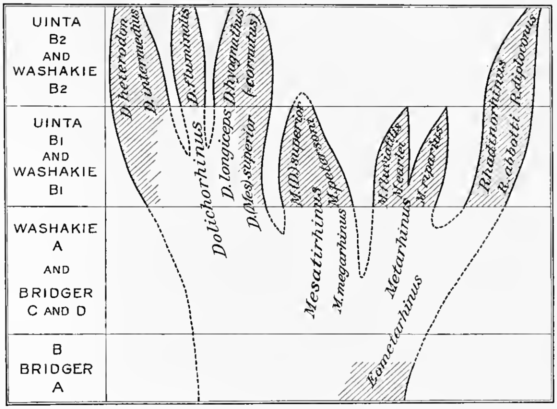

FIGURE 322.—Phylogenetic relations of the species of *Metarhinus, Mesatirhinus, Dolichorhinus,* and *Rhadinorhinus*

The author's theories (1919) as to the phylogenetic relations of these five phyla are expressed in Figure 322.

HISTORY OF DISCOVERY AND CLASSIFICATION

The separation of these five distinct phyla has been an extremely long and difficult undertaking, beginning with the work of Cope in 1872 and ending in 1919. Even now the position of *Sphenocoelus* and the relationship of *Rhadinorhinus* and *Megacerops* await elucidation. The chronologic record follows:

1872. Cope describes, under the name "*Palaeosyops vallidens,*" fragmentary upper and lower jaws from the Washakie Basin. This little-known species, probably from Washakie B, is now provisionally regarded as a primitive stage of *Dolichorhinus,* namely, *D. vallidens.*

1889. Scott and Osborn describe as "*Palaeosyops hyognathus*" a large lower jaw from Washakie B. This now proves to be *Dolichorhinus hyognathus.*

1891. Earle describes as "*Palaeosyops megarhinus*" a small skull from Washakie A, recognizing, however, its differences from the typical *Palaeosyops*. This is now known as *Mesatirhinus megarhinus*.

1894. Peterson explores horizon B 2 of the Uinta Basin and discovers a remarkable long-skulled form.

1895. This long-skulled form is described by Osborn as "*Telmatotherium cornutum*," which is now known to be a synonym of *Dolòchorhinus hyognathus*.

1895. Osborn also describes a smaller form from Uinta B 1 as "*Telmatotherium diploconum*." This is now known as *Rhadinorhinus diploconus*.

1895. Osborn also describes, from Uinta B 2, *Sphenocoelus uintensis*, a form that still remains problematical.

1895. Earle soon afterward points out the ancestral relationship of "*Palaeosyops megarhinus*" to "*Telmatotherium cornutum*," an affinity now recognized as that of *Mesatirhinus* to *Dolichorhinus*.

1895. Hatcher recognizes "*Telmatotherium cornutum*" as a new genus, namely, *Dolichorhinus*, possessing horns, but not directly ancestral to any of the Oligocene titanotheres.

1894–1906. American Museum explorers in the Bridger and Washakie Basins, under Peterson, Matthew, and Granger, bring together good material of the "*Palaeosyops megarhinus*" type.

1908. Osborn reviews the narrow-skulled or dolichorhine Eocene titanotheres with the following principal results:

(*a*) Hatcher's term *Dolichorhinus* is adopted, and *D. cornutus* is shown to be a synonym of *D. hyognathus*, both occurring in Washakie B. A new species, *Dolichorhinus intermedius*, is described.

(*b*) Earle's *Palaeosyops megarhinus* from Bridger B and Washakie A is made by Osborn the type of the new genus "*Mesatirhinus*," ancestral to *Dolichorhinus*. The new species *Mesatirhinus petersoni* is described from Bridger C.

(*c*) A related group, including small Eocene titanotheres with slender limbs and relatively short, narrow skulls, from Uinta B 1 and Washakie B, is recognized by Osborn as the distinct genus *Metarhinus*, including *M. fluviatilis*, *M. earlei*, and [?] *Telmatotherium diploconum*.

(*d*) The opinion is expressed that *Metarhinus* and *Dolichorhinus* represent the long-skulled form of the same stock that gave rise to the relatively broad-skulled *Manteoceras*.

1909. Douglas describes two new species of *Dolichorhinus* (*D. heterodon*, *D. longiceps*) from Uinta B 2.

1912. Riggs greatly extends our knowledge of the dolichorhines of Uinta B 1 and revises and expands the species *Metarhinus*, *Mesatirhinus*, and *Dolichorhinus*, establishing the new subfamily Dolichorhininae and basing the new genus *Rhadinorhinus* on the type *R. abbotti*, including also the "*Telmatotherium diploconum*" of Osborn.

1919. Osborn describes *Eometarhinus* from the upper part of the Huerfano formation, representing an extremely primitive ancestor of *Metarhinus*.

The original and the present determination of the synonymy of these species is thus as follows:

Palaeosyops vallidens = Dolichorhinus vallidens.
Palaeosyops hyognathus = Dolichorhinus hyognathus.
Palaeosyops megarhinus = Mesatirhinus megarhinus.
Telmatotherium cornutum = Dolichorhinus hyognathus.
Telmatotherium diploconum = Rhadinorhinus diploconus.

COMPARISON WITH MANTEOCERAS

There are in *Manteoceras*, *Mesatirhinus*, and *Dolichorhinus* resemblances which prove that these animals sprang from the same stock. They appear specially in the comparison of the skulls of *M. manteoceras* and *Mesatirhinus megarhinus;* in other words, the ancestral and atavistic characters of *Mesatirhinus* are those which it has in common with *Manteoceras*, among which are (1) preorbital concavities; (2) nasals long, decurved, truncate distally; (3) posterior nares compressed, or narrow space between the palatines and pterygoid plates; (4) zygomatic arches shallow; (5) occiput broadly depressed; (6) pit in the parietal vertex of the *Manteoceras* skull represented by a long slit in the *Mesatirhinus* skull; (7) angulation of the malars of *Manteoceras* represented by the suborbital shelf of *Mesatirhinus*. Their ancestral affinity to *Manteoceras* is also seen in (8) the position of the horns above the preorbital concavities; (9) the elongate form of the horn rudiments. There is a decided departure from the position of the horn rudiments of *Manteoceras* (Pl. XVII)—namely, in that in the Dolichorhininae the horn swelling is chiefly a protuberance of the nasal bones, whereas in *Manteoceras* the horn swellings are chiefly on the frontal bones, the nasofrontal suture of the dolichorhines being pushed back by the remarkable elongation of the nasals. (10) Another distinction is that in *Manteoceras* the horn swelling is decidedly in front of the orbit, whereas in *Mesatirhinus* it lies more directly above the orbit. Other differences appear in connection with the fact (11) that the face is relatively longer in the dolichorhines than in *Manteoceras*.

The face is relatively longer than in *Manteoceras*. Correlated with this is the fact that in *Metarhinus*, *Mesatirhinus*, and *Dolichorhinus* the grinders are farther forward with reference to the orbit than in *Manteoceras*—that is, in the members of these groups the postorbital process of the malar lies above the mesostyle of m^3, and in *Manteoceras* it lies above the parastyle of m^3. Similarly in *Dolichorhinus* the lacrimal lies above the mesostyle of m^2, in *Manteoceras* above the mesostyle of m^1. In *Dolichorhinus* this relation appears to spring as much or more from the backward displacement of the orbit (especially of its upper border) as from the forward displacement of the molar series. This oblique backward displacement of the orbit may have been correlated with the increased size of the nasofacial muscles, and with this factor may also have been correlated the hypertrophy of the posterior end of the nasals, the reduction of the anterior prong of the frontals, and exclusion of the frontals from the horn swelling.

The conclusion is that the dolichorhines sprang from the same stock as *Manteoceras* but that they diverged and radiated along lines of their own into persistent mesaticephalic and extreme dolichocephalic types.

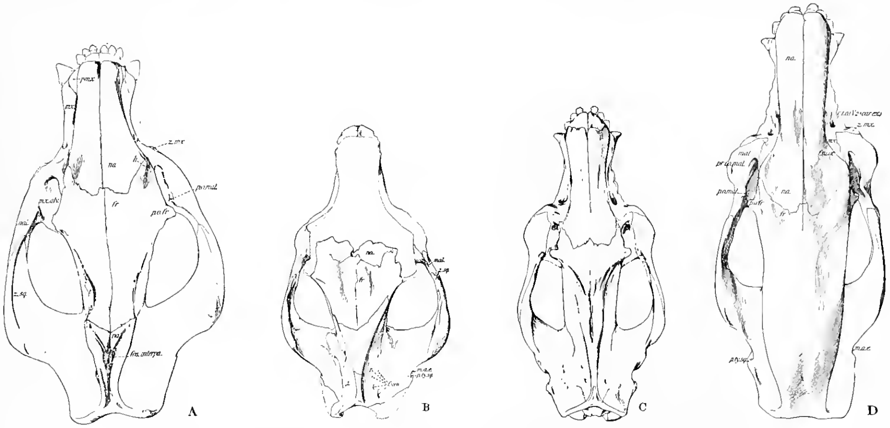

FIGURE 323.—Top view of the skull in the *Manteoceras-Dolichorhinus* group

One-eighth natural size. A, *Manteoceras manteoceras;* B, *Metarhinus earlei;* C, *Mesatirhinus petersoni;* D, *Dolichorhinus hyognathus.*

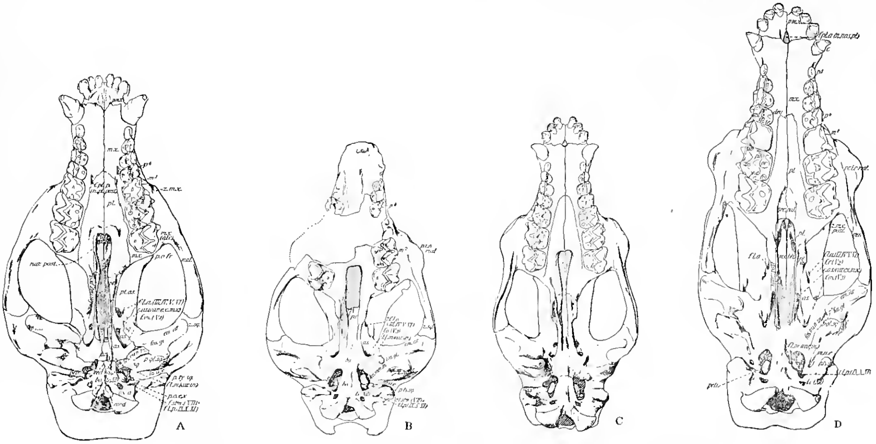

FIGURE 324.—Palatal views of the skull in the *Manteoceras-Dolichorhinus* group

One-eighth natural size. (See fig. 323.)

DOLICHOCEPHALY AND CYPTOCEPHALY IN THE MESATIRHINUS-DOLICHORHINUS PHYLUM

Elongation of the crowns of the grinding teeth, or subhypsodonty, generally characterizes the dolichorhines, from which we infer that they fed on harder kinds of food and may have adopted grazing as well as browsing habits. The members of the central dolichorhine phylum (*Mesatirhinus-Dolichorhinus*) afford the finest examples we have yet discovered, excepting only among the Equidae, of the changes in both skull and teeth which are correlated with progressive dolichocephaly, accompanied by progressive cyptocephaly,[27] or bending of the face downward on the cranial axis, as in many other grazing quadrupeds. Combined with this slowly acquired and only imperfectly attained cropping and grazing adaptation the cranium also converges toward the Oligocene titanothere type, as observed in the flattening of the top of the skull (*Dolichorhinus*), the rise of the horns (*Mesatirhinus, Dolichorhinus*), the incipient metamorphosis of the premolar and molar tooth

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[27] Cyptocephaly (κύπτω, κεφαλή) is a comparatively new term (first employed by Osborn as cytocephaly)

pattern (*Rhadinorhinus*). Yet so far as we know these long-headed animals of the *Mesatirhinus-Dolichorhinus* phylum were not destined to survive and give rise to any Oligocene titanothere but rather to terminate in an excessively specialized type.

CONVERGENCE OR KINSHIP CONTROL

These dolichorhines afford an illuminating illustration of kinship control in the simultaneous evolution of different character groups. Some of these character groups are predetermined or controlled by ordinal, others by family, others by generic affinities with related titanotheres. The general expression of kinship control may be summarized as follows:

1. Perissodactyl or ordinal kinship is shown, among other characters, in the independent progressive complication of the premolar-molar teeth, three of the premolars tending to acquire the pattern of the molars, although this pattern is less perfectly developed in other Perissodactyla.

2. Titanothere family kinship is indicated in the independent progression of the development of nasofrontal horns, the flattening of the top of the cranium, the obliteration of the sutures on the top of the cranium, and the elongation of the middle portion of the cranium.

FIGURE 325.—Leidy's cotypes of *Palaeosyops* (=*Mesatirhinus*) *junius*

Natural size. Crown view of premolar and molar in the museum of the Acad. Nat. Sci. Philadelphia. Bridger (?)B; level doubtful. A, Right fourth lower premolar; B, posterior part of third lower molar.

3. The subfamily kinship to the Manteoceratinae is indicated in the persistent subtriangular shape of the horns, in the development of an infraorbital shelf, and in the contracted posterior nares and broadening nasals.

In their progressive dolichocephaly, a tendency that strongly affects the middle region of the skull between the orbits and the auditory meatus, these animals (*Mesatirhinus-Dolichorhinus*) are partly independent of their subfamily, family, or ordinal relations and follow an extreme adaptive direction of their own in the elongation of the midcranial region and of the teeth.

In this special adaptation to their partial grazing habits the dolichorhines further parallel certain of the Equidae and other grazing animals, such as the cattle, in their cyptocephaly. (See figs. 213, 214.) The incisor teeth further acquire deep posterior pits, or pockets, analogous to the pits that are developed in the incisors of the upper Oligocene Equidae and that tend to become typical cropping teeth.

DIVERGENT OR INDEPENDENT EVOLUTION OF CHARACTER GROUPS IN THE DOLICHORHINES

The independent evolution of these four or five groups of characters as observed in the skull alone obviously affords only a partial picture of the play and interaction between the vast number of contemporaneous processes that are involved in the evolution of the members of this phylum. If we could similarly compare all parts of the vertebral column and of the limbs, we should probably discover many additional illustrations of this law of the evolution of groups of characters under the influence partly of kinship and partly of independent adaptation.

The principle of independence or divergence is well illustrated in the skull. In Figure 302 the skulls of *Manteoceras* and the *Mesatirhinus* group are compared as seen from the side. The palatal view of *Manteoceras*, *Metarhinus*, *Mesatirhinus*, and *Dolichorhinus* (fig. 324) brings out the resemblances and contrasts between these four forms. The superior view (fig. 323) also brings out the wide progressive divergences between these undoubtedly related forms.

We may also compare superior views (Pl. LXXX) of the skulls of *Metarhinus* and *Rhadinorhinus*, showing how the latter departs from the other members of this dolichorhine group in the abbreviation and pointing of the nasals and in the reduction of the infraorbital processes.

PROGRESSIVE DOLICHOCEPHALY IN MESATIRHINUS-DOLICHORHINUS

The dolichocephaly, which is the chief progressive character of the *Mesatirhinus-Dolichorhinus* phylum, is beautifully illustrated in the accompanying series of illustrations (figs. 339, 340).

A very important fact (see the following table) is brought out by the cranial indices and ratios in this series of species—namely, that while the skulls lengthen and become relatively narrower, the facial portion is not relatively abbreviated as it is in the *Manteoceras* phylum, because the faciocephalic index is the same in the terminal member of the series, *D. hyognathus*, as in *M. megarhinus*, the most primitive member of the series. In other words, in *Manteoceras* the face is abbreviated; in the dolichorhines it is not.

Cranial indices of Mesatirhinus and Dolichorhinus

	Cephalic index	Faciocephalic index	Molar-cephalic index
M. megarhinus	56–59	48	41
M. petersoni	51–52	48	39
D. superior	52	48	38
D. longiceps	[a] 47	49	35–37
D. intermedius	41–45	49	----------
D. hyognathus (=cornutus)	43–46	51–53	38
D. fluminalis	45	48	36

[a] Estimated.

In other words, while the ratio of breadth to length falls from 59 to 45 per cent, the ratio of the length of the face to the entire length of the cranium, or faciocephalic index, remains at 48. This is a very important distinction, because progressive abbreviation of the face is characteristic of all the true Oligocene titanotheres correlated with dolichocephaly but is not found in these dolichorines. We observe other correlated dolichocephalic changes in the skull—namely, (1) the occipital condyles are set broadly apart; (2) the external auditory meatus becomes widely open; (3) wide spaces arise between the cranial foramina; (4) the horn rudiments rise chiefly on the nasals and less on the frontals; (5) the nasals have a long exposure on the top of the skull; (6) there are correlated changes in the teeth.

The teeth also show the following correlations with doliochocephaly: (1) The opposite molar-premolar series become parallel; (2) the palate is narrowed, elongated, and arched; (3) the individual molar teeth are elongated or laterally compressed; (4) the premaxillary and mandibular symphyses become greatly elongated; (5) the jaws become long and slender, and there is an increasing distance between m_3 and the posterior border of the jaw, the coronoid becoming relatively low and backwardly recurved, its anterior edge oblique rather than transverse, and the chin shallow and sloping (hence the term *hyognathus*, or hog-jawed, applied by Scott and Osborn); (6) similarly the inferior molars become elongate; (7) the whole upper tooth row shifts forward with reference to the orbit.

The recently discovered *Eometarhinus* is described on pages 200, 419, 420.

Mesatirhinus Osborn

Plates XVII, L, LXXI, LXXII; text figures 26, 27, 33, 122, 211, 217, 219, 255, 302, 327–331, 333, 339–341, 483, 511–514, 516, 520–523, 526, 558, 559, 562–571, 586, 647, 656, 661, 686, 702, 713, 716, 724, 745

[For original description and type references see p. 182. For skeletal characters see p. 636]

Geologic horizon.—Bridger C and D and Washakie A.

Generic characters.—Middle Eocene titanotheres of small but increasing size; basilar length, 354–485 millimeters. Mesaticephaly progressing to dolichocephaly. Horns incipient, borne chiefly on the nasals; prominent infraorbital malar shelf; nasals elongate, laterally recurved; cranium profile convex; face deflected; sagittal crest gradually broadening; no secondary palate. Humerus short; tibia relatively long; carpus and tarsus narrow; astragalus with elongate neck; metapodials relatively elongate.

Geologic distribution.—There is the *Eometarhinus* of Huerfano B (Bridger A), and the *Mesatirhinus junius* of Bridger B. In Bridger C and D, also in Washakie A, there first appears a rich array of small titanotheres, which are readily distinguished from the contemporary species of *Palaeosyops*, *Telmatherium*, and *Manteoceras* by the generic characters enumerated above. These animals are related on the one side to *Metarhinus* and on the other, by progressive changes, to *Dolichorhinus*, and the phylum is therefore regarded as central. The phylum is divided into the smaller, more primitive species *Mesatirhinus megarhinus* and the partly contemporaneous, more progressive species *M. petersoni*. These species are contemporaneous in Bridger C 5, and both animals are found in Washakie A, which is evidence that they are contemporaneous and not successive species. At the summit of Uinta B 1 occurs the larger and more progressive "*Mesatirhinus*" *superior*, with partly flattened cranium. This animal is here referred to *Dolichorhinus*.

In the Uinta region *Metarhinus* is so abundant in the fluviatile sandstones of Uinta B 1 that the horizon is named the *Metarhinus* zone. The animals disappear at the summit of this zone in the "*Metarhinus* sandstones."

The synopsis of these species is as follows:

Mesatirhinus junius (Leidy)?, Bridger B, a diminutive animal. (See fig. 325.)

Mesatirhinus megarhinus (Earle), Bridger C and Washakie A. Skull small (about 354 by 170 mm.); cephalic index, about 53; faciocephalic index, 48; palatal crests narrow; nasofrontal horns incipient; premolars in less advanced stage.

Mesatirhinus petersoni Osborn, Bridger C and D and Washakie A. Skull of intermediate size (about 425 by 205 mm.); cephalic index, 49; parietal crest narrow; faciocephalic index, 48; premolars in more advanced stage.

Mesatirhinus (*Dolichorhinus*) *superior* Riggs, summit of Uinta B 1. Skull larger (485 by 240 mm.); cephalic index, 52; faciocephalic index, 48; parietal crest spreading; cranium flattened on top.

It is important to note that although these three species succeed each other progressively and this progression leads directly to *Dolichorhinus*, there is no proof of direct phyletic succession.

Measurements of Mesatirhinus megarhinus, M. petersoni, Dolichorhinus superior, and Metarhinus fluviatilis, in millimeters

	M. megarhinus				M. petersoni				D. superior, Field Mus. 12188 (type)	M. fluviatilis, Am. Mus. 1500 (type)
	Princeton Mus. 10008 (type)	Am. Mus. 1514	Am. Mus. 12202	Am. Mus. 1523	Am. Mus. 1571	Am. Mus. 1509	Am. Mus. 1556	Am. Mus. 12184 (type)		
Pmx–condyles	[a]354					[a]402		[a]425	485	[a]355
Mx–condyles			342			386				
Transverse, infraorbital, malar	[a]180		[a]180				183	205		[a]180
Transverse, zygomata			210				[a]212	[a]220	[a]255	[a]200
Transverse, condyle			92						89	
Face	[a]170					[a]195	205	[a]205	250	[a]170
Cranium			202			223				[a]190
Nasal–postorbital frontal process	168					178	190	195		
P^1–m^3	147	140	147	147	156	157	156	154	184	146
P^2–m^3		125	132	132	139	140	141	138		130
M^1–m^3	[a]77	80	83	82	89	91	90	87	105	85
P^4, ap	16	16	17	17	18	19	18	18		17
P^4, tr		22	22	22	23	23	23			23

[a] Estimated.

10008. Washakie Basin.
1514. Washakie A.
12202. Bridger C 5.
1523. Bridger C or D.
1571. Washakie A.
1509. Bridger D.
1556. Bridger D.
12184. Bridger D 3.
12188. Uinta B 1.
1500. Uinta B 1.

The figures show that *M. petersoni,* most specimens of which are from the higher levels of Bridger D, is considerably larger in all measurements than *M. megarhinus.* Both are much larger than the type of *Metarhinus fluviatilis* from Uinta B 1.

Mesatirhinus junius (Leidy)

Text figures 91, 325

[For original description and type references see p. 159]

Type locality and geologic horizon.—The type lower molar of *M. junius,* according to Leidy's description, was found near Fort Bridger, Wyo., at a geologic level that Granger places in Bridger B. If this geologic level is correct *M. junius* is the oldest known species in the *Mesatirhinus* phylum. Its geologic age must, however, be regarded as indeterminate.

Specific characters.—A doubtfully referred specimen, imperfectly known. M^1–m^3, 69 millimeters. A diminutive *Mesatirhinus* or *Metarhinus.*

Materials.—The type specimen (Acad. Nat. Sci. Philadelphia) is very fragmentary. The only other material that may be referred even provisionally to this species is a diminutive set of teeth, including m^1 to m^3 (Am. Mus. 12686), from level D 5 of the Bridger. The teeth present generic resemblances to those of *Mesatirhinus megarhinus* but are far smaller than in any known upper Bridger, Washakie, or Uinta titanothere, m^1–m^3 measuring only 69 millimeters, as against 85 in *Metarhinus fluviatilis.* The teeth are less hypsodont than in allied species; m^1 is relatively very small and m^3 very quadrate. A comparison of the lower molar with the type m_3 of *Palaeosyops junius* Leidy leaves the specific identity doubtful. The comparative measurements are as follows:

Measurements of teeth of species of Mesatirhinus, in millimeters

	M. junius?, Am. Mus. 12686; Bridger D 5	M. megarhinus, Am. Mus. 12202; Bridger C 5	M. fluviatilis, Am. Mus. 1500 (type); Uinta B 1	M. petersoni, Am. Mus. 1556; Bridger D	M. petersoni, Am. Mus. 1512; Bridger D
M_1–m_3	69	83	85	90	
M_1, ap	21		23	26	
M_1, tr	22			27	
M_3, ap	36				46

Mesatirhinus megarhinus (Earle)

Plate LXXII; text figures 106, 217, 324, 326, 328, 330, 331, 508, 510, 558, 560, 561, 685, 737

[For original description and type references see p. 170. For skeletal characters see p. 637]

Type locality and geologic horizon.—Washakie Basin, Wyo.; probably Washakie A. The species is also recorded from Bridger Basin, Wyo., *Uintatherium-Manteoceras-Mesatirhinus* zone, level Bridger C (=Washakie A).

Specific characters.—P^1–m^3, 140–147 millimeters; true molars, 77–83. Cephalic index, 56–59. Cranial length, premaxillaries to condyles, 354 millimeters (estimated); facial region rather short (about 170 mm.); faciocephalic index 48 (estimated); occipital condyles broad; premaxillary symphysis short; infraorbital shelf prominent. Tetartocones on p^3, p^4 very rudimentary. Nasofrontal horns incipient.

Materials.—The type (Princeton Mus. 10008) is badly preserved and unfortunately lacks the occipital condyles, which appear to be relatively broader in *Mesatirhinus* than in *Dolichorhinus.* The geologic level of the type is not definitely recorded, but is probably Washakie A.

The material in the American Museum referred to this species includes the following: From the Bridger Basin, skull, No. 12202 (level C 5); palates, Nos. 12206 (level C 5), 1519, 1523 (level unknown); lower jaws, Nos. 1520, 1551, 12207 (level C 5), 12199 (level C 5); from the Washakie Basin (level A), palates, Nos. 1513, 1514; lower jaws, Nos. 1575, 1577.

Mesatirhinus petersoni Osborn

Plates L, LXXI, LXXII; text figures 26, 27, 33, 122, 211, 217, 219, 255, 302, 327–331, 333, 339–341, 483, 511–514, 516, 520–523, 526, 558, 559, 562–571, 586, 647, 656, 661, 686, 702, 713, 716, 724, 745

[For original description and type references see p. 182. For skeletal characters see p. 641]

Type locality and geologic horizon.—Cattail Springs, Bridger Basin, Wyo.; *Uintatherium-Manteoceras-Mesatirhinus* zone (Bridger), level D 3. Also recorded from Bridger C (?) and Washakie A.

Specific characters.—P^1–m^3, 154–157 millimeters; true molars 87–90. Skull length, premaxillaries to condyles (estimated), 402–425 millimeters; cephalic index, 51–52; preorbital facial region (estimated), 195–205 millimeters; faciocephalic index 48. Other characters as in *M. megarhinus*—that is, broad occipital condyles, infraorbital shelf, etc.

Materials.—The type skull (Am. Mus. 12184) is from Bridger D 3 (fig. 327). Comparison of this animal with the type of *M. megarhinus* can leave no doubt that we have to do here with a more advanced stage of evolution. The skull is longer, the preorbital region especially. The grinding teeth occupy more space, and there is an average advance in all the premolar rectigradations, which prove that these differences in form and size are not merely due to fluctuations of size or differences of sex.

Other specimens (in the American Museum except as noted) referred to this species are, from the Bridger, skulls Nos. 1509 (level D) and 1556 (level D; now in British Museum), lower jaw No. 1567, lower jaw No. 12191 (level C 2); from Washakie A, skull No. 1571 and lower jaws Nos. 1512, 13178.

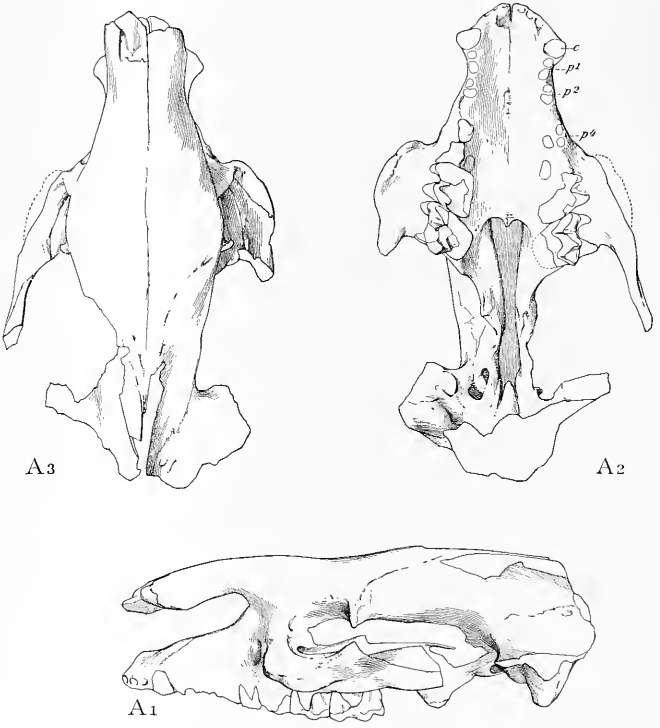

FIGURE 326.—Type skull of *Mesatirhinus megarhinus*

One-fourth natural size. Princeton Mus. 10008, Washakie Basin, Wyo., level Washakie A?. A_1, Side view (reversed); A_2, palatal view; A_3, top view.

Of these No. 1571, from Washakie A, fortunately has associated with it the fore foot, radius, ulna, astragalus, and pelvis. Another valuable skeleton (Am. Mus. 11659) is recorded from Bridger C 5, and a well-preserved forearm and manus in the Princeton Museum (No. 10013) came from Bridger C or D of Henrys Fork, Wyo.

From Washakie A comes a very progressive dolichocephalic specimen (Am. Mus. 1651) consisting of the three upper molars, which are strongly compressed laterally and measure collectively 96 millimeters. This specimen is provisionally referred to this species and appears to be an important and interesting transitional form leading into *Dolichorhinus.*

General characters of Mesatirhinus megarhinus and M. petersoni.—It is impracticable to describe *M. megarhinus* and *M. petersoni* separately, because it would involve duplication of description.

Sexual characters: Unfortunately the imperfect preservation of the canine teeth does not admit of the sharp separation of males and females that is possible for many of the series of skulls. Comparison of the teeth in the more perfectly preserved jaws, however, shows that the canines were decidedly smaller in the females than in the males.

Cranial elongation with age: There is considerable evidence that cranial elongation is not only a progressive but an age character—that is, one which appears in advanced years and through the "law of acceleration" will appear in earlier years of subsequent generations. For example, the space between the glenoid fossa and m^3 elongates with age, and correlated with it is the elongation of the ramus of the jaw between m_3, the anterior border of the coronoid process, and the condyle.

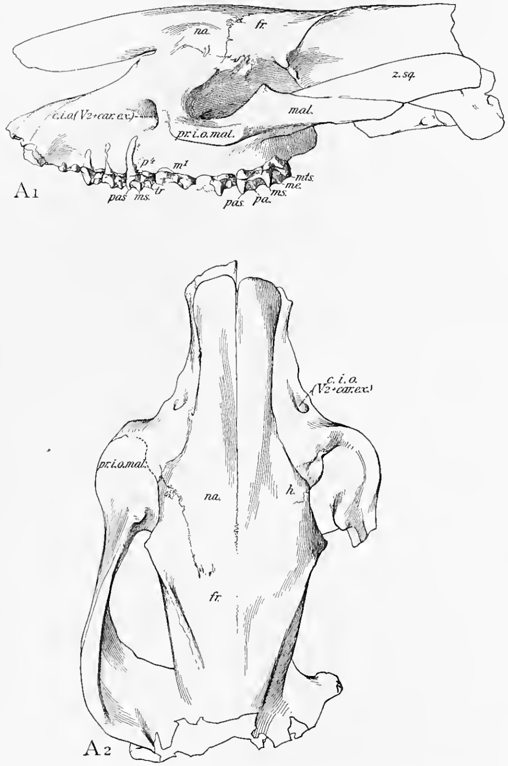

FIGURE 327.—Type skull of *Mesatirhinus petersoni*

One-fourth natural size. Am. Mus. 12184, Cattail Springs, Bridger Basin, Wyo., Bridger D 3. A1, Side view; A2, top view.

Skull.—The general characters of the skull are as follows: (1) Skull as a whole elongate, with considerable space between the glenoid process and the occipital condyles, leaving the auditory meatus open, as contrasted with the contemporary *Palaeosyops*, in which this space is abbreviated; (2) zygomatic arches relatively straight, slender, and gently arched outward; (3) on the malars an infraorbital shelf, which apparently increases progressively; (4) sagittal crest sessile and narrow as compared with *Limnohyops laticeps*; (5) nasals long, expanding and decurved distally; (6) premaxillary symphysis more abbreviate than in *Telmatherium*; (7) face moderately bent upon cranium, parietals convex in side view; (8) postorbital process of malar above posterior part of m^3. On comparing the side views of *Telmatherium cultridens* and of *Mesatirhinus petersoni* we see that in the former the premaxillary is stouter, vertically deeper anteriorly, and extends posteriorly farther up on the maxillary. In *T. ultimum* this is much more pronounced. In *Mesatirhinus*, in correlation with the smaller incisors and more slender maxilla, the premaxillary is shallower vertically, and the symphyseal surface is more delicate.

The skull of members of *Mesatirhinus petersoni* exhibits many marks of general affinity to those of their collateral relative *Manteoceras manteoceras*. Among these are (1) the shape of the symphyseal union of the premaxillaries; (2) the narrowing of the postnarial space between the pterygoids; (3) the sutural relations of the nasals, frontals, maxillaries, malars, and lacrimals, as seen in side view, with the exception of the position of the horn rudiment; (4) the concavities at the side of the face slightly above and in front of the orbits; (5) just above these concavities the prominent convexities of the nasals at their junction with the frontals above the orbits, extremely interesting as a very early stage of horn evolution and prophetic of the distinct horn base of *Dolichorhinus;* (6) presence of a long and narrow pit in the anterior portion of the sagittal crest.

Among the most significant resemblances to *Manteoceras* are also the similarity in the base of the cranium; the slender zygomata, constricted back of the orbit; and the underlying similarity in the dentition in spite of differences of proportion.

The skull differs markedly from that of *Manteoceras*, however, in the presence of infraorbital shelves and in its greater dolichocephaly. It also differs from *Manteoceras* in the shape of the occiput, shape of the skull top, and especially in the dentition. Its closer affinities, therefore, are with *Dolichorhinus*.

The detailed characters of the teeth exhibit a direct dolichocephalic adaptation of those of the *Manteoceras* type. The community of type, again, is due to a community of ancestry, the two lines running together perhaps prior to Wind River and Huerfano time.

More in detail: The superior view of the skull (fig. 328) exhibits the characteristic anterior expansion of the nasals, which measure transversely (Am. Mus. 1556, *M. petersoni*) anterior region 59 millimeters, mid-region 43, posterior region 84; the total length is 167. The nasals are separate anteriorly but firmly coalesced posteriorly; the lateral convexity just in front of their junction with the frontals (figs. 327, 328) represents the rudimentary stage in the evolution of the horn. The frontals are expanded above the orbits (91 mm., tr.), gradually contract posteriorly, and are bounded by the prominent supratemporal crests, which arise from the postorbital processes and in some adult individuals converge in the form of two broadly convex ridges into the short and narrow sagittal crest (10 mm.). Between these ridges there is a median depression. The suture between the frontals and parietals can apparently be made out in the Princeton skull (No. 10041, *Mesatirhinus petersoni?*). The parietals are best observed in the same skull and in Am. Mus. 1509 (*M. petersoni*). In the superior view of the skull as figured we observe also the short symphyseal union (42 mm.) between the premaxillaries (much more abbreviate than in *Dolichorhinus*), the prominent infraorbital shelf on the malars, and the slender section of the zygomatic arches.

In the inferior view of the skull of *M. petersoni* (fig. 328) we observe the converging incisive borders of the premaxillaries, the relatively narrow and transversely arched palate, which measures 152 millimeters from the incisive foramen to the posterior nares. The palatal portion of the palatines measures 70 millimeters in the midline and converges anteriorly; on either side of the posterior nares the convex inner surfaces of the palatines converge, and on the inner side of the narrowest portion of this postnarial space are placed the slender pterygoids, which are well defined. The conformation of this entire region is very characteristic of this genus as well as of *M. manteoceras*. The basioccipital region is best exhibited in the Princeton skull (No. 10041, *M. petersoni*), a very distinctive feature being the wide separation (28 mm.) by a plate of bone of the foramen ovale and foramen lacerum medium, the same plate measuring but 17 millimeters in the contemporary *Limnohyops laticeps*. The conformation of this important region of the skull, as well shown in Figure 333, includes the following noteworthy features: (1) The deep groove extending backward and inward on the inner side of the postglenoid facets, believed to have lodged an extension of the meniscal cartilage, as in the horse; (2) the prominent basioccipital and basisphenoid; (3) the narrow bridge of bone between the foramen condylare and the foramen lacerum posterius; (4) the continuity of the foramen lacerum medium and foramen lacerum posterius; (5) the peculiar inward extensions of the condylar facets; (6) the general elongation of the basicranial axis; (7) the open nature of the auditory meatus.

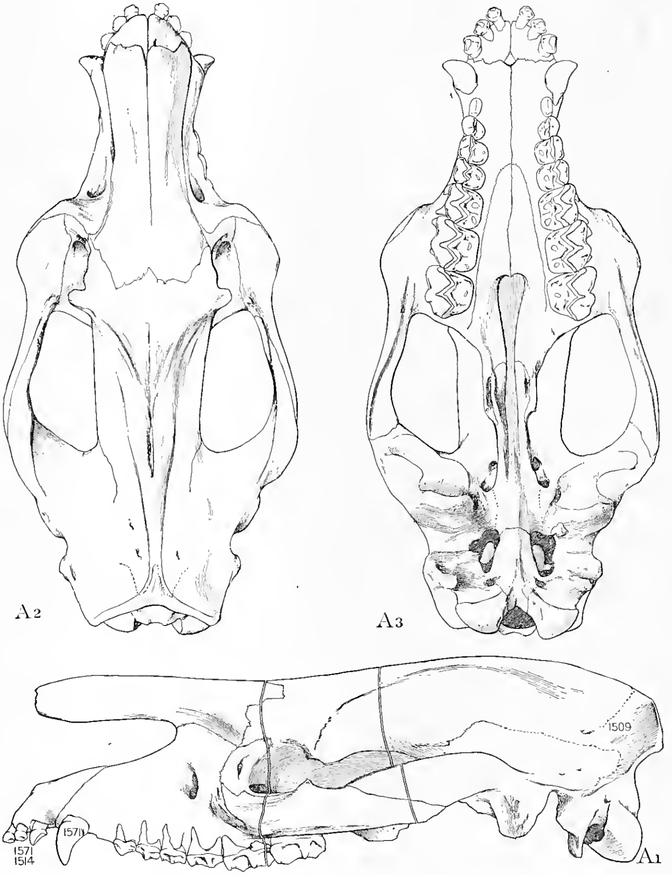

FIGURE 328.—Skull of *Mesatirhinus petersoni*

One-fourth natural size. A1, Side view (reversed); British Mus. (formerly Am. Mus. 1556), Big Bone Mountain, Henrys Fork, Bridger Basin, Wyo., Bridger D; occipital region restored from Am. Mus. 1509, Big Bone Mountain, Henrys Fork, Bridger Basin, upper Bridger; and Princeton Mus. 10041; incisors and canines from Am. Mus. 1571, Washakie Basin. A2, Top view; occipital region from Princeton Mus. 10041. A3, Palatal view; details of pterygoid region from Am. Mus. 1509 (see above); incisors from Am. Mus. 1571 (see above) and 1514 (*M. megarhinus*), La Clede Meadows, Washakie Basin; suture between basioccipital and exoccipital from Am. Mus. 12202 (*M. megarhinus*), Summers Dry Creek, Bridger Basin, Bridger C 5, lower level.

In the lateral view of the skull of *M. petersoni* (figs. 327, 328), we observe especially the horizontal suture connecting the maxillaries with the nasals, the lateral compression of the sides of the face at this point, the rudimentary horn convexities of the nasals, the scalelike overlap of the nasals by the frontals, the participation of the maxillaries in the anterior portion of the infraorbital shelf, the vertical extension of the lacrimals, the postorbital processes on the frontals and malars, the slender malar portion of the zygomatic arch, the comparatively slight upward curvature of the squamosal portion of the zygoma, the incipient arching of the parietal region, the greatly elongate and not deeply vertical temporal fossa, the wide space between the postglenoid and post-tympanic processes, the relations of the frontals, parietals, occipitals, and squamosals, and the formation of the temporal fossa.

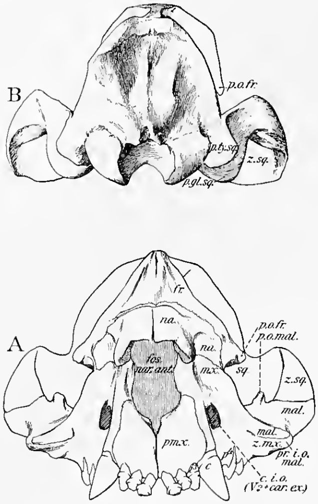

FIGURE 329.—Skulls of *Mesatirhinus petersoni*

One-fourth natural size. A, Front view of skull in British Museum (formerly Am. Mus. 1556); Big Bone Mountain, Henrys Fork, Bridger Basin, Wyo., upper Bridger, level D. B, Occipital view of Am. Mus. 1509; Big Bone Mountain, Henrys Fork, Bridger Basin, upper Bridger, level D.

The occiput is relatively broad and low, measuring (Princeton Mus. 10041, *M. petersoni?*) 107 millimeters transversely by 85 vertically. There is a deep depression in the superior portion of the occiput; the occipital condyles are widely divergent superiorly on either side of the foramen magnum.

The anterior view of the skull of *M. petersoni* (fig. 329, A) best illustrates the characteristic form and symphyseal junction of the premaxillaries, the stout lateral decurvature of the nasals, and the postero-lateral horn rudiments on these bones.

Dentition; influence of dolichocephaly.—In general the teeth show the dolichocephalic tendency, although they have not reached the extreme of elongation seen in the species of *Dolichorhinus;* they also are to be contrasted with those of the more mesaticephalic *M. manteoceras.* Thus it may be noted that *Manteoceras* and *Mesatirhinus* are separated by strong differences in the premolars and also in the molars. The premolars of *Mesatirhinus* are distinguished from those of *Manteoceras* as follows: (*a*) They are relatively longer as compared with their width; (*b*) in crown view p^2–p^4 appear more circular than in *Manteoceras* in consequence of the deuterocones being farther forward and the postero-internal part of the crown more evenly rounded out; (*c*) the tritocones are, on the whole, relatively larger and flatter externally; (*d*) the external cingula are better defined opposite the tritocone; (*e*) the protocone ribs on the ectoloph are more pronounced and narrowed; (*f*) the protoconules and tetartocones are better developed. Between typical members of *M. megarhinus* and *M. petersoni* the differences are of a progressive character—that is, in *M. petersoni* the deuterocones and tritocones are larger, the tetartocones and ectoloph ribs are much more pronounced.

Incisors.—The superior incisors (fig. 330) are arranged to form a forward-pointed arch—that is, the opposite series are less parallel to each other than in *T. cultridens* and less transverse in position than in *Palaeosyops.* The series is short-crowned, with convex anterior and convexo-concave posterior faces; the posterior cingulum foreshadows the marked development of the cingulum in *Dolichorhinus.* A noteworthy character is that i^3 is less caniniform than in *Telmatherium.*

Canines.—The canines are subround in section rather than laterally compressed as in *Telmatherium.* The enameled crown area measures vertically 36 millimeters and in base diameter 18 millimeters in certain specimens of *M. petersoni.* In the smaller specimens of *M. megarhinus* the crown measures 26 millimeters in length. The inferior canines (Am. Mus. 1576, 1575) are more slender and rounder toward the tip, with more feebly indicated anterior and posterior

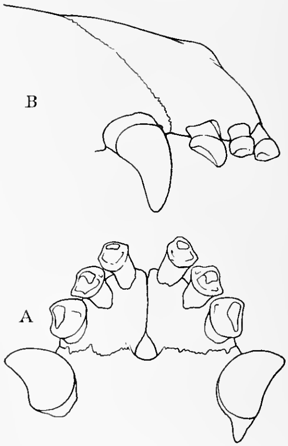

FIGURE 330.—Incisors, canines, and premaxillae of *Mesatirhinus*

One-half natural size. A, Crown view of *M. megarhinus*, Am. Mus. 1514, La Clede Meadows, Washakie Basin, Wyo.; B, side view of *M. petersoni*, Am. Mus. 1571, Washakie Basin.

ridges, a feature which at once distinguishes them from the lower canines of *T. cultridens*, in which these ridges are prominently marked.

Premolars.—The superior premolars especially exhibit the progressive rectigradations in the new cuspules, which, as well as the progressive changes of proportion, are subject to slight fluctuations. In the more advanced American Museum specimens (*M. petersoni*) the first superior premolar is separated from the canine by a narrow diastema, whereas in the less advanced Princeton Museum type of *M. megarhinus*, which represents a less dolichocephalic stage, it is in actual contact with the canine. The detailed characters are as follows: P^1 is bifanged, with a simple protocone, strongly compressed laterally, in which the proportions are typically 14 millimeters anteroposterior by 9 transverse; in the more progressive specimens (*M. petersoni*) the tritocone (a rectigradation) is seen as a rudimentary swelling of the posterior base of the crown, which is less conspicuous in *M. megarhinus*. P^2 is a highly characteristic tooth, suboval or slightly compressed transversely, the proportions (ap. by tr.) varying in different specimens from 15 by 13 to 16 by 16 millimeters; the proportions of this tooth are those correlated with mesaticephaly progressing into dolichocephaly; it is typically tricuspidate (protocone, deuterocone, tritocone); a generic feature is the excess of the large conic protocone over the small, externally flattened tritocone; the ectoloph is slightly cingulate (*M. petersoni*) but lacks the strongly accented cingulum around the base of the tritocone seen in *T. cultridens* and *T. validum*. P^3 is naturally a more progressive tooth, the breadth exceeding the length (ap. 14 millimeters, tr. 18, *M. megarhinus;* ap. 17, tr. 20, *M. petersoni*), the tritocone and protocone components of the ectoloph being more subequal, the basal external cingulum opposite the tritocone being more accented, and the deuterocone being more directly internal in position. P^4 still further marks this progression toward the molar type in its dimensions—17 by 22 millimeters (ap. by tr.) in *M. megarhinus*, as compared with 18 by 24 in *M. petersoni*. The external cingulum, varying in both species, is either partially indicated (Am. Mus. 1523, 1571) or extends across the outer face of the crown (Am. Mus. 1514, 1556); the less progressive individuals (Am. Mus. 1523, 1513, *M. megarhinus*) pass into more progressive stages (Am. Mus. 1556, 1509, *M. petersoni*) in which a faint rudiment of the protoconule is observed in p^2, p^3, and in Am. Mus. 1556 (*M. petersoni*) even a faint elevation of the tetartocone is observed (a rectigradation). Similarly the convex external rib of the protocone becomes more marked.

In comparing the premolar series in all these specimens it is seen that the external cingulum exceptionally almost or quite embraces the ectoloph, but that the internal cingulum never completely embraces the deuterocone, as in the type of *Metarhinus fluviatilis*. The premolar cingula are on the whole as progressive or more progressive than those of *T. cultridens* and *D. vallidens*. Another important progression is seen in the premolar ectolophs—namely, in certain specimens, Am. Mus. 1556, 1509 (*M. petersoni*) the tritocone ectoloph is flat, as in *D. vallidens* (Cope), whereas in other specimens, Am. Mus. 1571 (*M. petersoni*), 1513 (*M. megarhinus*), 12184 (type of *M. petersoni*), the tritocone ectoloph is more conic, as in *M. manteoceras*.

Comparative measurements of the superior premolars are given in the table on page 388.

The inferior premolars are more or less perfectly represented in six jaws in the American Museum collection, none of which, however, are certainly associated with skulls. P_1 is a small, conic or slightly flattened tooth, separated from the canine by a diastema 8 to 12 millimeters in length; a slight diastema (4 mm.) also separates it from p_2; p_1 is a typically single, rarely bifanged tooth, with a narrow, laterally compressed, recurved, pointed crown (9 by 6 mm.). P_2 is a bilobed tooth and elongate, but relatively less so than in *T. cultridens*—in fact, it is slightly more progressive than in that species; the typical measurements are 18 millimeters anteroposterior and 9 transverse; anterior to the elevated protocone is the beginning of the anterior valley and a rudiment of the antero-internal cusp (=paraconid); the much more depressed talonid similarly consists of a shallow, rudimentary crescent, opening inward. P_3, like its fellow in the upper jaw, shows more equal anterior and posterior lobes, on which the crescents and internal valleys and the cusps corresponding to the paraconid and entoconid of the molars are more accented; the typical proportions in *M. megarhinus* are 17 by 9 millimeters; in *M. petersoni* the typical proportions of p_2 are 19 by 10, but this tooth has only a rudiment of the prominent internal cusp corresponding with the metaconid of the molars. P_4 is still further advanced or submolariform, having a prominent internal cusp corresponding to the metaconid in the molars, each lobe consisting of two fairly defined crescents; it differs from m_1 in its smaller dimension (*M. megarhinus* 17 by 11 mm., *M. petersoni* 19 by 12) and in the nonelevation of the postero-internal cusp (entoconid). The cingulum is practically rudimentary or wanting in all these teeth.

Molars.—The *Mesatirhinus* or generic characters of the superior molars (Pl. LXXII) are seen in the following features: (1) The slight excess of anteroposterior over transverse diameters, especially in the more dolichocephalic *M. petersoni;* (2) the high, sharply pointed protocone (unworn height, 6 mm.); (3) the high, elongate external cusps (height of unworn paracone, 23 mm.); (4) the very sharp para-, meso-, and metastyles; (5) the reduced but still persistent protoconules (sometimes vestigial, Am. Mus. 1519, 1513, *M. megarhinus*); (6) the anterior and posterior cingula; (7) the vestigial metaconule seen in m^3 only in certain specimens (Am. Mus. 1556), the majority exhibiting no trace of this cusp; (8) the serrate external cingulum at the bottom of the ectoloph valleys, especially in the more progressive specimens.

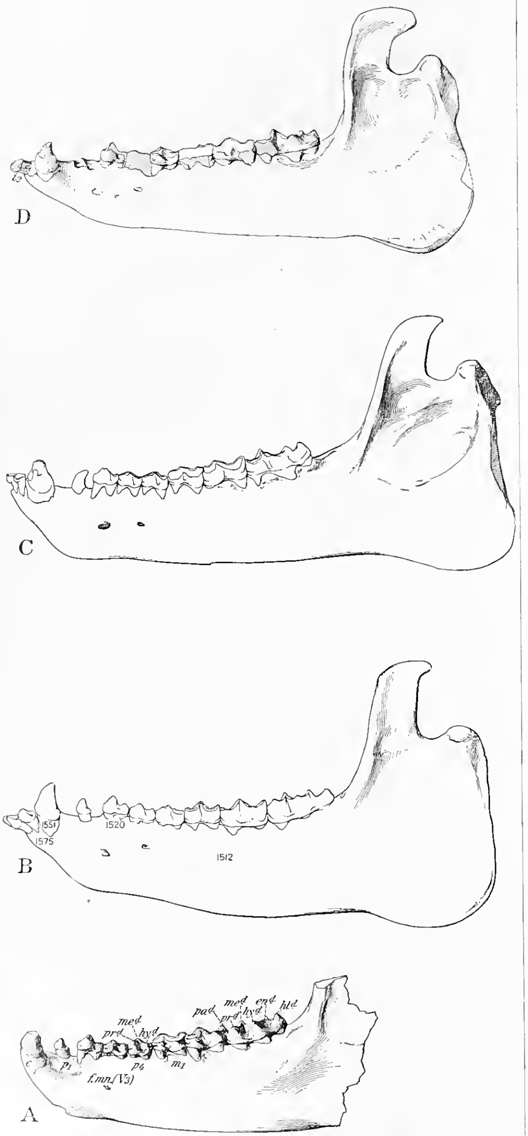

FIGURE 331.—Lower jaws of *Mesatirhinus*

One-fourth natural size. A, *M. megarhinus*, Am. Mus. 1520, Bridger Basin, Wyo., level unknown. B, *M. petersoni*, Am. Mus. 1512, La Clede Meadows, Washakie Basin, Washakie A; symphyseal region restored from Am. Mus. 1575 (*M. megarhinus*), La Clede, Washakie Basin; canine from Am. Mus. 1551 (*M. megarhinus*), Twin Buttes, Bridger Basin. C, *M. petersoni*, Am. Mus. 1567, Bridger Basin, level unknown; lower jaw of an old animal. D, *M. petersoni*, Am. Mus. 13178, north of Haystack Mountain, Washakie Basin, Washakie A; lower jaw of an old animal.

The superior molar series measures from 87 to 91 millimeters in *M. petersoni* and from 77 to 83 in *M. megarhinus*. The inferior molar series measures from 94 millimeters in *M. megarhinus* to 104 in *M. petersoni.*

The inferior molars are characterized by faint serrate, noncontinuous external cingula, which follow the curvature of the crown inward between the outer lobes, as distinguished from the cingula in *P. paludosus*, which form a straight line along the base of the outer border of the tooth. In the long, narrow m_3 (*M. megarhinus*, ap. 43 mm., tr. 19; *M. petersoni*, ap. 46, tr. 19) a serrate internal cingulum rises on the inner side of the hypoconulid but does not ascend so prominently as in *T. cultridens*. This hypoconulid is progressively conic in form; it is slightly more conic, more median in position, and less sharply crescentic or cupped on the inner side than in *T. cultridens;* but in certain specimens (Am. Mus. 1512, 1577) it has the more crescentic form of the *T. cultridens* type. In some molars (Am. Mus. 1512, 1575, 1520) faint rudiments of the metastylid fold are seen, but as a rule the internal valleys are open and smooth. Other teeth are too much worn to determine the presence or absence of the metastylid fold.

Lower jaws of M. megarhinus and M. petersoni.—The lower jaw of these animals is represented by a large number of separate jaws belonging to both species (see below). These jaws taken together afford very complete knowledge of the progressive, age, and sexual characters. There is a very marked disparity in size between the smallest (Am. Mus. 1520, *M. megarhinus*) and the largest (Am. Mus. 1512, *M. petersoni*).

Comparative measurements of Mesatirhinus and Metarhinus, in millimeters

	Mesatirhinus megarhinus, Am. Mus. 1520 (Bridger D?)	Mesatirhinus petersoni, Am. Mus. 1512 (Washakie A)	Metarhinus fluviatilis, Am. Mus. 1946 (Uinta B 2)
P_1–m_3	162	176	161
P_2–m_3	146	[a] 160	157
M_1–m_3	94	102	102
M_3, anteroposterior	43	46	46
Incisive border to angle	----------	325	----------

[a] Average.

The coronoid rises rather rapidly behind m_3, with a more or less rounded or angulate anterior border and with nearly parallel anterior and posterior contours until near its summit, when it suddenly curves back into a decided posterior hook. (Am. Mus. 1512, fig. 331.)

The condyle in *M. petersoni* is well raised (144 mm.) above the lower border of the angle and extends 107 millimeters behind m_3; it is more extended anteroposteriorly and less transversely than in *M. manteoceras*. The angle is very similar to that of *Eotitanops borealis* on a larger scale, with a slender and slightly incurved posterior border. The lower border of the ramus is concave below the coronoid, convex below the grinders, and rises gradually into a laterally compressed chin gently rounded on the inferior sûrface. The ramus increases in depth posteriorly. The symphysis measures 69 to 80 millimeters, and as seen from below the chin is sharply contracted to a width of 40 millimeters behind the canines. Below m_1 the rami attain in males the width of 20 millimeters. On the whole this is a progressive development of the *E. borealis* type of jaw, the chief difference being the broader coronoid.

Age characters.—In an aged, somewhat larger, more elongate, and perhaps more progressive jaw (Am. Mus. 1567), from the Bridger, there is a wider space (130 mm.) between the condyle and the posterior fang of m_3, the condyle itself is wider (57 mm.) and less extended anteroposteriorly, the gentle rounding of the posterior border of the angle seen in *E. borealis* and the typical *M. megarhinus* changes into a more decided, angulate projection of the posteroinferior border. Seen from behind, the border of the angle is marked by a sudden sharp inflection about two-thirds of the distance below the condyle. The condyle is more transversely extended.

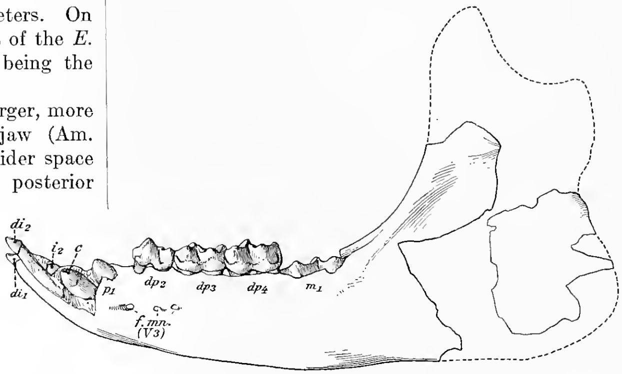

FIGURE 332.—Lower jaw of *Mesatirhinus* sp. with deciduous dentition

One-half natural size. Am. Mus. 12211, Summers Dry Creek, Bridger Basin, Wyo., Bridger C.

A small lower jaw (Am. Mus. 12211), from Bridger C, has deciduous incisors 1 and 2 and three deciduous premolars in place, with some of the replacing teeth below them. The incisors are chisel-shaped, somewhat like the adult incisors of *Lambdotherium*. The fourth deciduous premolar is more molariform than its successor, especially in the somewhat better development of the entoconid. The chin is very sloping. (See fig. 332.)

Mesatirhinus sp.

Large progressive skull (fig. 333).—There is interesting evidence (Princeton Mus. 10041) of the existence in Washakie B (?) of a much larger animal than *M. petersoni*, progressive at least in size toward *Dolichorhinus vallidens*. It differs from *Mesatirhinus superior* in the narrow sagittal crest.

Unfortunately only the occiput is preserved. It exhibits in the parietal profile a pronounced convexity; the parietal crests are also broadly divergent anteriorly and rounded, suggesting those of *Sphenocoelus*.

The superior dimensions are indicated by the following comparisons: The occiput measures 90 millimeters in height, as compared with 80 in *M. petersoni*; the occipital condyles measure 98 millimeters transversely, as compared with 86 in *M. petersoni*. The width across the postglenoid processes is 183 millimeters, as compared with 150 in *M. petersoni*.

This cranium may possibly belong to an animal with a dentition such as that which we have referred below to *D. vallidens*.

A progressive jaw from Washakie A.—A specimen (Am. Mus. 2355) from Washakie A at Glove Springs consists of the rami incomplete posteriorly, but including all the teeth. It belongs to the dolichocephalic *Mesatirhinus* series. It is much larger than the most advanced jaw of *M. petersoni* from Washakie A. The measurements are compared below:

Measurements of Mesatirhinus and Dolichorhinus, in millimeters

	Washakie A		Washakie B: D. hyognathus, Princeton Mus. 10273 (type)
	M. petersoni, Am. Mus. 1512	M. sp., Am. Mus. 2355	
P_1–m_3	[a] 175	192	240
P_2–m_3	164	177	213
M_1–m_3	103	112	120

[a] Estimated.

The postcanine diastema in this specimen is long (32 mm.). As in *Mesatirhinus* the canines are incurved as well as recurved.

Mesatirhinus (=Dolichorhinus) superior Riggs

Reference may be made here to the skull of *M.* (=*Dolichorhinus*) *superior*, which is fully described below (p. 405). This animal is intermediate in form between the two genera *Mesatirhinus* and *Dolichorhinus*, so that it might be placed in either genus with equal propriety. The skull and hypocone on m^3 of *M. superior* incline us to connect this skull with species of *Dolichorhinus*.

Dolichorhinus Hatcher

Plates XVII, XXIX–XXXII, XLVI, LII, LIII, LV, LXXI–LXXVII; text figures 27, 33, 105, 110, 125, 133–137, 140 210, 214–220, 254, 255, 302, 322–324, 335–337, 339–353, 483, 508–511, 520, 521, 579–585, 588–591, 647, 661, 685–686, 711, 724, 733, 737–740, 742, 743, 745

[For original description and type references see p. 177. For skeletal characters see p. 645]

Generic characters.—Animals of relatively large size, extremely dolichocephalic; cephalic indices 43 to 47; face relatively long; faciocephalic index 48 to 51; postorbital process situated above m^3; summit of cranium broadly flattened; space above small brain chamber filled with large air sinuses; occiput low and broad; relatively prominent supraorbital horn swellings on nasals; axis of face and middle part of skull bent downward. Astragalus of the long-necked type.

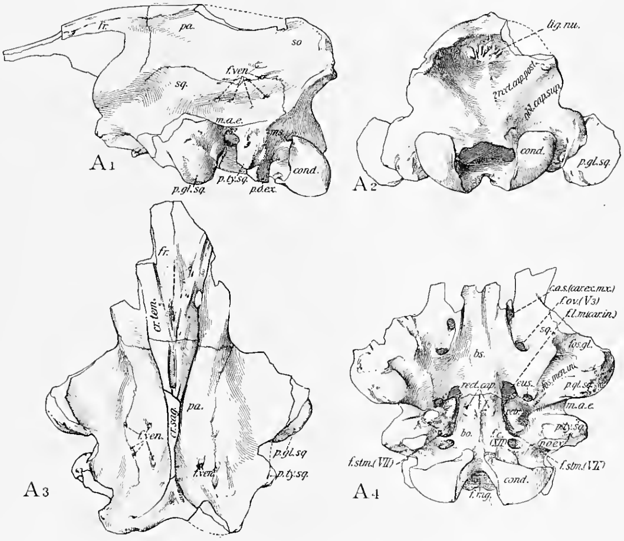

FIGURE 333.—Imperfect cranium of *Mesatirhinus petersoni?*

One-fourth natural size. Princeton Mus. 10041, Washakie Basin, Wyo., Washakie. A. A_1, Side view; A_2, occipital view; A_3, top view; A_4, basal view.

Dolichorhinus, appropriately named by Hatcher in reference to the elongation of the nasal region, is a titanothere in which we observe the dolichocephalic extreme. The genotype species, *D. hyognathus*, from Uinta B 2, is connected by transition forms in Uinta B 1, such as *Dolichorhinus longiceps* and especially *D. superior*, with the advanced structural stages of *Mesatirhinus*, namely, *M. petersoni*, so that there is no question that *Dolichorhinus* is a descendant of certain species of *Mesatirhinus*. Besides the highly progressive *D. hyognathus* and the more primitive *D. longiceps* there are several species of *Dolichorhinus* less clearly defined, a fact which indicates that this was a dominant and highly diversified form during the period of deposition of the river sandstones and flood-plain deposits of the levels Washakie B and Uinta B 1 and B 2 (see below).

History of discovery.—This animal first became known through Cope's personal exploration of the Washakie Basin exposures of 1872, which yielded his cotypes of "*Palaeosyops vallidens*"; this species apparently represents a distinct stage of *Dolichorhinus*, but unfortunately it is still known only from an imperfect lower jaw and some upper teeth. The next discovery was that of Scott, Osborn, and Speir, of the Princeton expedition of 1878, consisting of the large lower jaw which in 1889 Scott and Osborn made the type of the species "*Palaeosyops hyognathus*." The third step was marked by Peterson's discovery in 1894 on behalf of the American Museum of Natural History of several skulls and parts of skeletons in the Uinta Basin. These skulls aroused unusual interest because of the presence of well-developed horn bases above the eyes, in reference to which Osborn named the animals *Telmatotherium* "*cornutum*." He first considered that they represented a direct progressive transition from "*Telmatotherium vallidens*" (= *Manteoceras*) toward the Oligocene titanotheres, but, as Hatcher pointed out in 1895, the horn development in these animals is a parallelism rather than a direct approach to the Oligocene titanotheres, for accompanying these horns are other characters which exclude the animals from such ancestry. Hatcher accordingly separated the species as a distinct genus, *Dolichorhinus*. It was long believed that *Dolichorhinus* was confined to the Uinta Basin level B 2, to which Osborn gave the name *Dolichorhinus cornutus* zone. The animal certainly occurs in Uinta B 2, especially in the river-deposited sandstones, in very great abundance and may be considered as the dominant titanothere type of this deposition because it so far outnumbers all other types.

The next step in discovery was made by the American Museum expedition of 1906 in the Washakie Basin, during which Paul Miller found a beautifully preserved skull and jaws of a *Dolichorhinus* associated with parts of the skeleton and specifically identical with the type of *D. cornutus* prevailing in Uinta B 2. This discovery, together with evidence previously found, demonstrated the synchronism of the Washakie B 2 and the Uinta B 2 deposits. Further comparison of the jaws of this Washakie specimen with the type jaw of "*Palaeosyops hyognathus*," also from Washakie B, demonstrated that the species *D. cornutus* is a synonym of the earlier-described *D. hyognathus*. Exact study and comparison of all these specimens resulted in the opinion that "*Palaeosyops vallidens*" also belongs to the *Mesatirhinus-Dolichorhinus* group.

Among the crania that were at first included within the single species *D. cornutus* are two stages—an earlier stage, to which the name *D. intermedius* may be given, and a later stage, *D. hyognathus*. Akin to and possibly to be regarded as "mutations" of these stages are the species *D. heterodon* and *D. longiceps* of Douglass.

Geologic range and faunistic parallels.—The type of *Dolichorhinus cornutus* (=*hyognathus*) was found by Peterson in the sandstone at the top of Uinta B 2. The genus thus ranges downward through 700 feet of deposits to the type locality of *Dolichorhinus longiceps*, representing a long period of geologic time, in which we should expect considerable evolution of structural type as well as considerable changes in the contemporary mammalian life. In Uinta B 1, for example, *Dolichorhinus longiceps* is associated with *Metarhinus fluviatilis* and *M. riparius*. It is noteworthy, however, that *Dolichorhinus* seldom occurs in the same sandstone with *Metarhinus*, a fact indicating that these animals occupied somewhat different local habitats. It is also a striking fact that *Manteoceras* does not occur at all in Uinta B 1 or B 2 nor has it been found in Washakie B, while its relative *Mesatirhinus* occurs quite abundantly. This would appear to prove that *Dolichorhinus*, *Metarhinus*, and *Mesatirhinus* had different habitats and habits from either *Manteoceras* or *Telmatherium*, and that the conditions existing during the period of deposition of Uinta B 1 and B 2 were particularly favorable to the preservation of Dolichorhininae—namely, *Dolichorhinus*, *Metarhinus*, and *Mesatirhinus*. Among other ungulates no representatives of the Equidae or Tapiridae are found mingled with the dolichorhines. The hyracodont or light-limbed division of the rhinoceroses is represented by rare remains of *Triplopus*. The amphibious division of the rhinoceroses is represented by quite abundant remains of *Amynodon*. Among the Amblypoda, or giant quadrupeds, *Eobasileus* is very abundant and characteristic of the *Dolichorhinus* zone. Among the Artiodactyla the ancestral elothere *Achaenodon* occurs in the lower levels close to *Dolichorhinus*, and *Protelotherium* occurs in the uppermost levels. The giant flesh eaters *Mesonyx* and *Harpagolestes* are characteristic of this life zone.

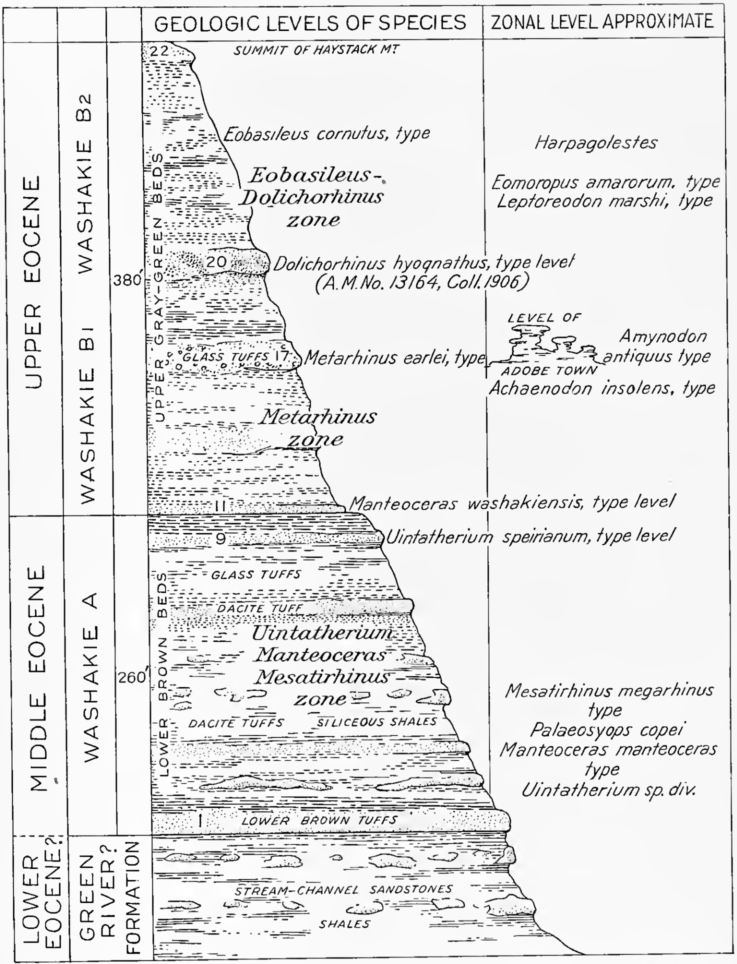

FIGURE 334.—Geologic section of the Bridger formation in the Washakie Basin

In general, the occurrence of the majority of these dolichorhine titanotheres in river sandstones associated with the remains of other fluviatile or river-border types, such as *Amynodon*, *Achaenodon*, and possibly *Eobasileus*, tends to favor the view that the dolichorhines which frequented the river borders were subject to being washed into the sandy deposits during periods of flood.

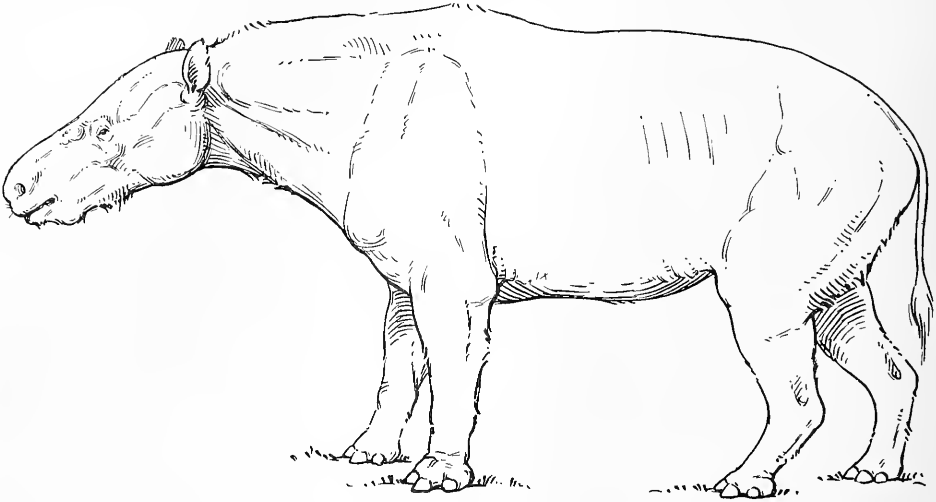

Figure 335.—Restoration of *Dolichorhinus longiceps*

By E. S. Christman, based on the mounted skeleton in the Carnegie Museum. One-fifteenth natural size.

The bodily proportions of the dolichorhines were similar to those of the existing forest-living pigs of Africa.

Habits of Dolichorhinus.—We may compare *Dolichorhinus* remotely with *Hippidium*, an aberrant South American Pleistocene horse, in which an excessively long skull is combined with exceptionally short metapodials, in contrast with those of typical horses.

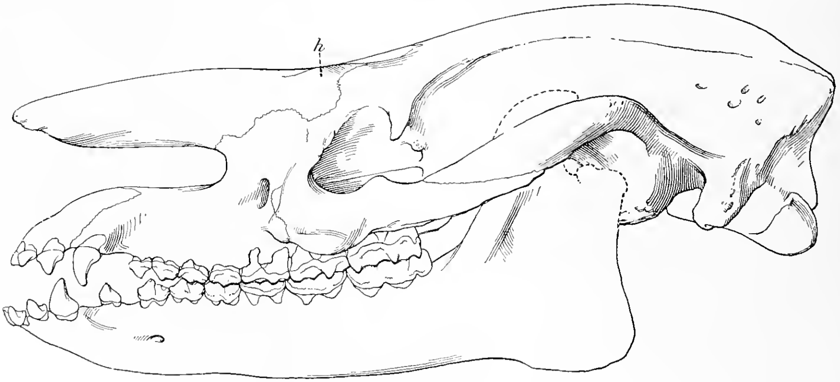

Figure 336.—Skull and lower jaw of *Dolichorhinus hyognathus*

One-fourth natural size. Skull, Am. Mus. 1851; lower jaw, Am. Mus. 1856. Both from White River, Uinta Basin, Utah, level Uinta B 2.

So far as we can judge from very sparse evidence, the feet of *Dolichorhinus* were surprisingly short, apparently indicating no increase in speed. *Dolichorhinus longiceps* may be described as dolichocephalic and brachypodal. (See p. 652.)

The muzzle was rather expanded, or truncate; the face was not so long as that of other titanotheres. The incisors were arranged in a semicircle and made some approach in form to the cropping incisors of the ruminant. These teeth were also partly cupped to facilitate prehension, as in the lower Miocene species of the horse. The diastema behind the canine tooth is longer than in other titanotheres, as in typical herbivorous forms. The canines in the males were moderately long, recurved, sharp edged, and may have been used in fighting, as by the existing camels; the offensive power of the front teeth was less, however, than in the short-jawed *Palaeosyops*. The cheek teeth, concerned in the comminution of food, were relatively long crowned, with pointed cusps, and constituted an elaborate cutting and triturating apparatus. The movement of the more slender mandible was partly vertical, partly oblique, since the wearing of the cheek teeth gives evidence of an oblique shearing action. Adapted to these conditions were the length and proportions of the chewing muscles and their angles of action. (See below for details.)

It is therefore probable that since the food evidently required finer cutting and better trituration than the food of *Palaeosyops*, *Dolichorhinus* was either a browser on harder materials or a grazer, perhaps coming out from the forests at night into the open grassy places or searching for smaller twigs, like the Indian rhinoceros (*R. unicornis*). The bending down of the facial upon the cranial axis is a characteristic of many grazers, whereas the bending up of the facial axis is generally characteristic of browsers.

Directing attention, on the other hand, to the progressive backward shifting of the hinder border of the posterior nares to what is known as the "secondary palate," Riggs (1912.1, p. 36) has advanced the hypothesis that *Dolichorhinus* was a river-frequenting form which perhaps fed upon submerged plants, like the moose. The backward shifting and closure of the hinder border of the palate is an obvious advantage to animals feeding partly in the water and is characteristic of many water-living forms.

General characters of the genotype, D. hyognathus.—The elongate skull, the broad, flattened, and sutureless cranial region, the elongate nasofrontal horns are characters partly of progressive dolichocephaly, partly of family affinity to the Oligocene forms. The features of the main line of *Dolichorhinus* are the extreme narrowing and lengthening of the skull and zygomatic arches, the convex upward arching instead of a concave saddle shape of the skull top, the broad infraorbital shelf, the shallow jaws, the parallel series of grinding teeth, and especially the extremely long, narrow nasals. The horns are borne chiefly on the nasals, as in *Mesatirhinus*, in contrast with *Manteoceras*, in which they are borne chiefly on the frontals. The occiput is low, possibly in correlation with the bending down of the cranium. In palatal view we observe the marked backward extension of the posterior nares and the formation of a secondary palate. The jaw is distinguished by its long, slender, recurved coronoid process and its depressed angle. These characters combine to constitute this animal one of the most peculiar and distinctive of the whole titanothere series.

At a first glance the long skull suggests that of a horse, but a closer examination shows that, although both are dolichocephalic, the resemblance is entirely superficial; the horse has a primitive short cranium (brachycrany) and an enormously long face (dolichopy) or preorbital region. *Dolichorhinus* has an elongate, highly modified cranium (dolichocrany) and postorbital region and a relatively short face (brachyopy). As compared in detail with the skull of a horse that of *Dolichorhinus* furnishes an instructive mingling of convergent resemblances to other long-headed ungulates and divergent hereditary differences. Among the convergent resemblances in *Dolichorhinus* are (1) the lengthening of the whole skull, especially of the face; (2) the bending down of the anterior half of the skull; (3) the backward prolongation of the palate; (4) the semicircular or cropping arrangement of the incisors; (5) the prominence of the orbits; (6) the forward extension of the masseter muscle, the anterior slip in *Dolichorhinus* being attached to the infraorbital shelf.

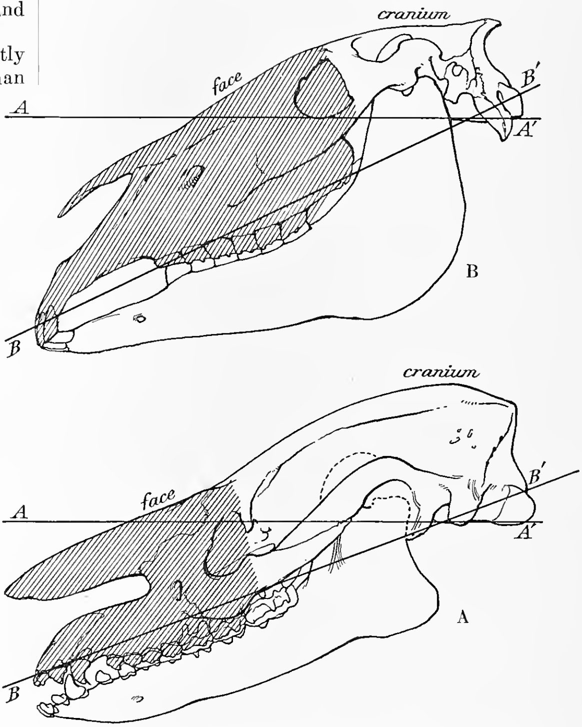

FIGURE 337.—Skulls of *Dolichorhinus hyognathus* (A) and modern horse (B)

One-sixth natural size. These show analogous and divergent adaptations to grazing habits. *A-A′*, Basicranial axis; *B-B′*, basipalatal axis.

Among the divergent hereditary differences characteristic of the titanotheres and shown in *Dolichorhinus* are (1) the lengthening of the middle part of the skull; (2) the development of supraorbital horn swellings; (3) the character of the teeth; (4) the shape of the lower jaw; (5) the broadening of the top of the skull; (6) the relatively short crowns of the grinding series.

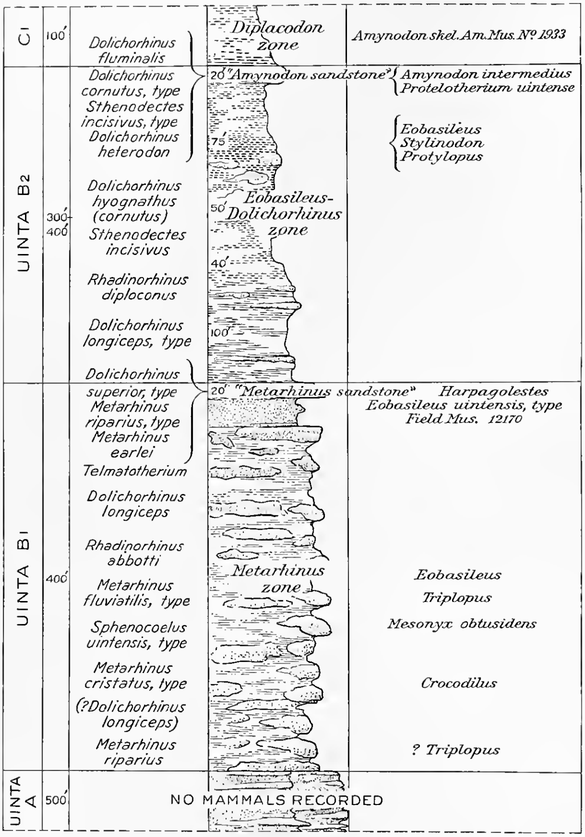

FIGURE 338.—Geologic section of the *Eobasileus-Dolichorhinus* and *Metarhinus* zones in the Uinta Basin

As a whole the grinding series is short (206 mm.) in proportion to the length of the skull, the molar index being 38. Correlated with molar dolichocephaly the inner and outer cones of the molar teeth are closely approximated and the crowns are elongated and narrowed. In adaptation to harder kinds of food the crests and cones are elongate or subhypsodont; both the parastyles and mesostyles are very sharp and prominent.

The backward and downward prolongation of the bony palate is a very distinctive feature. In early stages (*D. intermedius*) the secondary palate is rudimentary and lies much above the plane of the primary palate; in later stages it descends and lies on the same plane as the primary palate, also extending very far backward (*D. fluminalis*).

In the comparison of numerous dental series we observe that the male teeth are somewhat larger, including the robust, sharp-edged canines, whereas the female jaws are more slender and the canines smaller and rounder, with shorter enamel caps. Sex apparently does not affect the development of the osseous horns, which are practically similar in the male and female skulls.

Synopsis of species.—The following summary gives the principal features of the species assigned to *Dolichorhinus:*

UPPER LEVELS

D. hyognathus (Osborn) = *D. cornutus* Osborn. Summit of Uinta B 2 and middle of Washakie B 2. Cranium large, most progressive, broad and convex, length 550 millimeters, breadth 240, cephalic index 46, faciocephalic index 53; broad secondary palate; horns well developed.

D. fluminalis Riggs. Summit of Uinta B 2. Distinguished by extreme backward prolongation of secondary palate. Length, type skull, 520 millimeters, breadth 233, cephalic index 45, faciocephalic index 48.

D. intermedius Osborn. Uinta B 2. A broad form with elongate skull; length 485 millimeters, breadth 223 (estimated), cephalic index 45 (estimated), faciocephalic index 49; horns less prominent; secondary palate less extended posteriorly.

D. heterodon Douglass. Summit of Uinta B 2. Similar to *D. intermedius*. Length 487 millimeters; cephalic index not determined; faciocephalic index 50.

LOWER LEVELS

D. longiceps Douglass. Base of Uinta B 2. Very abundant; more primitive; probably ancestral to *D. hyognathus*. Horns incipient. Large size, length 545 millimeters, breadth 260; cephalic index of type 47; faciocephalic index 48; cranial roof narrow, less arched.

D.? vallidens (Cope). Washakie B(?). Imperfectly known teeth, more primitive than those of *D. hyognathus*.

D. (*Mesatirhinus*) *superior* (Riggs). Summit of Uinta B 1. Smaller and more primitive. Horns very rudimentary. No secondary palate.

Summary of cranial indices in Dolichorhinus

Species	Cephalic index	Faciocephalic index
D. hyognathus, Am. Mus. 13164, ♀	46	53
D. hyognathus, Am. Mus. 1851, ♀ (type of Telmatherium cornutum)	43	51
D. intermedius, Am. Mus. 2001	[a] 45	49
D. intermedius, Am. Mus. 1837 (type)	[a] 41	49
D. heterodon, Carnegie Mus. 2340 (type)		50
D. fluminalis, Field Mus. 12205 (type)	45	48
D. longiceps, Carnegie Mus. 2347 (type)	47	48
D. longiceps, Am. Mus. 1852, ♀	42	48
D. superior, Field Mus. 12188	52	48?

[a] Estimated.

The extremes of these specific indices are also presented above.

Dolichorhinus vallidens (Cope)

Plate LXXIV; text figures 95, 341, 353

[For original description and type references see p. 162]

Geologic horizon.—Washakie Basin, Wyo., level Washakie B.

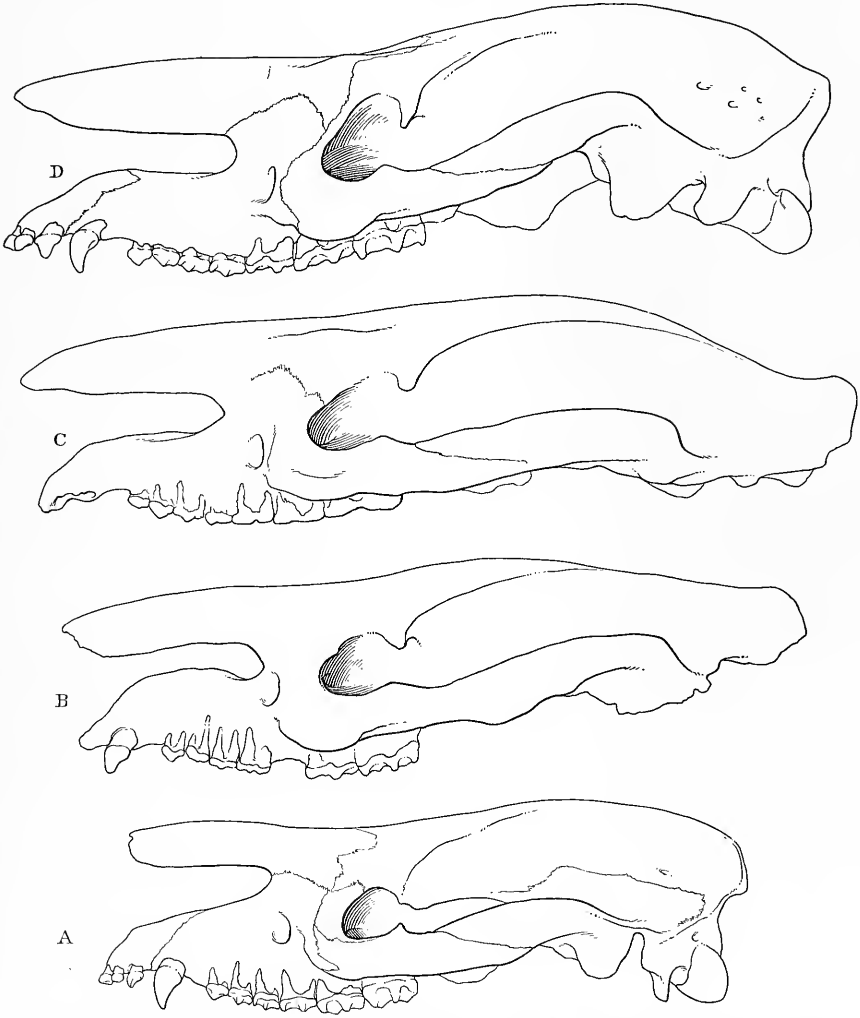

Figure 339.—Skulls showing progressive dolichocephaly in the *Mesatirhinus-Dolichorhinus* phylum

Side view. One-fourth natural size. A, *Mesatirhinus petersoni*, British Mus. (formerly Am. Mus. 1556), Big Bone Mountain, Henrys Fork, Bridger Basin, Wyo., Bridger D; B, *Dolichorhinus superior*, Field Mus. 12188 (type), Uinta Basin, Utah, Uinta B 1; C, *D. longiceps*, Carnegie Mus. 2347 (type), Uinta Basin, Uinta B 2; D, *D. hyognathus*, Am. Mus. 1851, White River, Uinta Basin, Uinta B 2.

Specific characters.—P^1–m^3, 185 millimeters (estimated); m_1–m_3, 123; ectolophs of superior premolars with a broad basal spreading of the protocone convexities; tritocones more flattened than in *D. intermedius;* p^2, p^3 of same proportions as in *D. hyognathus;* lower premolars less compressed and more primitive than in *D. hyognathus;* hypoconulid of m_3 elongate; in general more primitive than either *D. intermedius* or *D. hyognathus.*

As shown above, the imperfectly preserved upper and lower jaws, the cotypes of Cope's original description, were not found together. Nevertheless it now appears probable though not certain that the lectotype lower jaw (Am. Mus. 5098) and at least one of the original upper dentitions (Am. Mus. 5097) do pertain to the same species.

Doubtful reference.—The reference of these types to *Dolichorhinus* is provisional; if the jaws are correctly referred the cranium is apparently much less dolichocephalic than that of *D. hyognathus* or *D. longiceps.* Comparison with *Dolichorhinus superior* is also difficult and unsatisfactory; in *D. superior* the premolars appear to be different in contour, also their cingula are not so heavy; the measurements of the superior teeth (p^1–m^3) in these two species are approximately the same—185 millimeters (estimated) in *D. vallidens* and 182 in *D. superior.* The hypocone on m^3, probably absent in *D. vallidens*, is present and strong in *D. superior.* The upper teeth of *D. vallidens* (paratype) are structurally ancestral to those of *Diplacodon,* but so also are the upper teeth of *Mesatirhinus petersoni.*

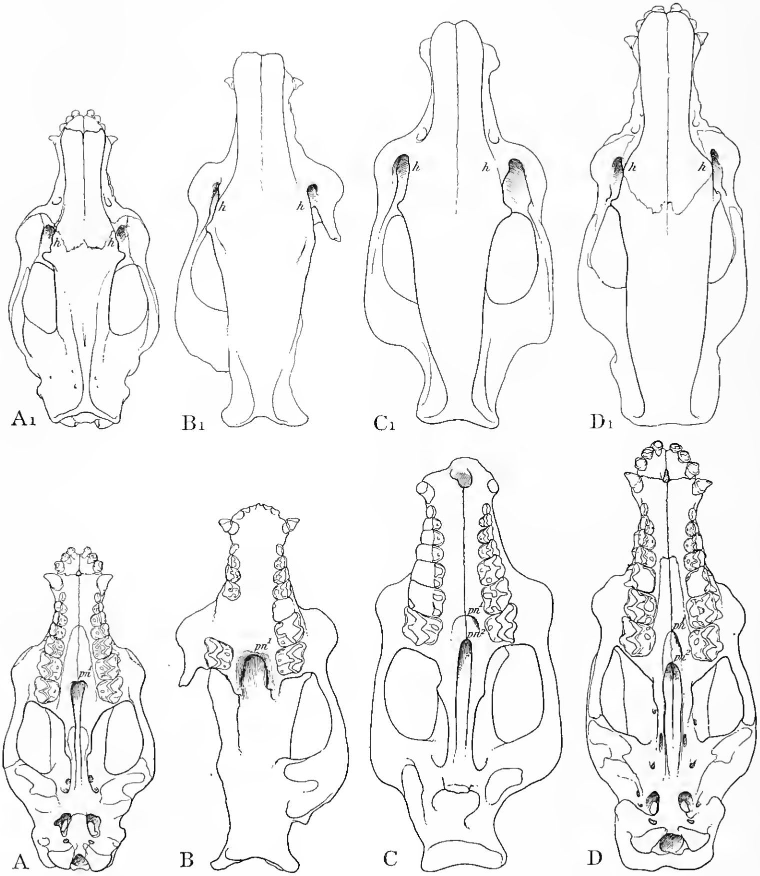

Figure 340.—Skulls showing progressive dolichocephaly in the *Mesatirhinus-Dolichorhinus* phylum

Top and palatal views. One-eighth natural size. A, A_1, *Mesatirhinus petersoni*, British Mus. (formerly Am. Mus. 1556), Big Bone Mountain, Henrys Fork, Bridger Basin, Wyo., Bridger D; B, B_1, *Dolichorhinus superior*, Field Mus. 12188 (type), Uinta Basin, Utah, Uinta B 1; C, C_1, *D. longiceps*, Carnegie Mus. 2347 (type), Uinta Basin, Uinta B 2; D, D_1, *D. hyognathus*, Am. Mus. 1851, White River, Uinta Basin, Uinta B 2. pn^1, Primary border of the posterior nares; pn^2, secondary border of the posterior nares.

History.—The species was at first referred by Cope (1885.1, p. 700) to the genus *Palaeosyops.* Earle also assigned this animal to *Palaeosyops.* Osborn at first regarded it as belonging to the genus *Manteoceras* but subsequently recognized the prevailing dolichocephalic characters and placed the animal near *Dolichorhinus.*

Lectotype lower jaws of D. vallidens (Am. Mus. 5098).—Comparison with typical lower jaws of *D. hyognathus* from both Washakie B 2 and Uinta B 2 shows that *D. vallidens* was a smaller animal and somewhat more primitive in the details of the lower premolars. (See fig. 353.)

The chin is only partially preserved and with it the root of the right canine, which is stouter than in supposed females of *D. hyognathus.* The first lower premolar, as indicated by the alveolus in Cope's drawing

(1885.1, pl. 52, fig. 3), appears to have had but one root. P_2 is shorter anteroposteriorly and less compressed than in the typical *D. hyognathus;* its posterior V is also smaller as compared with the protoconid and less sharply developed. P_3 is not preserved. P_4 is also less compressed, the posterior V lower and more primitive in form than in *D. hyognathus.* The true molar series is considerably shorter, but the posterior half of m_3 and especially the hypoconulid are relatively longer and more compressed. The space between m_3 and the ascending ramus was less. Comparative measurements are as follows:

Measurements of Dolichorhinus vallidens and D. longiceps?, in millimeters

	D. vallidens, Am. Mus. 5098, lectotype jaw	D. longiceps?, Am. Mus. 1852
Front of canine to hinder border of m_3	230	275
Front of p_4 to hinder border of m_3	146	165
Length of true molar series	123	139
P_2, ap. by tr	19×11	23×11
P_4, ap. by tr	23×13	25×15
M_3 (anterior lobe), ap. by tr	55×20	60×23
M_3, length of hypoconulid	14	15

The specimen under consideration is distinguished from jaws of *M. manteoceras* by the longer molar series and more elongate hypoconulid on m_3.

Upper teeth of the paratype of Dolichorhinus vallidens (Am. Mus. 5097).—The characters of the premolar ectolophs are so constant in all the many specimens of *D. hyognathus* that the marked differences which they present in the paratype of *D. vallidens,* approaching as they do the characters of the *Mesatirhinus* premolars, appear to establish the specific separation.

The whole series of upper grinding teeth (p^1–m^3) of *D. vallidens* is estimated at 185 millimeters, as compared with 177 in *D. intermedius* and 206 in *D. hyognathus.*

Comparison with Dolichorhinus hyognathus.—As noted above, the superior grinding series is shorter than that of *D. hyognathus* (185 mm. (estimated), as compared with 206), and the detailed anteroposterior and transverse measurements of the crowns of the only perfectly preserved teeth, p^2, p^3, are practically identical with those of the average *D. hyognathus,* as shown below:

Measurements of upper premolars in species of Dolichorhinus, in millimeters

	D. intermedius, Am. Mus. 1837 (type)	D. vallidens, Am. Mus. 5097 (paratype)	D. hyognathus (average)
P^2 anteroposterior	13	15	15
P^2, transverse	9	10	9.8
P^3, anteroposterior	18	20	20
P^3, transverse	20	22	22
P^3, internal lobe, anteroposterior	16	19	21
P^4, internal lobe, anteroposterior	19	22	23

The linear ectoloph measurements of the true molars are intermediate between those of *D. intermedius* and *D. hyognathus.* The ectolophs of the premolars of *D. vallidens* (fig. 341, B) afford the most distinctive character—namely, the broad festoon and the basal spreading of the convexities of the protocone, a primitive character which relates these teeth to the *Mesatirhinus* stage. The deuterocones of p^{2-4} are more primitive and the tritocones are more flattened than in the *D. intermedius* type.

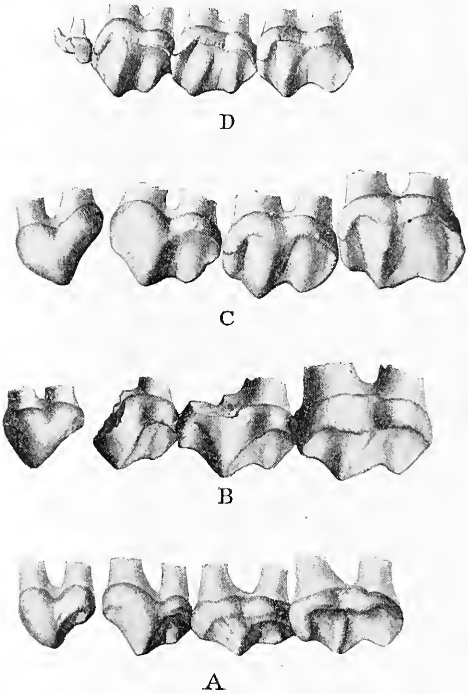

FIGURE 341.—Upper premolars of *Mesatirhinus, Dolichorhinus,* and *Metarhinus*

Outer side view. Natural size. A, *Mesatirhinus petersoni,* British Mus. (formerly Am. Mus. 1556), Big Bone Mountain, Henrys Fork, Bridger Basin, Wyo., Bridger D; B, *Dolichorhinus vallidens,* Am. Mus. 5097 (paratype), reversed, Mammoth Buttes, Bitter Creek, Washakie Basin, Wyo., Washakie B; C, *Dolicharhinus hyognathus,* Am. Mus. 1850, White River, Uinta Basin, Utah, Uinta B 2; D, *Metarhinus fluviatilis,* Am. Mus. 1946, White River, Uinta Basin, Utah, Uinta B 1.

These characters tend to show that so far as indicated by the paratype *D. vallidens* is somewhat more primitive than either *D. intermedius* or *D. hyognathus.*

Comparison with M. petersoni and other forms.—The superior grinding teeth of this paratype resemble those of certain specimens of *M. petersoni* on a larger scale. The progressive distinctions are (*a*) the presence of a cingulum on the inner side of p^1; (*b*) the quite complete cingulum on the inner side of p^3 and p^4 and the somewhat more flattened and elevated ectolophs of p^{2-4}, which are less elevated, however, than in *D. hyognathus;* (*c*) the external cingula of the molar teeth are a shade more prominent; (*d*) the protoconule and metaconule have nearly vanished, although inconspicuous vestiges still persist.

The faint rudiments of the tetartocone folds of the premolars are less marked than in certain specimens of *M. petersoni.* The ectolophs of the superior premolars are readily distinguished from those of *M. manteoceras* by the flattening of the tritocones. The ectoloph of p^1 is simple and sharply convex. That of p^2 consists of a prominent protocone convexity which spreads downward into a broad cingulum bounding the base of the tritocone (the same region in *D. hyognathus* is strongly constricted); the tritocone ectoloph is nearly flat or very slightly convex. In p^3 the protocone ectoloph is a convex ridge spreading toward the base into a cingulum, while the tritocone ectoloph is very gently convex but without a rib. P^4 has the convexity opposite the apex of the protocone, while the outer face of the tritocone is slightly convex and the basal cingulum is nearly continuous across the ectoloph. The above-mentioned features enable us to distinguish the upper premolars from those of *Manteoceras* and of both *D. intermedius* and *D. hyognathus.*

Summary.—In the lectotype lower jaw of *D. vallidens* the premolars are decidedly more primitive than in *D. hyognathus.* In the paratype upper dentition of *D. vallidens* the premolars are somewhat more primitive than in *D. hyognathus.* It is thus not certain that the lectotype and paratype belong to precisely the same stage of evolution; but, on the other hand, there is no evidence that they are specifically distinct.

Comparative measurements, in millimeters, showing progressive proportions of skull and teeth of Dolichorhinus

	D. superior, Field Mus. 12188 (type)	D. intermedius		D. vallidens, Am. Mus. 5097	D. heterodon, Carnegie Mus. 2340 (type)	D. fluminalis, Field Mus. 12205 (type)	D. "longiceps," Carnegie Mus. 2347 (type)	D. longiceps?, Am. Mus. 1852	D. hyognathus						
		Am. Mus. 1837 (type)	Am. Mus. 2001						Am. Mus. 13164	Am. Mus. 1850	Am. Mus. 1851	Am. Mus. 1845	Am. Mus. 1848	Field Mus. 12167 (D. "cornutus")	Average
Premaxillaries to condyles	485	462	[a] 485	------	487	520	[a] 555	[a] 550	542	------	550	------	------	595	550
End of nasals to middle top of occiput	------	475	475	------	492	------	590	573	580	593	570	------	[a] 565	------	575
Face, anteroposterior	------	230	241	------	245	------	[a] 270	270	[a] 290	[a] 260	280	------	------	------	270
Cranium, anteroposterior	------	236	248	------	240	------	[a] 285	283	------	320	288	290	310	------	298
Transverse zygomata	224	[a] 190	[a] 223	------	------	233	[a] 264	230	250	------	[a] 240	215	------	285	231
P^1–m^3	184	179	177	[a] 185	189	171	197	202	205	208	208	------	------	214	206
P^2–m^3	------	165	164	------	173	------	178	185	186	185	187	------	------	------	186
P^2–p^4	------	57	57	------	58	------	60	62	65	61	65	------	------	------	62
M^1–m^3	103	109	105	------	114	105	115	118	119	120	122	131	------	135	123
P^1, ap. by tr	------	------	12×10	------	------	------	15×10	15×11	18×11	16×9	15×10	------	------	------	15×10
P^4, ap. by tr	------	19×21	20×25	------	22×25	------	21×29	20×26	23×29	22×25	23×27	25×30	------	------	22×27
M^1, ap. by tr	------	31×32	30×?	------	33×32	------	35×?	36×33	36×33	36×30	34×34	35×33	------	------	35×33
M^2, ap. by tr	------	39×38	------	------	42×41	------	39×40	41×39	43×42	41×38	43×43	47×41	------	------	42×40
M^3, ap. by tr	------	36×37	39×39	------	39×38	------	39×?	40×37	42×42	43×35	45×?	47×41	------	------	44×39

[a] Estimated.

12188. Uinta B 1.
1837. Female. Uinta B 2.
2001. Uinta B 2.
5097. Washakie B.
2340. Uinta B 2 (upper level).
12205. Uinta B 2.
2347. Uinta B 2 (low level).
1852. Female. Uinta B 2.
13164. Washakie B 2.
1850. Male. Uinta B 2.
1851. Female. Uinta B 2 (type of *Telmatotherium cornutum*).
1845. Uinta B 2.
1848. Uinta B 2.
12167. Uinta B 2.

The above table shows the dolichocephalic proportions of the cranium proper and of the true molars and the smaller dimensions of *D. intermedius* and the intermediate proportions of the type of *D. heterodon.* The type of *D. longiceps* and the type of *D. "cornutus"* agree well in size with the skulls of *D. hyognathus.* The well-preserved skull from the Washakie Basin (Am. Mus. 13164), which is referred to *D. hyognathus,* does not differ greatly in measurements from the type of *Dolichorhinus "cornutus"* and the other Uinta B specimens. The skulls of *D. hyognathus,* from Uinta B, show a considerable difference in size, ranging from the relatively small skull No. 1852 to the very large skull No. 1845.

Measurements of the lower jaws of these species are given on page 416.

Dolichorhinus (Mesatirhinus) superior Riggs

Plates LXXV–LXXVII; text figures 137, 339, 340

[For original description and type references see p. 190]

Type locality and geologic horizon.—Uinta Basin, Utah, *Metarhinus* zone, top of the "*Metarhinus* sandstones," summit of Uinta B 1. *D. superior* comes from a horizon 200 to 400 feet above that at which *D. longiceps* is commonly found. The type was found in the same ledge and associated with one of the more advanced stages of *Metarhinus* (*M. earlei*). Thus *D. superior* is contemporary with a more advanced stage of development of *Dolichorhinus* and with the last of the *Metarhinus* phylum (Riggs).

Specific characters.—"Skull 485 by 255 millimeters, molar series 182 millimeters, nasals free to a point over last premolar, infraorbital process present, arches slender anteriorly, nasals infolded at margins, sagittal area expanded, canines small, p^2 and p^3 oblique to axis of series. Molars relatively small, strong hypocone on m^3, posterior nares opening opposite the anterior margin of last molar." (Riggs, 1912.1, p. 26.)

Materials.—The only specimen known is the type skull in the Field Museum (No. 12188), described below. This important form is transitional between *Mesatirhinus* and *Dolichorhinus*. On the whole it appears to be a primitive species of the genus *Dolichorhinus*. The original description by Riggs is as follows:

> This genus [*Mesatirhinus*], reported for the first time from the Uinta formations, is apparently indigenous to the Bridger and Washakie Basins. It is represented in the Field Museum collections by a single specimen—an incomplete skull collected by Mr. J. B. Abbott from the top of the *Metarhinus* sandstones near gilsonite vein No. 2. The right arch is wanting, together with the basioccipital and condyles. The dentition is anatomically complete excepting the incisors.
>
> The skull presents striking similarities with the earlier representatives of *Dolichorhinus*. From the dorsal view, the nasals, facial, and supracranial regions appear very similar, though the cranial region does not have the pronounced downward curve characteristic of *Dolichorhinus*. In the palatal view more marked differences are noticeable. The premolars are more primitive, the molars smaller, and the posterior narial opening is unmodified. In these characteristics the specimen in hand resembles *D. heterodon* [28] from upper Uinta B more closely. However, it differs from that species in having a strong hypocone on the last molar and in the whole facial profile. In our present knowledge of these many closely related forms, this species may be regarded as the largest and most highly specialized representative of *Mesatirhinus*.

This animal occurs geologically at the very summit of Uinta B 1 (upper A of Riggs), fully 300 feet above the first occurrence of *Dolichorhinus longiceps*. This fact is important, because otherwise it would certainly be considered the direct ancestor of *Dolichorhinus*, since it affords a complete structural transition to this genus, as shown in the comparative outlines displayed in Figure 339. This is another very interesting instance of the survival of a primitive stage side by side with a progressive stage. We have an analogy in existing nature in the survival of the hippopotami of Liberia and the Nile regions of Africa, namely, *H. liberiensis* and *H. amphibius*, the former extremely primitive, the latter rather progressive.

Although the profile and the top views (figs. 339, 340) of the cranium of *D. superior* are closely similar to those of *D. longiceps*, the palatal view is less similar because of the entire lack of the secondary palate, which in its various stages of development is so characteristic of *Dolichorhinus*. In *D. superior*, moreover, the horn cores are even more rudimentary than in *D. longiceps*. There is a wide orbital-nasal area, and a sharp downward curve of the nasals. The species is also related to *M. petersoni* in its cephalic index, which is 52 as compared with 47 in *D. longiceps*—in other words, the skull is less dolichocephalic than that of the typical *Dolichorhinus*.

The opening of the posterior nares is opposite the margin of the second molar tooth, or in the same position as the primary nares of *Dolichorhinus*. The crowns of the molar teeth are somewhat shorter or more brachyodont than in *Dolichorhinus*. The molar cephalic index, or ratio of the length of the grinding series to basilar length of skull, is estimated as 38, the same as in *D. hyognathus*.

Dolichorhinus intermedius Osborn

Plate LXXIII; text figures 125, 342, 343

[For original description and type references see p. 184]

Type locality and geologic horizon.—Uinta Basin, Utah; *Eobasileus-Dolichorhinus* zone (Uinta B 2).

Specific characters.—As compared with *D. hyognathus*, of inferior size; p^1–m^3, 179 millimeters; m^{1-3}, 109; length, premaxillaries to condyles, 462; transverse zygomata, 190 (estimated); cephalic index of type 41, of paratype 45; faciocephalic index 49. Secondary palate present but less developed than in *D. hyognathus;* infraorbital shelf of malar relatively narrow; premolars less progressive with subconic deuterocones; all cingula less robust; nasals more pointed or less expanded distally.

This species when described in 1908 was regarded by Osborn as a structural ancestral stage, or ascending mutation toward the typical *D. hyognathus*. It now appears to be a dwarfed and somewhat more primitive form, which thus coincides in some of its characters with *D. longiceps* (the true ancestor of *D. hyognathus*) except that the horn bases appear to be more distinct. It might perhaps be regarded as a side or dwarfed phylum related to or identical with the *D. heterodon* of Riggs.

Materials.—The type is the skull Am. Mus. 1837, representing the main characters of this species. Another skull (Am. Mus. 2001) is somewhat less typical. These skulls are recorded from Uinta B 2.

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[28] Douglass, Earl, Carnegie Mus. Annals, vol. 6, p. 310, 1910.

The more exact level, however, is not stated. Only from their less progressive condition does it appear probable that they belong to a somewhat lower geologic stage than the typical *D. hyognathus*.

Proportions.—These animals are smaller than those referred to *D. hyognathus*. The type skull belongs to a young adult female with canines proportioned as in the females of the type species. The total length (462 mm.) is somewhat inferior to that of the older animal (Am. Mus. 2001), in which the length is 485 millimeters, as compared with an average of 550 in *D. hyognathus*. Similarly the superior grinding series measures 179 millimeters, as compared with 156 in *Mesatirhinus petersoni* and 206 in *D. hyognathus*.

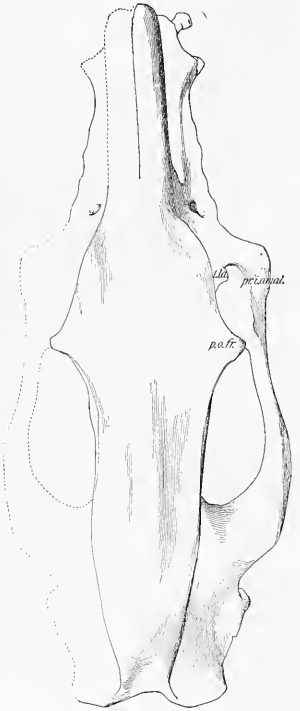

FIGURE 342.—Skull of *Dolichorhinus intermedius*

Top view. One-fourth natural size. Am. Mus. 1837 (type), White River, Uinta Basin, Utah, Uinta B 2.

Comparison with D. (cornutus) hyognathus.—The crania are of inferior dimensions throughout. The nasals are narrower anteriorly; the horns are less prominent and are borne entirely on the nasal bones; the flattened vertex of the skull in the parieto-occipital region is relatively narrow.

The incisors, as shown by i^3, preserved in Am. Mus. 2001, are deeply pitted or pocketed, posteriorly. P^1 is a small, simple tooth, less broadened anteriorly than in any specimens of *D. hyognathus*. The common characters as compared with *D. hyognathus* in p^2–p^4 are: (1) The crowns are less hypsodont throughout; (2) the protocone convexities on the ectolophs are more convex or less sharply constricted; (3) the tritocone convexities, on the other hand, are somewhat more prominent; (4) the deuterocones are more rounded or conic, and there is less prominence of the internal cingula and of the protoconules. All these characters indicate a lesser degree of progression.

Additional note on Dolichorhinus intermedius.—Three skulls in the Carnegie Museum from Uinta B 2 (middle levels), Nos. 3094, 3095, 3096, collected by Doctor Douglass, are referred to this species. The principal dimensions of two of these are given below:

Measurements of skulls of Dolichorhinus intermedius, in millimeters

	3094	3096
Pmx–condyles	472	462
Transverse zygomata (estimated)	170	
P^1–m^3	176	
P^1–p^4	70	
M^1–m^3	103	

Dolichorhinus longiceps Douglass

Plates XXX–XXXII, LXXIII, LXXV–LXXVII; text figures 135, 136, 254, 335, 339, 340, 343–346, 353, 589–591, 724

[For original description and type references see p. 188. For skeletal characters see p. 651]

Type locality and geologic horizon.—Uinta Basin, Utah; *Eobasileus-Dolichorhinus* zone (Uinta B 2). Geologic range 300 to 400 feet.

Specific characters.—Horn bases small; cranium large, 530–550 millimeters; breadth, 264–240; cephalic index 44–47; secondary palate in early stage of development, lying above level of primary palate; cranial vertex narrow posteriorly; premolars with relatively feeble internal cingula.

Geologic distribution.—The type skull of this primitive and clearly defined species, recorded by Douglass as "700 feet below Uinta red beds," would place the type well down in Uinta B 2. The four skulls (Field Mus. 12175, 12176, 12193, 12200) collected by Riggs extend from the lower to the upper portion of Uinta B 2 or the "upper *Metarhinus* beds" of Riggs. These specimens are somewhat smaller and less specialized than the type; they vary in length from 525 to 560 millimeters.

Type.—The type skull of Douglass has been distorted from right to left and from above downward, so that the left upper part is tilted and overhangs the left temporal fossa and orbits. The right premaxillo-maxillary rostrum is flat, and the general wearing plane of the left tooth row is tilted toward the right, while the parietofrontal vertex above the squamosal region is squeezed up into a long anteroposterior convexity.

This distortion makes it difficult to determine what are the real structural differences from *D. hyognathus*, but the judgment of Douglass in separating this species is fully confirmed by the skulls discovered by Riggs in Uinta B 1 and B 2. One skull (Am. Mus. 1852), presumably that of a female in regard both to measurements and to characters, appears to bridge over the differences between this species and the type of *D. cornutus* (=*hyognathus*), as shown in the following measurements:

Measurements of Dolichorhinus longiceps and D. hyognathus, in millimeters

	D. longiceps, Carnegie Mus. 2347 (type)	D. hyognathus	
		Am. Mus. 1852 (a transitional form)	Am. Mus. 1851 (type of Telmatotherium cornutum)
Tip of nasals to occipital crest (lateral)	590	--------	577
Premaxillary to condyle	[a] 555	[a] 550	550
Transverse zygomata	264	230	[a] 240
Face, anteroposterior (premaxillary to postorbital process, frontal)	[a] 270	270	280
Cranium, anteroposterior (postorbital frontal to condyle)	[a] 285	283	288
P^1–m^3	197	202	208
P^1–p^4	79	78	82
M^1–m^3	115	118	122
P^1, ap. by tr	15×11	--------	15×10
P^4, ap. by tr	21×29	20×26	23×27
M^1, ap. by tr	35× ?	36×33	34×34
M^2, ap. by tr	39×40	41×39	43×43
M^3, ap. by tr	39× ?	40×37	45×45

[a] Estimated.

Thus these measurements indicate that as compared with the type of *T. cornutum* (=*D. hyognathus*) the type of *D. longiceps* is somewhat broader and its tooth dimensions slightly less, except that p^4 is wider.

Field Museum skulls.—The four skulls as described by Riggs (1912.1, p. 33) are somewhat smaller, less specialized than the type, and range in length from 525 to 560 millimeters. One of the largest, a finely preserved skull, is shown in Plate LXXVI. There is little evidence of incipient horn cores. The nasals overhang the margins of the premaxillaries, which are somewhat narrower than in the type of Douglass. Compared with the type of *D. intermedius*, the smaller *D. longiceps* skull (Field Mus. 12193) approaches closely in size; the dental series is similar in length; the premolars are more advanced in structure. In the palate there is a ridge between m^2 and m^3 corresponding to the primitive position of the posterior narial border, which is bridged over by the outgrowth of thinner plates from the lateral margin of the palatal bones so that the nares have receded to a point behind the hamular processes of the pterygoids; the plates of this secondary palate are, however, so thin that they are often broken through, so that the secondary border of the posterior nares can not be precisely determined. The secondary palate in this species is pierced by a pair of foramina; its posterior extension is an enfoliate process free from the lateral walls and probably attached to the inferior margins of the vomer (Riggs).

A mandible associated with the incomplete skull of *D. longiceps* (Field Mus. 12200) is relatively strong, curved in the ramus, and broad at the angle. The skeleton of this same specimen, which was found near the base of Uinta B 1, is described on page 651.

The detailed measurements of these skulls are given in the following table:

Measurements of Dolichorhinus by Riggs, in millimeters

	D. longiceps, Carnegie Mus. 2347 (type)	D. cornutus, Field Mus. 12167	D. longiceps				D. fluminalis, Field Mus. 12205 (type)
			Field Mus. 12175	Field Mus. 12176	Field Mus. 12193	Field Mus. 12200	
Skull:							
Length, incisors to condyles	[a] 545	595	550	[a] 560	530	[a] 535	520
Breadth across arches	260	285	247	255	[a] 240	--------	233
Breadth above orbits	--------	--------	[a] 134	130	--------	132	116
Postorbital process to condyles	[a] 310	--------	305	305	295	264	--------
Last molar to condyles	--------	300	263	280	258	259	--------
Length of free nasals	152	--------	170	[a] 160	--------	--------	137
Greatest breadth of nasals	81	--------	79	--------	--------	--------	57
Postglenoids to condyles (median line)	--------	140	122	121	115	114	--------
Length of molar-premolar series	197	214	212	200	192	198	171
Length of molar series	115	135	131	124	121	122	105
Length of crown of canine	--------	40	24	--------	--------	--------	32
Diameter of crown of canine	--------	22	17	--------	16	--------	18
Length of diastema	15	16	14	--------	23	--------	--------
Narrowest point in sagittal area	40	--------	52	40	45	54	44
Breadth of orbitonasal area	--------	--------	--------	67	--------	--------	--------
Mandible:							
Length, condyles to incisors	--------	--------	--------	--------	--------	400	--------
Height, condyles above angle	--------	--------	--------	--------	--------	159	--------
Length of molar-premolar series	--------	--------	--------	--------	--------	209	--------
Length of molar series	--------	--------	--------	--------	--------	123	--------
Length of crown of canine	--------	--------	--------	--------	--------	29	--------
Diameter of crown of canine	--------	--------	--------	--------	--------	16	--------
Depth of ramus from base of p_3	--------	--------	--------	--------	--------	70	--------
Depth of ramus from base of m_3	--------	--------	--------	--------	--------	57	--------

[a] Estimated.

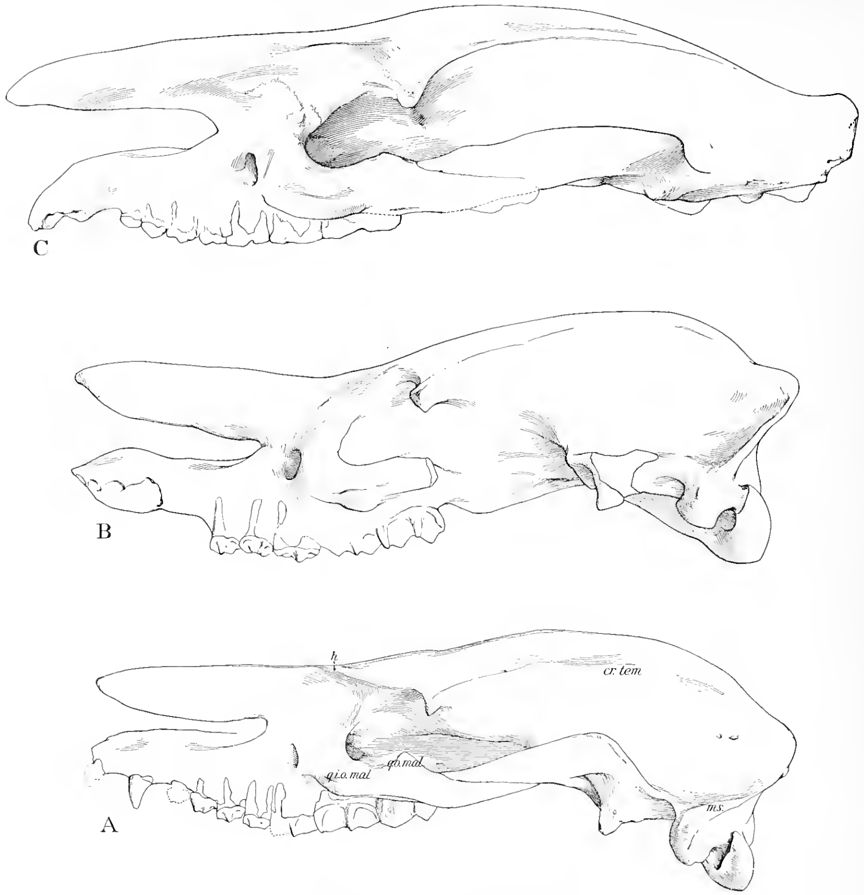

FIGURE 343.—Skulls of *Dolichorhinus*

From White River, Uinta Basin, Utah, level Uinta B 2. One-fourth natural size. A, *D. intermedius*, Am. Mus. 1837 (type), reversed; B, *D. heterodon*, Carnegie Mus. 2340 (type), reversed; C, *D. longiceps*, Carnegie Mus. 2347 (type), "from the lowest level at which fossils were found in horizon B" (Uinta B 2).

Measurements of Dolichorhinus heterodon, D. longiceps, and D. hyognathus, in millimeters

	D. heterodon, Carnegie Mus. 2340 (type)	D. longiceps		D. hyognathus, Am. Mus. 1851 (type of Telmatotherium cornutum)
		Carnegie Mus. 2865	Carnegie Mus. 2347 (type)	
Pmx–condyles	487	[a] 485	[a] 555	550
Transverse zygomata	240	[a] 225	[a] 264	[a] 240
M^1–m^3	114	119	115	122
P^4, ap. by tr.	22×25	21×26	21×29	23×27
M^1, ap. by tr.	33×32	32×33	35× ?	34×34
M^2, ap. by tr.	42×41	42×42	39×40	43×43
M^3, ap. by tr.	39×38	42×42	39× ?	45× ?

[a] Estimated.

Additional observations on Dolichorhinus longiceps.—A skull in the Carnegie Museum (No. 2865) referred by Mr. Peterson to *D. longiceps* is associated with a complete fore limb and other parts of the skeleton. It was found at a low level in Uinta B 1. It differs from the type of *D. heterodon* in having a larger m^3; it appears to be smaller than the type of *D. longiceps* in skull dimensions but somewhat larger in the second and third upper molars.

Mr. Peterson's description (1914.3) of this skull, with the mandible and hyoid bones, is in substance as follows:

> The specimen (No. 2865) consists of the greater portion of the skull, the posterior part of the mandible of the left and fragments of the right side, the hyoid arch, the cervical vertebrae, two dorsal and two lumbar vetebrae, together with the fore limb and foot practically complete.

Cranium and mandible.—The cranium is somewhat smaller than in the type of *Dolichorhinus longiceps*, the sagittal area of the parietals is more compressed laterally, the zygomatic portion of the squamosal is slenderer and less expanded laterally, and the basicranial axis has a greater bend. These characters together with the slightly larger teeth constitute the most marked differences in the two crania compared, but that they should be regarded as of specific value is rather questionable. The base of the skull has received some crushing fore and aft, a fact to which the greater curvature of the basicranial axis may partly be due.

The sudden downward bend of the occiput of *Dolichorhinus heterodon*, the flatter frontal region, the smaller preorbital ledge, and the smaller and more delicate nasals seem to separate that species more widely from the present specimen. Furthermore, the difference in the geological horizons in which *D. heterodon* and the present specimen were found is to be considered. The former came from horizon "Lower C," while the latter was found in the lower part of horizon "Upper A" of the Uinta sediments.

The high coronoid process and its sudden backward turn at the top, so characteristic of the mandible of *Dolichorhinus*, is well shown in this specimen. The angle is much compressed laterally, the temporal fossa is located high up but is quite deep, and the horizontal ramus has but small vertical diameter.

Measurements	Millimeters
Length of skull from anterior border of the orbit to top of occiput	365
Anteroposterior diameter of upper molar series	125
Transverse diameter of frontals at postorbital processes	145
Depth of mandible at m_3	71
Length of stylohyal, approximately	168
Anteroposterior diameter of basihyal, median line	15

Hyoid arch.—The hyoid arch may best be compared with that of the tapir, because in that genus there is apparently no extended anterior appendix or process such as is seen on the basihyal of the horse or the rhinoceros. However, the bone as a whole, especially its anterior border, is relatively heavier than in the tapir. The thyrohyal is unfortunately broken off on both sides. This element was perhaps relatively less developed than in *Tapirus terrestris*. The ceratohyal is also unfortunately broken off at the upper end, but its length was no doubt proportionately equal to that of the American tapir, while the shaft is less constricted anteroposteriorly. The epihyal is not present; this bone no doubt was nodular in character, as is the case in *Tapirus terrestris*. The anterior portion of the shaft of the stylohyal is rounder in cross section than in the tapir or the horse, but the upper end is flattened and terminates in enlarged processes, the superior attached to the hyoidial portion of the temporal bone and the inferior somewhat more obtusely rounded, extending downward and outward. This riblike upper end of the stylohyal is more suggestive of the rhinoceros or the horse than of the tapir. (See figs. 344 and 345.)

Dolichorhinus hyognathus (Osborn)

[*Telmatherium cornutus* Osborn]

Plates XVII, XLVI, LII, LIII, LV, LXXI, LXXII; text figures 27, 33, 105, 110, 215, 217–219, 254, 255, 302, 336, 337, 339–341, 346–353, 483, 511, 520, 521, 579, 580, 582–585, 588, 647, 661, 686, 737, 743, 745

[For original description and type references see pp. 169, 173. For skeletal characters see p. 645]

Type locality and geologic horizon.—Uinta Basin, Utah; summit of *Eobasileus-Dolichorhinus* zone (Uinta B 2). This animal is very abundant within its known geologic range through the upper 200 feet of Uinta B 2. The type specimen of *D. cornutus* (=*hyognathus*) and most of the crania in the American Museum collection were found by Peterson in the upper or "*Amynodon* sandstones," at the summit of Uinta B 2, but the animal has also been recorded by Peterson 150 feet below the summit of B 2. It is not thus far recorded in Uinta C. A single specimen has been found in the Washakie Basin, Wyo., on the 180-foot level of Washakie B 2.

Specific characters.—Skulls large, 550 by 240 to 595 by 285 millimeters; relatively narrow, cephalic indices 46 to 43; face relatively long, faciocephalic index 53 to 51; grinding series p^1–m^3, average 206 millimeters; molar-cephalic index 38; horn cores very prominent; face decidedly bent down on cranium—that is, cyptocephalic; secondary palate broad and nearly on the same plane with the primary palate; premolar ectolophs more hypsodont; premolar protocone convexities sharply ridged; molars with prominent cones and crests; vestigial protoconules; hypocones of m^3 very distinct.

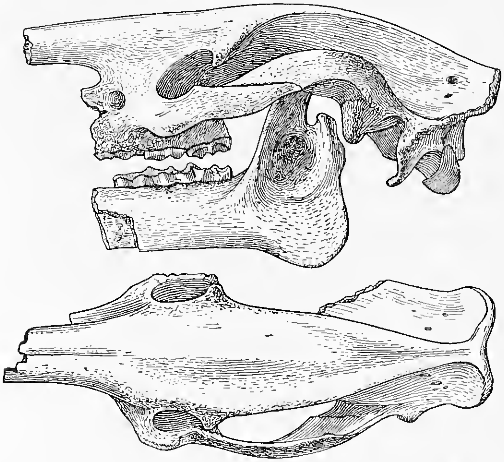

FIGURE 344.—Skull referred to *Dolichorhinus longiceps?*, side and top views

One-sixth natural size. After Peterson. Carnegie Mus. 2865.

This animal, from Uinta B 2, represents the most advanced stage known of this series. It appears to be a progressive descendant of *D. longiceps* from the base of Uinta B 1. The crania are somewhat larger in all dimensions than those of *D. longiceps* or *D. intermedius*, and the parieto-occipital vertex is broader.

Synonymy.—The male jaw, type of *D. hyognathus* (Princeton Mus. 10273), was found by the Princeton expedition of 1878 in Washakie B 2. When compared with the female skull and jaw (Am. Mus. 13164) found at the 185-foot level of Washakie B 2, it can not be separated specifically. Thus they must both be referred to *D. hyognathus*. These specimens in turn closely resemble in form and measurement the females in Uinta B 2 which were first referred to *D. cornutus*. Thus *D. cornutus* can not be separated specifically from *D. hyognathus*.

Materials.—No other Eocene titanothere is represented by so rich cranial material as this species. The numerous skulls and jaws, although uniformly recorded from the *Dolichorhinus* (*cornutus*) *hyognathus* zone (Uinta B 2 and Washakie B 2), were undoubtedly found at somewhat different levels and may represent different stages of mutative progression, although it seems impracticable to separate them into species. These crania are enumerated below.

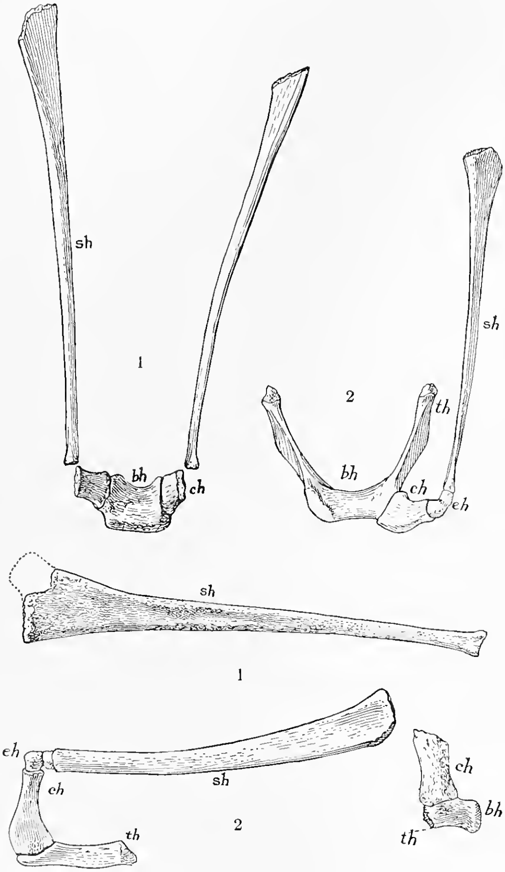

FIGURE 345.—Hyoid apparatus of *Dolichorhinus longiceps?* (1, 3) compared with that of a modern tapir, *Tapirus terrestris* (2)

One-half natural size. After Peterson. The two upper figures show a front view, the three lower a side view. This almost unique fossil belongs with the skull and jaws previously figured (fig. 344) and other bones comprising the specimen Carnegie Mus. 2865. bh, Basihyal; th, thyrohyal; ch, ceratohyal; eh, epihyal; sh, stylohyal. Compare the hyoid bones of *Brontops* sp. (Am. Mus. 518, fig. 425).

Washakie B 2:
- Princeton Mus. 10273, type of *D. hyognathus;* jaw of an aged animal.
- Am. Mus. 13164, skull and jaws of a young adult female; m^3 slightly worn, associated with parts of skeleton, fore limb, and parts of vertebrae.

Uinta B 2:
- Am. Mus. 1850, skull of a young adult male; m^3 just appearing.
- Am. Mus. 1845, skull of a young adult; m^3 in place but unworn.
- Am. Mus. 1851, skull (type of *Telmatotherium cornutum*) of aged female; m^3 well worn.
- Am. Mus. 1852, skull of young female; m^2 slightly worn.
- Am. Mus. 1848, very old skull; m^3 greatly worn, sex indeterminate.
- Am. Mus. 1843, anterior part of skull of large size, associated with complete backbone and humerus.
- Am. Mus. 1849, parts of skull and fragments of skeleton doubtfully recorded as of base of Uinta B 2.
- Field Mus. 12167, skull from Uinta B (1 or 2).

Jaws.—Besides the type of *D. hyognathus* from Washakie B 2, we have the jaws Am. Mus. 13164, associated with a skull. Also from Uinta B 2 we have thirteen jaws more or less completely preserved, including Am. Mus. 1834, 1836, 1840, 1852, 1854, 1855, 1856, 1857, 1858, 1941, 2008.

Skull.—The affinities of the skull of these animals to that of *Mesatirhinus petersoni* are apparent in many details of structure, but, as above noted, there is a very marked progressive advance, which is bridged over partly by the intermediate stages of *D. intermedius* and *D. longiceps.* The affinity to *M.* (=*Dolichorhinus*) *superior* is still closer. The full description which follows is based principally on the female skull Am. Mus. 1851 (type of *Telmatotherium cornutum*) and the superb skull and jaws, also of a female (Am. Mus. 13164), from Washakie B 2.

In the superior aspect (fig. 346) we are immediately struck by the extraordinary elongation of the nasals, which extend behind the line between the orbits and occupy a little less than one-half of the entire length of the skull. The longitudinal suture persists between the nasals and is traceable a short distance back between the frontals. These bones expand to 129 millimeters immediately above the orbits and are convex both anteroposteriorly and transversely; the line of junction between the frontals and parietals is obliterated. The vertex is here arched both transversely and longitudinally. The supratemporal ridges, now wholly lateral in position, follow the superior border of the supratemporal fossa; the top of the cranium is expanded slightly to 108 millimeters and then contracts to 62 millimeters just in front of the junction with the occipitals. This flattened arching and spreading of the vertex of the skull naturally differs both according to age or growth and the progressive stage of evolution which the skull represents. The superior view also displays the comparatively long and slender zygomatic arches, which reach a maximum width of 245 millimeters and an average width of 231, as compared with 550, the total length of the skull.

Horns.—The nasals diverge suddenly into the osseous horns, which lie directly above the orbits, whereas in *M. manteoceras* the horns lie in front of the orbits; they present an outward-directed elongate-oval convexity, to the posterolateral portion of which only the frontals contribute. On the vertex between the horns are gentle longitudinal valleys separated by median longitudinal convexities; the horn bases thus actually rise decidedly above the surrounding surfaces and overhang the orbits. A biologic fact of interest is that the horns appear to be developed as strongly in the female as in the male skulls and are not at this stage a distinctively sexual character; in none of the crania are they distinctly rugose, as in some of the male crania of *M. manteoceras*. Under these horn swellings, which are 127 millimeters apart, the nasals narrow to 66 millimeters, then broaden again to 76 at the widest point near their extremities.

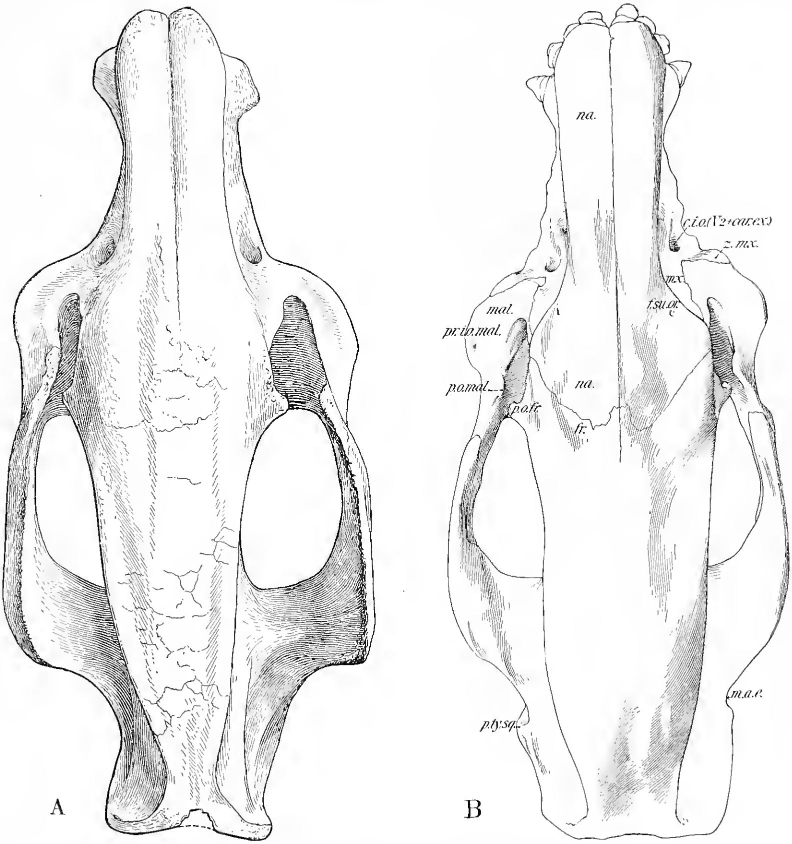

FIGURE 346.—Skulls of *Dolichorhinus*

Top view. One-fourth natural size. A, *D. longiceps*, Carnegie Mus. 2347 (type), Uinta Basin, Utah, Uinta B 2; after Douglass. B, *D. hyognathus*, Am. Mus. 1851, White River, Uinta Basin, Utah, Uinta B 2.

Palatal aspect.—As seen from below (fig. 347), the elongation of the palate, in which the palatine and maxillary plates take about equal share, is a most striking feature. The posterior nares open behind m^3. A kind of secondary palatal plate is formed by the backward and upward extension of the dorsal surface of the palatine. In this compressed postnarial chamber the maxilloturbinals appear as prominent paired eminences, as in Am. Mus. 13164. The extreme elongation of the posterior nares is unique among perissodactyls. The pterygoid plates of the alisphenoid are elongate and depressed on either side of the long and narrow postnarial depression. The palatines do not crowd into the postnarial space as in *M. manteoceras*. The infraorbital malar plates constitute a very prominent shelf, the anterior part of which is shown by the sutures to be composed of the maxillaries. To this prominent infraorbital shelf was probably attached an anterior slip of the masseter muscle, as in many other mammals with weak zygomata. Behind these projections the malars are seen to present a long and comparatively narrow edge. The lacrimals are larger and have a broader extension on the face than in any other species. The lacrimal tubercle is preserved in one skull, as in the *Palaeosyops* series.

Among the most striking results of progressive dolichocephaly are those seen in the conformation of the articular facets for the condyles of the jaw. The postglenoid processes are narrow and tuberous; the glenoid facets are not transverse in position but directed obliquely forward, as if their outer borders were drawn out anteriorly by a stretching of the skull. In *M. manteoceras* these glenoidal facets are more directly transverse. The whole basicranial region is correspondingly elongate, the bridge of bone separating the foramen ovale and the foramen lacerum medium now measures 42 millimeters as compared with 27 in *M. petersoni* or 17 in the brachycephalic *Limnohyops laticeps*.

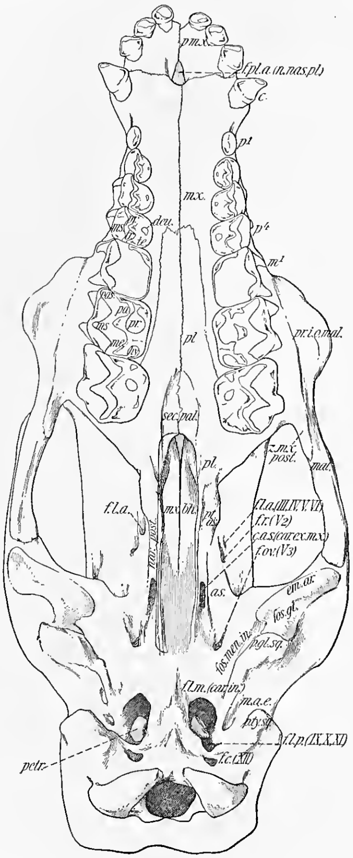

FIGURE 347.—Skull of *Dolichorhinus hyognathus*

Palatal view. One-fourth natural size. Am. Mus. 1851 (type of *Telmatotherium cornutum* Osborn). Supplementary details from Am. Mus. 1845. Both specimens from White River, Uinta Basin, Utah; Uinta B 2.

The anterior aspect of the skull (fig. 348) exhibits the extraordinarily long premaxillo-maxillary rostrum, which extends horizontally backward into the floor of the narial chamber, the total length being 144 millimeters. The infraorbital shelves are well shown. The infraorbital foramina are deep and narrow; the nasals are vertically decurved at the sides, so that they form three sides of a square. The projection of the nasal horns, although the animal is a female, is admirably illustrated.

The lateral aspect of the skull (fig. 349) shows that the midcranial concavity characteristic of *Manteoceras* and the Oligocene titanotheres is replaced in this species by the prominent frontoparietal convexity, the lowest point of the cranium in the upper profile being above the orbits between the horns. The suture between the maxillary and the nasals is similar in form to that in related species, the nasofrontal junction being above the orbit. The failure of the frontals to send forward a spur overlapping the enlarged nasals is well shown. A broadly concave space (68 mm.) separates the narial notch and the orbit, and the infraorbital foramen issues 33 to 40 millimeters in front of the orbit. The maxillaries contribute to the anterior portion of the infraorbital process, the chief convexity being formed by the malars. Below the orbits the malars are gently concave, as in the related species of this genus. Other characteristic dolichocephalic features are the limited vertical extent of the zygomatic portion of the squamosal, the great fore and aft thickening of the postglenoid processes, and the widely open external auditory meatus.

The occipital view (fig. 348), best shown in Am. Mus. 1845, is highly characteristic. The height of the occiput, 142 millimeters from the basioccipital to the supraoccipital crest, approximately equals the width across the middle of the occiput. Above the foramen magnum two prominent ridges diverge and terminate in tuberous convexities in the upper lateral portions of the crest.

The interior structure of the skull, including that of the narial and cranial cavities, is shown in Figure 254.

Dentition in general.—The grinding teeth are more or less perfectly preserved in most of the crania and jaws; three specimens afford a complete knowledge of the upper and lower cutting teeth.

Incisors.—The superior series has a semicircular arrangement (Am. Mus. 1851); the median pair are separated by a considerable diastema (12 mm.). The incisors increase in size regularly from i^1 to i^3. They exhibit convex anterior faces, more flattened posterior faces, with a median convex ridge. The posterior cingulum rises to form a distinct cup in i^1, less marked in i^2 and i^3. I^3 is fully incisiform (in contrast to its caniniform shape in the contemporary *Telmatherium*); it exhibits a narrow antero-external cingulum besides the postero-internal, obliquely sloping cingulum; it differs from other incisors in its more elevated crown. A narrow diastema (9 mm.) separates i^3 from the canine.

The inferior incisors are also arranged in semicircular series, have obtusely pointed crowns and evenly convex anterior faces, slightly recurved concave posterior faces, and a pronounced median rib, which expands into the basal cingulum. The transverse measurements of the broadest part of the crown in Am. Mus. 1856, a female, are respectively i^1, 14 millimeters; i^2, 17; i^3, 16. The entire breadth of these teeth in this specimen is 72 millimeters.

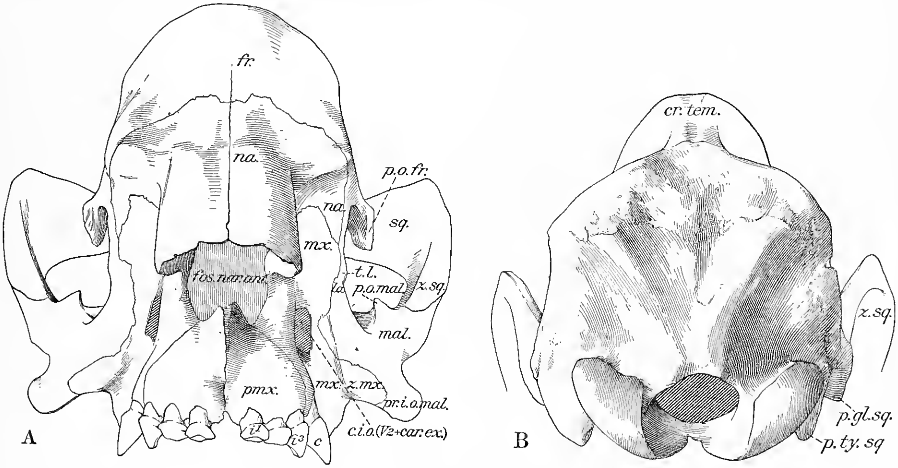

FIGURE 348.—Skulls of *Dolichorhinus hyognathus*

Front and occipital views. One-fourth natural size. A, Am. Mus. 1851 (type of *Telmatotherium cornutum* Osborn), front view. B, Am. Mus. 1845, occipital view. Both specimens from White River, Uinta Basin, Utah; Uinta B 2.

Canines.—The sexes are sharply distinguished by the size of the lower canines: in the males the enameled crown of the tusks measures vertically 41 millimeters, in the females only 27. The fine male tusks preserved in Am. Mus. 1850 (ap. 24 mm., tr. 21) are laterally compressed, with sharply defined antero-internal ridges and somewhat less prominent posterior cutting ridges. No internal basal cingulum is observed in this specimen. In the female tusks (No. 1856, ap. 18 mm., tr. 15) the anterior and posterior ridges are less prominent, but a large, obtuse posterior basal cingulum is observed. The lower canines are more obliquely placed and recurved than in *T. cultridens*. There is a conspicuous antero-internal cingulum, but the lingual side of the base of the crown is smooth in the middle basal portion only; elsewhere it is cingulate. The posterior cingular ridge is slightly less acute than in *T. cultridens*.

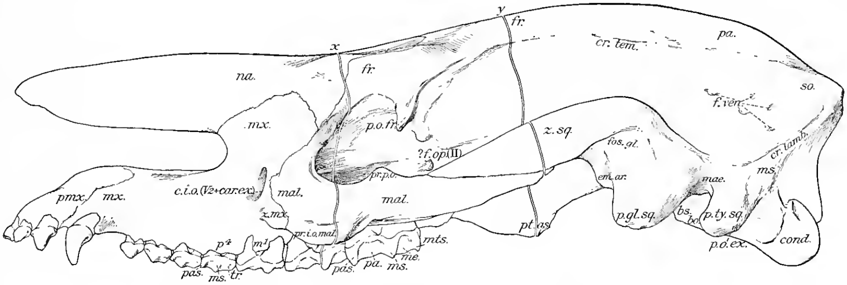

FIGURE 349.—Skull of *Dolichorhinus hyognathus*

Side view. One-fourth natural size. Am. Mus 1851 (type of *Telmatotherium cornutum* Osborn). White River, Uinta Basin, Utah, Uinta B 2. *x*, *y*, Section lines in Figure 255.

In the upper canines also the difference between the sexes is sharply marked, the male tusks in Am. Mus. 1850 measuring (ap. by tr.) 24 by 20 millimeters and having a vertical height of 42, whereas the female tusks of the type (Am. Mus. 1851) measure 18 by 15 and have an estimated crown height of 27.

Upper premolar-molar series.—The distinctive ectoloph characters of p^2–p^4 are a sharp vertical protocone rib or ridge, a flattened to gently convex tritocone, and a well-elevated ectoloph. In general this series is long, averaging 202 to 208 millimeters in length. The true molars are very strongly dolichocephalic in certain specimens (as in Am. Mus. 1850), in which the anteroposterior considerably exceeds the transverse measurement of each tooth. In other specimens, however (as in Am. Mus. 1851, type), the anteroposterior and transverse diameters are more nearly subequal. In most specimens the external cingulum is sharply defined, although there is considerable variation in this respect also. The ectoloph cusps and internal cones are subhypsodont, or elevated (paracone 34 mm. high, protocone 23 mm.). The internal cusps (the deuterocones of the premolars and the protocones and hypocones of the molars) throughout the series are rounded at the apices and are decidedly convex internally as compared with those in the *Telmatherium* phylum. Vestigial protoconules appear in the molars of Am. Mus. 1850. Small, more or less cingulate hypocones appear variably in m^3. A well-defined and sometimes broad internal cingulum extends around the lingual side of the premolars in the more progressive specimens (Am. Mus. 1850, 1851, 1852). P^2–p^4 in crown view appear more subcircular in outline than in *Telmatherium*.

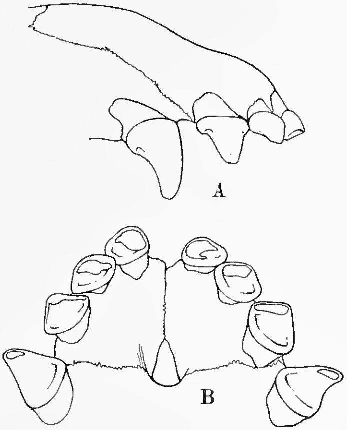

FIGURE 350.—Upper incisors and canines of *Dolichorhinus hyognathus*

One-half natural size. A, Am. Mus. 1851, White River, Uinta Basin, Utah, Uinta B 2, side view; B, Am. Mus. 1845, White River, Utah, Uinta B 2, crown view.

Premolars.—Of the superior premolars, p^1 is separated by a slight diastema (15 mm.) from the canine and is a bifanged, narrow, laterally compressed tooth (ap. 16 mm., tr. 9) with convex buccal and more concave lingual faces. The posterobasal lobe is becoming well defined. P^2 is more subcircular than in *M. petersoni*, its proportions being 20 by 19 millimeters, a condition which is due to the more anterior position of the deuterocone. The protocone and tritocone are subequal, but the protocone is much more prominent externally, the tritocone being still nearly flat. A rudimentary protoconule is observed (Am. Mus. 1850). In p^3 (ap. 20 mm., tr. 21) the inner portion of the crown is broader, a rudimentary protoconule is seen, a slight spur foreshadowing the tetartocone extends back from the deuterocone, the protocone exhibits a narrow but sharply convex buccal face, the tritocone is slightly convex, with a basal cingulum. In p^4 the ectoloph rises to 21 millimeters, the external cingulum is more continuous, and the inner side of the crown is relatively broader, the crown measuring 22 by 24 millimeters. In these premolars (p^3, p^4) the tetartocone rudiments are of the faintest character; in well-worn teeth they are not perceptible at all. *D. hyognathus* has less progressive tetartocones than *T. ultimum* but is very highly specialized in respect to the peculiar subcircular form of p^2–p^4.

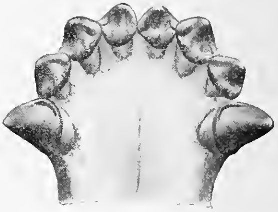

FIGURE 351.—Lower incisors and canines of *Dolichorhinus hyognathus*

One-half natural size. Am. Mus. 1856, White River, Uinta Basin, Utah, Uinta B 2; crown view.

D. hyognathus presents a considerable advance beyond *D. vallidens* and some advance beyond *D. intermedius* in the elevation of the ectoloph as a whole; the increased symmetry of the protocones and tritocones, especially in p^3, which is a much more progressive tooth than in *D. vallidens;* and the more nearly subcircular form of p^2–p^4.

A specific dolichocephalic feature of the inferior premolars is the spacing of p_1 in the midst of the long diastema between the canine and p_2, as seen especially in the type of *D. hyognathus,* in which this diastema measures 52 millimeters, the diastema in front of p_1 measuring 25 and that behind 14. These diastemata naturally increase as the individuals advance in age, and they are affected by individual growth, by the stage of evolution, and by the sex. In the female (Am. Mus. 1856) the total diastema between the canine and p_2 is 42 millimeters, nearly in the center of which lies p_1. The lower premolars are well preserved in Am. Mus. 1856, from which the following descriptions and measurements are taken: P_1 is a laterally compressed tooth, measuring (ap. by tr.) 15 by 8 millimeters, with the posterobasal lobe well defined and bearing a distinct cusp. In p_2 (ap. 23 mm., tr. 11) the protocone, which is somewhat less prominent (16 mm.), relatively, exhibits the antero-internal concavity and a rudiment of the antero-internal cusp (=paraconid); the posterior lobe (=talonid) is more distinctly of the

FIGURE 352.—Left upper canine of *Dolichorhinus hyognathus*

One-half natural size. Am. Mus. 1850; external view.

molar type and has a rudimentary fold analogous to the metastylid. In p_3 (ap. 23 mm., tr. 12) still further progress is made, there being quite a decided antero-internal valley and a well-defined posterior basin. In p_4 (ap. 24 mm., tr. 15) we find a submolariform tooth including a high metaconid and rudimentary paraconid but lacking the distinct entoconid.

Molars.—The superior molar series varies in length from 118 to 131 millimeters and in addition to the characters enumerated above exhibits a very broad and prominent antero-internal extension of the cingulum, the crown of m^2 being broader in front (43 mm. through parastyle) than it is behind (32 mm. through metastyle). In some specimens (Am. Mus. 1852) the hypocone of m^3 rises as a small but sharp and distinct cusp but is not so prominent as in the type of *Rhadinorhinus diploconus*. In other specimens (Am. Mus. 1851) it is less prominent and more cingulate. The proportions of the molars are given in detail in the table (p. 416).

The inferior molar series measures 138 millimeters in the female (Am. Mus. 1856). A very distinctive feature is the infolding of the external cingulum between the outer lobes of the tooth, which is, however, less marked in the type than in most other specimens. In the Princeton type of *D. hyognathus* (Princeton Mus. 10273) the only molar preserved is m_3, which measures (ap. by tr.) 64 by 25 millimeters, agreeing almost exactly with specimens in the American Museum. There is no proof of sexual inferiority in the female grinding teeth (m_3, ap. 62 mm., tr. 28), and we should not expect it, because the females require as much food as the males or more. In the type m_3 there are rudimentary folds on the inner valleys, and the hypoconulid has a crenulate internal cingulum.

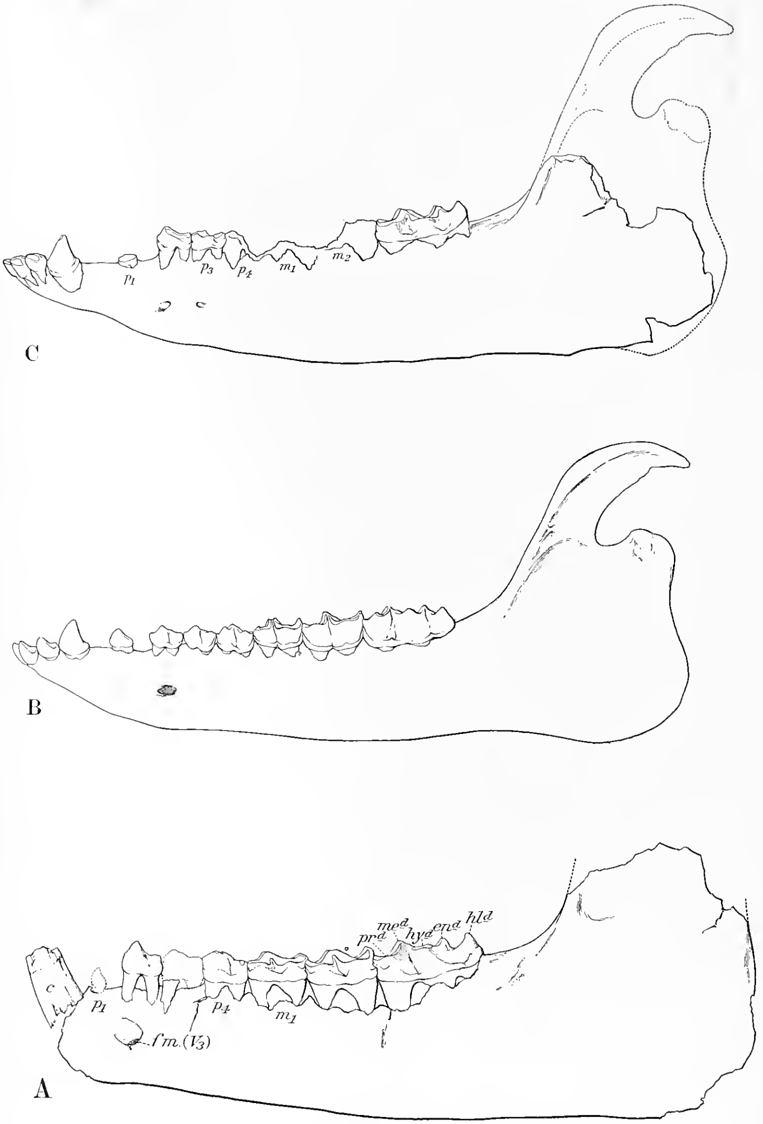

FIGURE 353.—Lower jaws of *Dolichorhinus*

A, *D. vallidens*, Am. Mus. 5098, one of the cotypes of "*Palaeosyops*" *vallidens* Cope, here regarded as the lectotype; Mammoth Buttes, Bitter Creek, Washakie Basin, Wyo.; Washakie B?. B, *D. hyognathus*, Am. Mus. 1856; White River, Uinta Basin, Utah, Uinta B 2; coronoid from Am. Mus. 1852 (*D. longiceps?*), White River, Uinta Basin, Utah, Uinta B 2. C, *D. hyognathus*, Princeton Mus. 10273 (type); White River, Uinta Basin, Utah, Uinta B 2; coronoid and angle restored from Am. Mus. 1852 (*D. longiceps?*). A one-half natural size; B and C one-fourth natural size.

In the more perfectly preserved m_3 of a female specimen (Am. Mus. 1856) the external cingulum is very feebly marked except opposite the external valleys.

The internal valleys are more prominent and conspicuous, and the hypoconulid is reduplicate. In the more worn m_2 of the same specimen (ap. 43 mm., tr. 25) these internal valley folds have been worn away, and the same is true of the still smaller m_1 (ap. 35 mm., tr. 20). The external cingulum is more sharply accented in some specimens (as in Am. Mus. 1855) than in others.

Jaw of Dolichorhinus hyognathus.—The somewhat fractured and crushed type jaw (Princeton Mus. 10273) presents the distinctively long and shallow ramus and shallow sloping symphysis that are characteristic of this species. (See fig. 353.) The measurements given below serve to determine the variations due to age, to sex, and in a measure to the progressive evolution of this type.

Measurements of Dolichorhinus hyognathus, in millimeters

	Washakie B 2		Uinta B 2			
	Am. Mus. 13164, ♀	Princeton Mus. 10273, ♂ (type)	Am. Mus. 1855, old ♂	Am. Mus. 1854, old ♂	Am. Mus. 1852, old ♀	Am. Mus. 1856, ♀
Condyle to incisive border	448	----------	----------	----------	445	430
Depth, condyle to angle	+135	----------	----------	----------	----------	[a]148
Depth, ramus behind p_2	58	65	65	65	53	54
Depth, ramus behind m_2	59	79	75	----------	55	60
Depth, ramus behind m_3	74	95	95	----------	----------	79
Length of symphysis	109	115	114	[a]112	102	117
Least width of chin	59	57	62	61	55	55
Free height of coronoid	----------	----------	----------	----------	65	----------
Thickness of ramus below m_2	----------	32	26	25	----------	29
Vertical thickness of symphysis posteriorly	----------	----------	37	34	27	30
Canine to m_3	268	[a]300	276	----------	270	274
P_1–m_3	230	[a]246	233	----------	223	238
P_2–m_3	213	[a]218	210	----------	194	207
M_1–m_3	138	[a]137	142?	----------	127	138
Transverse diameter of m_3	26	27	----------	----------	(?)	27

[a] Estimated.

We observe that the specimen from Washakie B (Am. Mus. 13164), a female, is practically similar in its measurements to the females found in Uinta B 2. (Am. Mus. 1852 may belong to the species *D. longiceps.*)

The most perfectly preserved rami are those of the females Am. Mus. 13164 (Washakie B) and 1856, from which Figure 353 B is taken.

The symphysis is greatly elongated (114 mm.) in the type of *D. hyognathus.* The ramus increases very gradually in depth from 50 millimeters in front of p_2 to 85 in front of m_3, being of moderate thickness (26 mm.) In the female jaw Am. Mus. 13164 (from Washakie B) the angle is produced moderately downward and backward, the condyle not being so greatly raised (138 mm.) above the angle as in the brachycephalic types. The most distinctive feature is the coronoid, which is produced backward so as to overhang both condyle and angle.

Dolichorhinus heterodon Douglass

Plate LXXIII; text figures 133, 134, 343

[For original description and type references see p. 187]

Type locality and geologic horizon.—Uinta Basin, Utah; horizon Uinta B 2 or C 1 (Douglass).

Specific characters.—A small, aberrant form, possibly related to *D. intermedius;* distinguished by somewhat larger size, p^1–m^3 189 millimeters, faciocephalic index 50. Secondary palate above level of primary palate; large occipital condyles; premolars and molars with heavy internal and external cingula; a distinct mesostyle and a prominent parastyle on p^4; premolar ectolophs very oblique. Agreeing with *D. intermedius* in general skull and tooth characters and especially in the marked anteroposterior convexity of the parietal vertex.

Materials.—Represented by the type specimen only, in the Carnegie Museum (No. 2340). As shown by the accompanying measurements this type represents an animal distinctly smaller than *D. hyognathus* and closely allied to *D. intermedius,* of which it may be a somewhat more progressive successor.

Among its primitive features is the elevation of the secondary palate above the plane of the primary palate. The secondary palate is present in the type specimen but has not yet grown downward near the horizontal plane of the primary palate as in *D. cornutus.* Among its progressive features distinguishing it from *D. intermedius* are the heavier internal and external cingula of the upper premolars and molars, the well-developed mesostyle on p^4, and the prominent parastyle on p^3, p^4. A very rudimentary mesostyle is observed on p^3, which is a rare feature among titanotheres, as ordinarily mesostyles are not developed in the premolars.

Comparative measurements of Dolichorhinus, in millimeters

	D. heterodon, Carnegie Mus. 2340 (type)	D. intermedius	
		Am. Mus. 2001	Am. Mus. 1837 (type)
Skull:			
Pmx to condyles	487	[a] 485	463
End of nasals to middle top of occiput	492	473	476
Face, anteroposterior (pmx to postorbital frontal)	245	247	227
Cranium, anteroposterior (postorbital frontal to condyles)	240	250	236
Transverse zygomata	-------	[a] 225	[a] 190
Dentition:			
P^1–m^3	189	177	180
P^1–p^4	76	72	72
M^1–m^3	114	105	109
P^1, ap. by tr	-------	12×10	-------
P^2, ap. by tr	17×17	16×17	16×16
P^3, ap. by tr	20×20	19×20	17×20
P^4, ap. by tr	22×25	21× ?	19×21
M^1, ap. by tr	33×32	31× ?	32× ?
M^2, ap. by tr	42×41	37×39	40×38
M^3, ap. by tr	39×38	38×38	35×37

[a] Estimated.

Dolichorhinus fluminalis Riggs, 1912

Plates LXXV–LXXVII; text figure 140

[For original description and type references see p. 191]

Type locality and geologic horizon.—Uinta Basin, Utah; "*Amynodon* sandstones," summit of *Eobasileus-Dolichorhinus* zone (Uinta B 2).

Specific characters.—Extreme backward extension of secondary palate. Skull rather small, 520 by 233 millimeters, cephalic index 45; faciocephalic index 48; molar-premolar series 171 millimeters; molar cephalic index 36. Nasals narrow and slightly tapering; posterior nares open between hamular processes; postorbital processes of jugal back of the last molar; incipient horn cores in the form of narrow ridges. Molar series relatively short; canines short and recurved.

Materials.—The only specimen known is the type skull in the Field Museum (No. 12205).

Specific relations.—The high geologic level, namely, the summit of Uinta B 2, is to be especially noted—that is, this animal occurs contemporaneously with the most advanced specimen of *D. hyognathus.* Like *D. heterodon* it appears to be related as a much more progressive form to *D. intermedius,* with which it agrees in the angulate form of the narial recess (which is rounded in *D. hyognathus*), in the tapering nasals, in the position of the postorbital processes of the jugal behind m^3 (which process is in front of m^3 in *D. hyognathus*). The face is relatively short, the faciocephalic index being 48; in *D. hyognathus* it is 53 to 51. The molar series is relatively short, the index being 36, while in *D. hyognathus* it is 38. Moreover, the skull and dentition is smaller than in *D. hyognathus* and is highly specialized in the extension of the secondary palate, the broad occipital vertex, straight tooth row, and extreme dolichocephaly of the basicranium.

In his original description Riggs observes (1912.1, p. 36):

> *D. fluminalis* displays a high degree of specialization in the postnarial characters. The nares are bridged over so as to obliterate almost all evidence of their primary position. In this process the opening has receded to a point back of the hamular processes. This recession, noted in less degree in other species, is evidence of a secondary adaptation to aquatic habits of feeding. Other characters of the skull in this species would not indicate that this animal was aquatic in its general habits. Like many other terrestrial mammals it probably fed upon submerged plants. The slenderness and delicate modeling of the skull would suggest an animal lighter of limb and more active than other species of this genus. In the development of horns the type of this species is more advanced than the type specimen of *D. cornutus* [*hyognathus*]. Its narrower sagittal area, its strongly recurved canines, and much smaller molars readily distinguish it from that species.

Sphenocoelus Osborn

Text figures 111, 354

[For original description and type references see p. 174]

Sphenocoelus appears to be referable to the subfamily Dolichorhininae. This animal may be an aberrant derivative of *Mesatirhinus*, but it is clearly distinguished from *Dolichorhinus*. The type skull of *Sphenocoelus*, so far as preserved, resembles that of *Metarhinus riparius* Riggs in general form and in many details. *Sphenocoelus* may therefore be closely allied to that type.

Geologic horizon.—Uinta B 1.

Characters.—Of extreme dolichocephalic type. Base of cranium with the basisphenoid laterally compressed to afford space for a pair of bony pits in the roof of the pharynx; a sessile sagittal crest; occiput low; occipital condyles excessively broad; glenoid facets oblique as in *Dolichorhinus;* external auditory meatus widely open inferiorly.

Geologic distribution.—The geologic level of the only known specimen (the type) is the middle portion of Uinta B 1 or "upper *Metarhinus* zone" of Riggs, where remains of this animal are found associated with *Dolichorhinus longiceps* but especially with the *Metarhinus fluviatilis* type. The type specimen (Am. Mus. 1501), consisting of the posterior part of the skull only, affords further proof of the wide adaptive radiation of the titanotheres. Although our present knowledge is confined to the posterior half of the type skull, it appears that this animal, although aberrant, probably belongs not far from the *Mesatirhinus-Dolichorhinus* phylum.

The name *Sphenocoelus* was applied to this form by Osborn because of the presence of two cavities in the alisphenoid bones on each side of the basisphenoid, which thus appears to form a septum between two elongate oval cavities, whose function is unknown. It may be conjectured that they lodged diverticula of the epithelial lining of the oral cavity or that the "pits" were mere antra, or hollow spaces, the outer wall of which became extremely thin or even partly incomplete. Similar thin-walled or partly open cavities occur on either side of the basisphenoid in certain specimens of the two-toed sloth (*Choloepus hoffmanni*).

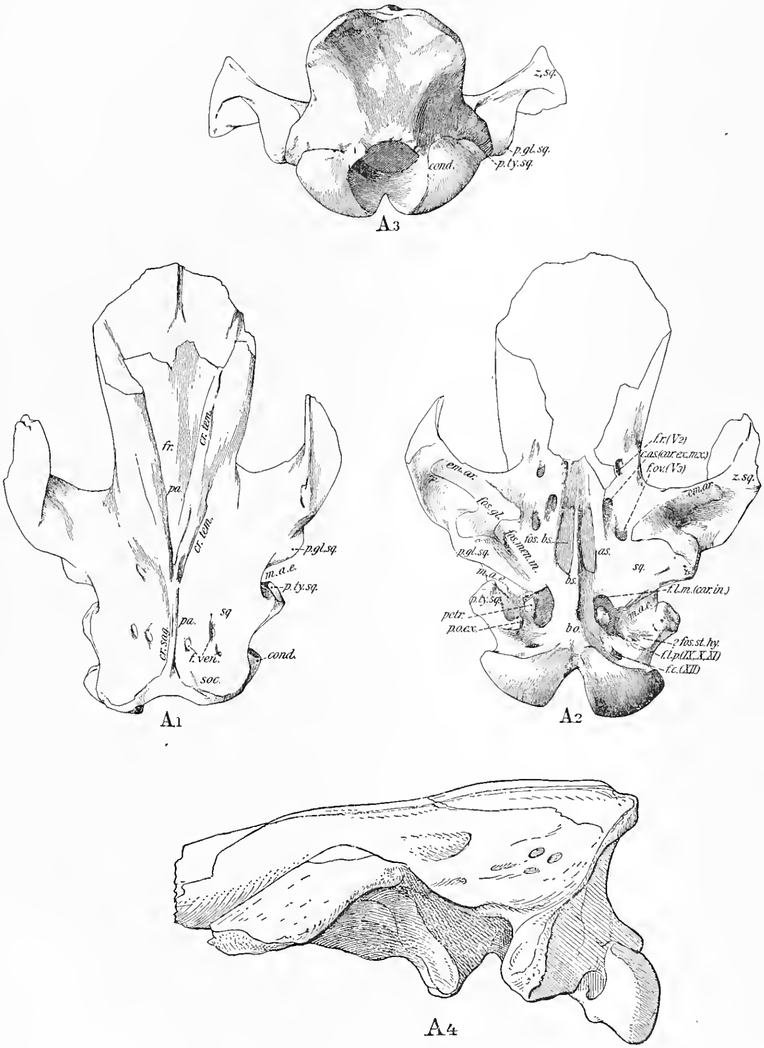

FIGURE 354.—Skull of *Sphenocoelus uintensis*

One-fourth natural size. Am. Mus. 1501 (type); Wagon Hound Bend, White River, Uinta Basin, Utah, Uinta B 1. A1, Top view; A2, basal view; A3, occipital view; A4, side view.

When this peculiar skull was first described the relationship of the animal to which it belonged was entirely uncertain. Now, after more detailed study of the Eocene titanothere skull in general and especially of the skull of *Dolichorhinus*, it appears that *Sphenocoelus* is certainly an aberrant titanothere and not a chalicothere (suborder Ancylopoda), as at first suggested. The chief considerations in favor of this view are the following: (1) The large alisphenoid canal relates it to the Perissodactyla; (2) the wide space between the foramen ovale and foramen lacerum medium (40 mm.) removes it from affinity with all other perissodactyl families except the Brontotheriidae and Equidae; (3) the basicranial region and especially the elongate, oblique form of the glenoid facets for the lower jaw is strikingly similar to that of *Dolichorhinus hyognathus*, although the postglenoid processes are somewhat different in form; (4) the detailed relations of the foramen rotundum, alisphenoid canal, foramen ovale, tympanic fossa, foramen condylare, as well as the form of the petrosal bone and of the paroccipital processes, point in the same direction; (5) the form of the temporal, sagittal, and occipital crests, the arrangement of the venous postparietal foramina, the spacing of the postglenoid and posttympanic processes (see top view in fig. 354), are all clearly foreshadowed in the brain case Princeton Mus. 10041 (figs. 713, 716), which is provisionally regarded as a very progressive *Mesatirhinus*.

Generic distinctions.—Mingled with all these points of resemblance to *Dolichorhinus* are striking generic differences, such as the pair of pits already mentioned, the short sagittal crest diverging into raised temporal ridges, the excessively large and broad condyles, and, as indicated in the widely separated postglenoid and post-tympanic processes, an extreme degree of dolichocephaly.

Sphenocoelus uintensis Osborn

Text figures 111, 354

[For original description and type references see p. 175]

Type locality and geologic horizon.—Wagon Hound Bend, White River, Uinta Basin, Utah; *Metarhinus* zone (Uinta B 1).

Specific characters.—Occipital condyles of striking breadth (131 mm.); occiput of moderate height (130 mm.), of considerable breadth (117 mm.); width across zygomatic arches (230 mm.) about the same as in *D. hyognathus.* The sagittal crest short (89 mm.) and thin (8 mm.) in posterior cranial region. Diverging, rounded supratemporal ridges.

Materials.—The only specimen known is the type skull in the American Museum (No. 1501). The most striking fact about *Sphenocoelus* is that although more specialized in certain points than *Dolichorhinus* it is geologically older than *D. hyognathus,* as it comes from Uinta B 1. *Sphenocoelus* may at present be regarded as a descendant of a certain type of *Mesatirhinus* (such as Princeton Mus. 10041, a brain case) which retained the narrow occipital crest but otherwise paralleled *Dolichorhinus.*

The sphenoid pit measurements are approximately as follows: Length 41 millimeters; width 13; depth 22. They are distinctly roofed over dorsally with bone. The function of these basicranial pits is entirely conjectural. Nothing similar has been observed in other Perissodactyla.

The occipital condyles exceed in width (131 mm.) those of even the very broad type of *D. hyognathus.* The glenoid facets exhibit a long, obliquely transverse extension, so characteristic of *D. hyognathus*; the postglenoid processes also have a peculiar obliquity. In front and to the outer sides of the postglenoids the squamosals are deeply concave.

Conclusion.—The peculiar pits remove this animal from any other known genus or species; it is possible that they are not constant characters. The various distinctive characters, while somewhat extreme, appear to be paralleled or foreshadowed in the member of the *Mesatirhinus-Dolichorhinus* series.

Eometarhinus Osborn

Text figures 156, 355

[For original description and type reference see p. 200]

This recently discovered *Eometarhinus* is recognized as ancestral to *Metarhinus* and is thus the earliest known member of the *Metarhinus* phylum.

Geologic horizon.—The type specimen was found 205 feet below the top of the Huerfano formation, in Huerfano B (*Eometarhinus-Trogosus* zone).

Generic characters.—Small; ancestral to *Metarhinus;* with rudimentary frontonasal horn; nasals elongate; overhanging premaxillaries, decurved as in *Metarhinus;* no infraorbital shelf; characters apparently intermediate between those of the *Metarhinus* and *Mesatirhinus* phyla.

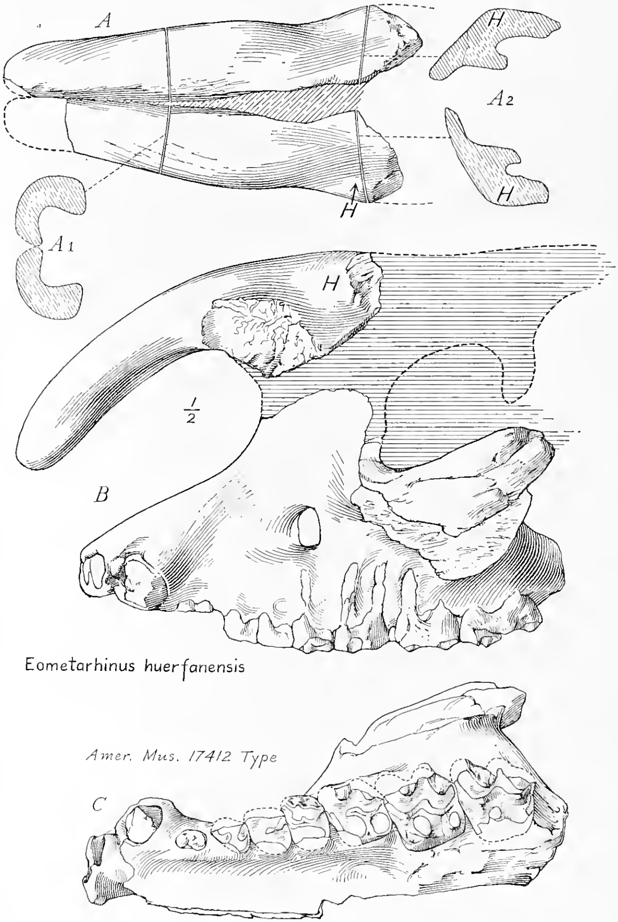

FIGURE 355.—Type skull of *Eometarhinus huerfanensis*, from Huerfano B

One-half natural size. A, nasals, top view; A_1, anterior nasal sections; A_2, posterior nasal sections; B, side view; C, palatal view with crown view of dentition. H, horn rudiments.

Type species.—*Eometarhinus huerfanensis.* (See below.)

Original description.—Osborn writes (1919):

> This new genus and species from the upper Huerfano is founded upon the anterior portion of a skull (Am. Mus. 17412)

representing an animal widely distinct in all its characters from the contemporary *P. fontinalis* and more closely related to the other group of middle Eocene titanotheres to which *Metarhinus*, *Mesatirhinus*, and *Dolichorhinus* belong. The most surprising character in an animal of this geologic antiquity is the very rudimentary osseous horns at the junction of the nasals and frontals, indicating the horn rudiment, a very ancient character in this phylum. The nasals are long, arched, decurved, and revolute on lateral borders, thus resembling the rhadinorhinal type in the metarhine group. The malars below the orbits are prominent. There was probably no infraorbital shelf, as in *Rhadinorhinus*. The comparative measurements of *Eometarhinus*, of *Mesatirhinus megarhinus*, and of the contemporary *Palaeosyops fontinalis* are shown below.

Eometarhinus huerfanensis Osborn

Text figures 156, 355

[For original description and type reference see p. 200]

Type locality and geologic horizon.—The type specimen was found near the Huerfano-Muddy divide, 3 miles west of Gardner, in the Huerfano Basin, Colo., 205 feet below the top of the Huerfano formation, in the *Eometarhinus-Palaeosyops fontinalis* zone (Huerfano B).

Specific characters.—Inferior in all measurements to *M. megarhinus*. Premolars with small deuterocone. P^1–m^3, 124 millimeters; p^1–p^4, 53; m^1–m^3, 72.

Materials.—This species is known from the type skull (Am. Mus. 17412) and from two referred specimens—a fragment of a lower jaw (Am. Mus. 17013) with the first and second molars preserved (Osborn, 1919.494, fig. 7, B), and the right and left fourth lower premolars with a fragment of a canine (Am. Mus. 17416). Both of these specimens are from approximately the same level as the type and from the same general locality. Doubtfully referred to this species are three fragmentary upper molars (Am. Mus. 17415), found 3 miles north of Gardner, on the lowest level of the upper Huerfano (Huerfano B), or 200 to 300 feet below the level of the type.

General characters.—The principal skull characters are noted above under the generic description. The dental formula is normal. The premolars are small, apparently very simple in pattern. The anteroposterior diameters of the molars appear to exceed the transverse; as they are in fractured condition, no accurate measurements can be taken. Apparently a hypocone on m^3.

Measurements of Eometarhinus, Mesatirhinus, and Palaeosyops, in millimeters

	Eometarhinus, Am. Mus. 17412	Mesatirhinus megarhinus, Am. Mus. 12202	Palaeosyops fontinalis, Am. Mus. 17425
P^1–m^3	124	147	[a] 146
P^2–m^3	109	133	[a] 131
M^1–m^3	72	83	83
P^4, anteroposterior	14	17. 5	16. 5
P^4, transverse	[a] 18	23	21. 5
M^1, anteroposterior	21	25	23
M^1, transverse		26. 5	26
M^3, anteroposterior	25. 5	28	29
M^3, transverse		31	34

[a] Estimated.

A tibia, found in association with the type skull, measures 275 millimeters (estimated) in extreme length.

Metarhinus Osborn

Plates LII, LXXI, LXXIV, LXXVIII–LXXX; text figures 123, 124, 138, 139, 219, 302, 323, 324, 341, 356–361, 404, 407, 509, 521, 522, 573–578, 647, 745.

[For original description and type references see p. 183]

Animals of medium or small size, divergent in structure, and probably different in habit and habitat from members of the *Mesatirhinus-Dolichorhinus* series, hence the name *Metarhinus;* perhaps of fluviatile or semiaquatic habit; skull with rudimentary horns, elongate expanding nasals, orbits prominent; opposite sides of the upper jaw firmly united, proportions mesaticephalic; persistent sagittal crest and narrow occipital condyles.

Geologic horizon.—This group of small animals is at present found only on one geologic level—namely, Uinta B 1 and Washakie B 1, which may be known as the *Metarhinus* zone. It originally sprang from the same ancestral stock as *Mesatirhinus megarhinus*, but in these "metarhines" dolichocephaly was arrested and mesaticephaly persisted. The four or five known species exhibit a considerable number of characters in common which afford ground for regarding them as a related natural group of the smallest titanotheres of the period; they are truly dwarfed forms. The skull is very broad across the orbits, which are notably prominent; immediately in front of the orbits the face contracts; the nasals are long and expand distally. There is some evidence that the phylum divides into two lines, consisting of broad-headed and narrow-headed forms that run parallel throughout the period represented by Uinta B 1.

The remains of these animals are very abundant, and the genera *Metarhinus* and *Dolichorhinus* are equally well represented (Riggs, 1912.1, p. 24) in Uinta B 1. The remains are usually associated in the same ledges and were apparently deposited under the same conditions. In one ledge of sandstone a large part of an articulated skeleton of *D. longiceps* was so mingled with the skeleton of a young *Metarhinus* that it was at first mistaken for a young animal of that genus. In other ledges, however, *Metarhinus* is very abundant and *Dolichorhinus* is absent. Other genera occurring in the same life zone are the more rare *Rhadinorhinus*, the giant amblypod *Eobasileus*, the small hyracodont *Triplopus*, and two large creodonts, *Mesonyx* and *Harpagolestes*. Occasionally crocodiles and numerous turtles are found, also beds of fresh-water clams. Reeds, leaves, and branches of trees are abundant in the upper sandstones of the *Metarhinus* zone.

Geologic occurrence in channels.—It is evident that our knowledge of this *Metarhinus* zone fauna is confined to that of the intrusive sandstone ledges of stream origin, because fossils are rarely found in the shales which alternate with these ledges (Riggs, 1912.1, p. 24). Skulls are often embedded in the semigravelly layers and have their narial or orbital cavities filled with pebbles which could be carried only by rapidly flowing water. Another evidence of stream action lies in the complete dissociation of the various skeletal elements; seldom are the lower jaws associated with the skulls, or so many as two vertebrae found articulated. In the exceptional instances where the whole skeletons are but little disturbed they are found embedded in the fine-grained homogeneous sandstone apparently deposited in more quiet water, such as deep pools or eddies.

This prevailing mode of occurrence supports Osborn's theory that these animals were of semiaquatic or fluviatile habits, as indicated by tne name given to the type species of the genus, *M. fluviatilis.*

Generic characters.—Small titanotheres, basilar length 355 to 415 millimeters. Persistently mesaticephalic; postcanine diastema short; orbits very prominent, with projecting infraorbital shelves; nasals expanding distally; narial opening deeply recessed at sides; premaxillary symphysis greatly elongated; snout moderately broad; rudimentary horns on frontonasal suture; sagittal crest high and thin. Incisor teeth small, cingulate; canine teeth small, pointed, recurved; grinding teeth subhypsodont; premolars rather progressive; hypocone of m^3 present or absent; hypoconulid of m_3 small, conic.

Historical notes.—The type species of this genus was recognized by Osborn (1908.318) from a specimen found in Uinta B 1, which had been confused previously with *Mesatirhinus megarhinus.* This is a very small animal, perhaps the primitive member of the series. At the same time Osborn recognized in Washakie B a second species, *M. earlei,* distinguished from *M. fluviatilis* by its much greater size and the lesser prominence of the orbits. After the successful expedition of 1910 in the Uinta Basin, Riggs (1912.1) added *M. cristatus,* an animal of intermediate size but of the same proportions as *M. fluviatilis,* also *M. riparius,* an animal of larger size with an apparently longer and narrower skull.

Osborn placed in the genus *Metarhinus* the species *M. diploconus,* which Riggs (1912.1) on excellent grounds removed to the new genus *Rhadinorhinus.* It is possible that the *Palaeosyops junius* of Leidy, from Bridger B, a very diminutive form, represents an ancestral form of this metarhine phylum.

Is Metarhinus diphyletic?—Riggs (1912.1, p. 27) regards the genus as including two phyla, one containing *M. fluviatilis* and *M. riparius,* which were more primitive and had longer heads and larger canines, the other containing *M. earlei* and *M. cristatus,* which were relatively shortheaded and had somewhat more progressive teeth. The restudy of these forms by cephalic indices partly sustains Riggs's opinion, but indices can be depended upon only when a considerable number of skulls can be measured, because the effect of crushing is deceiving. The indices actually taken are as follows: *M. earlei,* 63, 61, 60, 60, 60; *M. cristatus,* 60 (estimated); *M. fluviatilis,* 58, 56; *M. riparius,* 55, 51.

It would appear from these indices that *M. earlei* contains the forms with broadest heads and that *M. riparius* contains the forms with narrowest heads. There are also other characters which may divide these animals into two phyla, as shown below.

Phyla of Metarhinus

M. riparius	M. earlei, M cristatus, M. fluviatilis
More elongate skulls.	Broad-faced skulls.
Hypocone on m^3 constant.	Hypocone on m^3 variable.
Canines larger (? males).	Canines smaller (? females).
Frontals narrow.	Frontals broad.
Supracranial areas lyre-shaped.	V-shaped sagittal area.
Smaller molars.	Molars relatively large.

The synopsis of these species in chronologic order is as follows:

Metarhinus fluviailis Osborn. Middle of Uinta B 1; skull small, moderately broad (length 352 mm., breadth 205; cephalic index 56–58); a hypocone on m^3.

Metarhinus earlei Osborn. Summit of Uinta B 1 and Washakie B; skull somewhat larger (length 405 mm., breadth 255, or 338 : 245); somewhat broader (cephalic index 60–63); rudiments of a secondary palate; no trace of hypocone.

Metarhinus cristatus Riggs. Lower level of Uinta B 1; type skull of intermediate size (length 385 mm., breadth 240; cephalix index 60); hypocone present, cingulate; similar to *M. fluviatilis.*

Metarhinus riparius Riggs. Summit of Uinta B 1; skull larger (length 406 mm., breadth 210, or 406 : 210; cephalic index 51–55, estimated); apparently longer and narrower; a hypocone on m^3.

Metarhinus fluviatilis Osborn

Plates LII, LXXI, LXXIV; text figures 123, 341, 356–358, 404

[For original description and type references see p. 183. For skeletal characters see p. 644]

Type locality and geologic horizon.—White River, Uinta Basin, Utah; *Metarhinus* zone (Uinta B 1); abundant.

Specific characters.—Relatively short, broad skull, length 352 millimeters, breadth 205, or 355: 200; cephalic index 56 to 58. Eye socket small; circumorbital ridges prominent; premaxillary symphysis elongate; basicranial region short; sagittal crest high and prominent. Grinding teeth subhypsodont, m^3 with a rudimentary "cingulum hypocone" in the type.

Geologic distribution.—Uinta B 1 is the horizon of the type specimen (Am. Mus. 1500) and of the referred specimen (Am. Mus. 1877). Similar but somewhat more progressive forms showing the same diminutive measurements and probably representing higher mutations or species occur in Uinta B (Uinta B 2 of this monograph) according to Peterson's field records (1893)—namely, Am. Mus. 1946, 1864, 2059 (a tiny jaw), 1865. Riggs, however (1912.1, p. 21), reports no species of *Metarhinus* in Uinta B (Uinta B 2 of this monograph), nor have we found any specimens referable to *M. fluviatilis* in upper levels of Uinta B 1. It is possible that the line between B 1 and B 2 is not drawn at the same point by these two observers.

General characters and habits.—The type skull (Am Mus. 1500) is supplemented by a crushed skull (Am. Mus. 1877). Of the two skulls known neither includes the complete nasals nor affords a knowledge of the nasofrontal horn. We can not therefore speak positively as to this character. A further knowledge of these animals is afforded by Am. Mus. 1946, from Uinta B 1 (see geologic note above), which includes a palate with superior teeth associated with a jaw and parts of the pes and of the limbs. Also recorded from Uinta B 1 we find a series of upper teeth, which differ from those of the type in that the external cingulum is absent and the tetartocones on p^3 are somewhat more advanced. From Uinta B 2 also are recorded the American Museum jaws 1865 and 2059. The latter is a very small jaw.

This animal is by far the most diminutive of the known upper Eocene titanotheres—in fact, it may be described as a dwarfed form. The specific name, *M. fluviatilis*, was assigned by Osborn on the ground that the animal was probably a river-living animal. In size it is appreciably smaller than the known specimens of *M. earlei*, although the teeth are larger than those of the doubtfully referred *Metarhinus junius* from the Bridger.

Specific distinctions.—Distinctions from *Metarhinus megarhinus* are found in both the progressive and the adaptive characters. In its progressive characters, although it is an animal of inferior size, *M. fluviatilis* presents an advance upon *M. megarhinus* in the increased hypsodonty of the molar teeth, the increased strength of the external cingulum, the decidedly sharp and compressed parastyle, the upward curvature of the anterior portion of the grinding series, a character pointing toward the Oligocene brontotheres. The protoconids or anterior crests of p_{2-4} are ridged, and the cusps corresponding to the metaconid are better developed. The tooth progression is thus parallel with that of *Dolichorhinus* in certain respects, divergent in others.

The adaptive characters are most interesting. We observe especially that the narial openings are carried very far back on the sides of the face, so that a very narrow space is left between the orbits and the narial notch (a feature observed also in *M. earlei* and *Rhadinorhinus diploconus*). The region across the orbits shows unusual breadth (partly attributable to crushing), because the orbits as a whole are prominent and the circumorbital ring appears to be elevated and the eye sockets themselves are small. This feature is analogous to that in the Oligocene brontotheres, in which the orbits are small. We might therefore conjecture that these animals had adopted aquatic habits, because although the orbits are invariably prominent, the eyes tend to become smaller in all swimming ungulates. A pes provisionally referred to *M. fluviatilis* (from Uinta B 1) has slender metapodials, which would indicate cursorial rather than amphibious habits. The habitat must be left an open question until the skeleton becomes definitely known.

Correlated with a relative shortening and broadening of the skull is the narrowing of the occipital condyles. It is difficult to discover the reason for the elongation of the maxillary symphysis. The symphysis appears to be elongate partly because of the deep recession of the narial openings.

Detailed description.—The skull of this species exhibits a great number of interesting characters, because it presents a wide departure from the skull of all other Eocene titanotheres except those of the little group to which it belongs. It is a curious mixture of adaptive, progressive, and conservative characters. Among the last may be mentioned the relative elongation and height of the sagittal crest. The skull is sharply characterized specifically by the combination of the above characters with a prominent infraorbital shelf, a prominent antorbital bridge, and a prominent postorbital process. The superior view of this peculiar skull exhibits the elongate symphyseal union of the premaxillaries, recalling that of *Dolichorhinus*, the broadened posterior portion of the nasals, the deep lateral depression of the face, or antorbital fossae in front of the orbits, the prominent lateral projection of the orbits, the relatively short supratemporal ridges, which rapidly unite posteriorly, the prominent, narrow sagittal crest. The general resemblance of this aspect of the skull to that of *Rhadinorhinus diploconus* is quite apparent. The palatal view brings out distinctive features. The posterior narial space is long and narrow with parallel sides, the palatines not projecting inward as in *Manteoceras manteoceras*. As compared with that of *R. diploconus* it appears to afford the following important differences: In *M. fluviatilis* the basicranial region appears to be less dolichocephalic, the zygomata are relatively heavier, the infraorbital shelf (wanting in *R. diploconus*) is very prominent. The anterior view of the skull exhibits a prominence above the orbit which possibly represents a supraorbital frontonasal horn element; it may, however, be due to crushing. The lateral aspect of the skull is equally distinctive, as it exhibits the deep narial notch separated from the orbit by a very narrow interval, the prominent antorbital bridge concealing the infraorbital foramen, and the sharp and deeply depressed infraorbital shelves. The peculiar elevation of the front of the upper jaw may be partly increased by crushing but appears to be correlated with a similar upward flexure of the front part of the lower jaw (figs. 356, 358). The third molar is somewhat farther back with reference to the orbit than in *Dolichorhinus*.

Dentition of type and referred specimens.—Some of the "referred" specimens are recorded from Uinta B 1 and may well belong to a more progressive species than *M. fluviatilis*. The following description of the dentition includes the referred Uinta B 1 specimens which may belong to more progressive mutations or species than the type of *M. fluviatilis*.

The teeth of this diminutive titanothere are represented by the very much worn and somewhat crushed series of the type (Am. Mus. 1500, Uinta B 1) and by the perfect grinding teeth of Am. Mus. 1946, Uinta B 1, with which is associated the lower dentition; also by the complete dentition of another jaw (Am. Mus. 2059, Uinta B 1) and possibly by a more fragmentary upper jaw (Am. Mus. 1864) from Uinta B 1.

Incisors: The six upper incisors, as seen from the lower side, are arranged in a semicircle, much as in *Dolichorhinus*. They have smooth, gently convex anterior faces and increase gradually in size from i^1 to i^3, a tooth which is separated from the canine by a narrow diastema. The inferior incisors as exhibited in Am. Mus. 2059 are intermediate between the *Mesatirhinus megarhinus* and *Dolichorhinus* types, pointed by wear, increasing in size very gradually from i_1 to i_3, and having smoothly concave posterior surfaces bounded by a sessile cingulum.

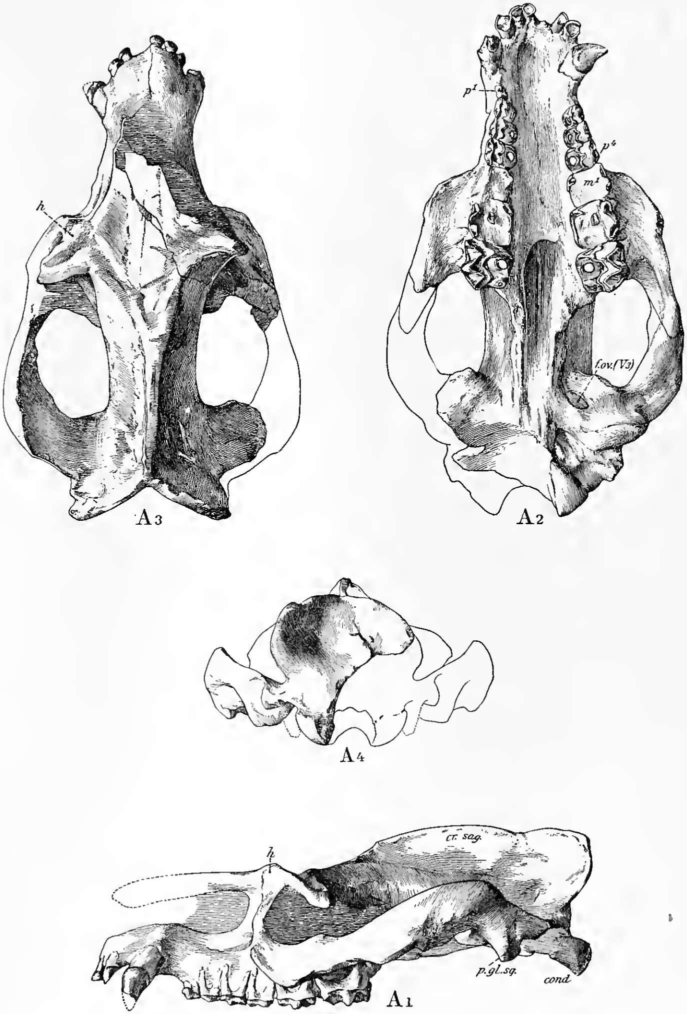

FIGURE 356.—Skull of *Metarhinus fluviatilis*

One-fourth natural size. Am. Mus. 1500 (type); White River, Uinta Basin, Utah; Uinta B 1. A_1, Side view (crushed downward); A_2, palatal view; A_3, top view; A_4, occipital view.

Canines: The superior canines are also of the *M. megarhinus* form and although much crushed in the type exhibit evidence of smoothly rounded sides swelling toward the base of the crown and accented by very delicate anterior and posterior ridges. The coronal measurements (ap. by tr.) are 17 by 16 millimeters. In Am. Mus. 1946, although probably a male, the canines are still smaller (ap. 18 mm., tr. 16). The inferior canines in jaw Am. Mus. 1946 are finely preserved except at the tips, measuring 15 by 14 millimeters; they exhibit a strong antero-internal cingulum at the base. In the other jaw (Am. Mus. 2059), obviously a female, the canines are much smaller (height 18 mm., ap. 13, tr. 12), with strong antero-internal cingulum, slightly recurved apex, and somewhat expanding base. The incisors and canines as a whole seem to foreshadow the short swollen type seen in the Oligocene Brontotheriinae.

Superior premolar-molar series: The grinding series, although of diminutive dimensions (145 mm. in the type, which includes p^1, and 137+ mm. in the longitudinally crushed cotype), are really more progressive in character than those of *M. megarhinus* in the following respects: (1) P^2 has a subquadrate instead of elongate subtriangular crown, the trito- and deuterocones being subequal; (2) m^3 has an elevated postero-internal cingulum, which forms a subfunctional hypocone in the type; (3) the ectolophs of p^2, p^4, as well as of the molars, are relatively more elevated.

Premolars: The premolars of the type measure (ap. by tr.), p^2, 13 by 14 mm.; p^3, 15 by 19; p^4, 17 by 23. The internal cingula are well defined and progressive, completely surrounding the deuterocone of p^2 and nearly surrounding the deuterocone of p^4. The external cingula of p^2, p^3 are not well marked across the protocone but are very pronounced opposite the tritocone; in p^4 they are strongly developed opposite both cusps, and the protocone "rib" was also pronounced, all marks of relatively advanced specialization.

The coronal pattern is exhibited much better in Am. Mus. 1946, in which the premolar measurements (ap. by tr.) are, p^2, 15 by 17 millimeters; p^3, 15 by 20; p^4, 17 by 23.

FIGURE 357.—Right lower premolars (p_1–p_4) of *Metarhinus fluviatilis*

Crown view. Natural size. Am. Mus. 1946; White River, Uinta Basin, Utah, Uinta B 1.

The most significant features of the premolars in this specimen (No. 1946) are as follows: (1) The deuterocones are large and give a well filled out subquadrate inner contour to p^3, p^4; (2) the tritocones are very large and progressive, especially in p^3, p^4, and have subflat ectoloph faces except in p^2, which has a more convex tritocone ectoloph; (3) the protocones (antero-external cusps) have large, sharply defined external ribs; (4) no tetartocones are yet present; (5) the external cingula are very advanced, rising into prominent parastyles, faintly continuous across the protocone base in p^3, p^4, and better defined opposite the tritocone; the external cingulum of p^4 at the base of the tritocone surrounds a sharp protuberance, emphasizing the gentle protuberance seen here in *M. megarhinus*; (6) the internal cingula are well defined but still incomplete opposite the deuterocone, the posterior cingulum of p^3, p^4 very broad; (7) the internal cones of the premolars and molars are relatively elevated, and they have very thick enamel, these conditions causing the partly worn tips to be sharply truncate.

Allowing for differences in wear and for some differences in level, we conclude that, from the evidence of the premolars, No. 1946 is related to or referable to *M. fluviatilis.*

The inferior premolars, measuring 59 millimeters in Am. Mus. 1946, are also more advanced than those of *M. megarhinus.* P_1 is more advanced than in that species; it is more elongate, has a larger posterobasal swelling, a lower, rounder tip, and a faint rudiment of the anterior valley. There is a faint external cingulum on the anterior and posterior end. Its measurements are 10 by 6 millimeters (ap. by tr.). P_2 is also more advanced than in *Mesatirhinus*, with a lower trigonid, a somewhat higher talonid, and better-defined anterior and posterior valleys. Its measurements are 16 by 95 millimeters. In p_2–p_4 the protoconid forms a high, blunt transverse ridge, extending internally into the cusp analogous to the metaconid. In p_3 (ap. 16 mm., tr. 10) the molariform tendency is still more pronounced, the posterior lobe being stronger, with rudiments of the internal styles appearing. P_4 (ap. 18 mm., tr. 13) exhibits a somewhat more accented external cingulum, and the cusp analogous to the entoconid is much more elevated than in *Mesatirhinus* and only less elevated than in the molars.

Molars: The lower molars do not differ greatly from those of *M. petersoni*, except that they are of slightly smaller size (98 to 103 mm.), have the external cingula a little better defined, are perhaps slightly more hypsodont, and have a more conic hypoconulid on m_3. In *M. fluviatilis*, as in *M. megarhinus*, the hypoconulid of m_3 is of small size and variable (or progressive) from a crescentic to conic form.

Lower jaws of Metarhinus fluviatilis; type and referred specimens.—The type skull lacks the jaw. The superior grinding series (Am. Mus. 1946) is associated with the jaws, and they are also found in the nearly perfect jaw of Am. Mus. 2059 and in the left ramus of Am. Mus. 1865, which is from Uinta B 1. The diminutive jaw forming Am. Mus. 2059 barely exceeds in length the jaws of certain specimens of *Eotitanops borealis*, but the rami are relatively deeper, and the dentition is of course far larger and more advanced.

Measurements of the lower jaws of specimens of *Mesatirhinus* and *Metarhinus* are given in the accompanying table:

Measurements of species of Mesatirhinus and Metarhinus, in millimeters

[Specimens in Am. Mus. except 12195, which is in the Field Museum]

	Mesatirhinus			Metarhinus				
	M. megarhinus, Bridger No. 1520	M. petersoni, Bridger		M. earlei, Washakie B, No. 13179	M. sp., Uinta B, No. 1859	M. fluviatilis, Uinta B		M. riparius Uinta B 1 (upper Metarhinus beds), No. 12195
		No. 1567	No. 1512			No. 1946	No. 2059	
Incisive border to angle			325	325	[a] 350		280	
Incisive border to condyle				325	350		285	338
Posterior border of jaw to m_3		132	112	[a] 90	90		78	
Depth below m_3		74	83	79	86		62	
P_1–m_3	162	168	172	169	195	161	157	172
M_1–m_3	94	99	103	106	[b] 118	102	98	110

[a] Estimated.

[b] Average.

These jaws are distinguished by the laterally constricted chin, correlated with the constricted premaxillaries above; also by the slender rami with the lower borders slightly downcurved below the grinders and upcurved below the coronoid, extending back into an angle which is produced posteriorly, as in *Mesatirhinus.* With the exception of the chin, the jaw, so far as known, was of the *Mesatirhinus* type. The anterior border of the coronoid is decidedly angulate in character; the coronoid itself rises with nearly parallel anterior and posterior borders to a gently recurved tip. These characters suggest those of a dwarfed collateral of *M. megarhinus.* In the supposed female (Am. Mus. 2059) the ramus appears much deeper and more slender than in Am. Mus. 1946.

The type of Heterotitanops parvus Peterson—is it a young Metarhinus?—A very young, perhaps a fetal skeleton in the Carnegie Museum (No. 2909), the type of *Heterotitanops parvus* Peterson (figs. 150–152), may possibly represent *Metarhinus fluviatilis.* It was found lower down in Uinta B 1 than any other known mammalian remains. The type of *Metarhinus fluviatilis* was also found by Mr. Peterson in Uinta B 1. According to W. K. Gregory its reference to *Metarhinus* or to some closely allied genus is indicated by the following facts:

1. The deciduous cheek teeth, in size and appearance, bear to the adult dentition of *Metarhinus fluviatilis* much the same relation as the deciduous dentition of Oligocene titanotheres (Pl. XXIII) bears to the permanent dentition—that is, the deciduous molars are more molariform than the permanent premolars, and they are elongate anteriorly and have more widely open external V's and less prominent mesostyles.

2. The large upper and lower grinding teeth that have not wholly emerged from the alveoli are probably not m^1 and m_1, as supposed by Peterson, but dp^4 and dp_4. The anteroposterior diameters as given by Peterson are dp^4 21 millimeters, dp_4 25, dimensions nearly as great as in m^1 and m_1 of the *Metarhinus fluviatilis* type and apparently large enough for dp^4 and dp_4 of that species. The resemblance of dp^4, dp_4 to m^1 and m_1 of that species seems sufficiently striking to indicate congeneric relationship. The measurements of dp_4 are also not inferior to those of dp_4 in *Mesatirhinus* sp. (Am. Mus. 12211).

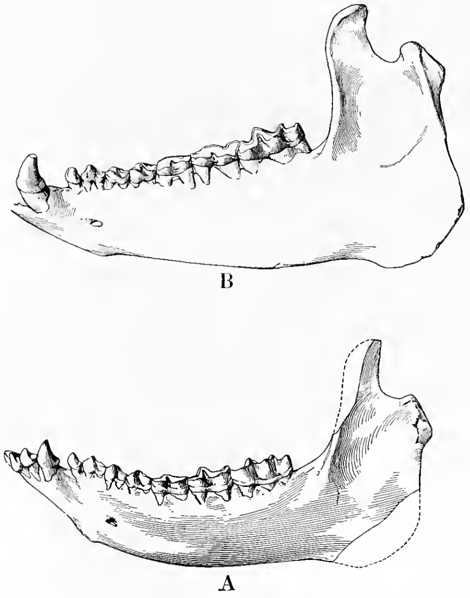

FIGURE 358.—Lower jaws of *Metarhinus*

One-fourth natural size. A, *M. fluviatilis,* Am. Mus. 2059, White River, Uinta Basin, Utah, Uinta B 1; B, *M. earlei,* Am. Mus. 13179, northwest point of Haystack Mountain, Washakie Basin, Wyo., Washakie B.

3. The deep lateral excavation of the anterior nares, which leaves a very narrow bridge of bone between the narial sinus and the orbit, a feature characteristic of *Metarhinus* and its near allies, is strongly marked also in the specimen under consideration.

4. In the side view the form of the lambdoidal ridges of the occiput is not dissimilar to that of *Metarhinus*; however, these ridges do not unite above into a narrow median crest as they do in *Metarhinus fluviatilis* but form a flattened vertex which suggests that of *Dolichorhinus intermedius*. Possibly the median crest of the adult *M. fluviatilis* may be derived by the upgrowth of these lambdoidal ridges toward the midline. At any rate the form of occiput seen in *Heterotitanops* is not seen elsewhere outside the subfamily Dolichorhininae. In brief the animal named *Heterotitanops parvus* may provisionally be regarded as the young of *Metarhinus fluviatilis*.

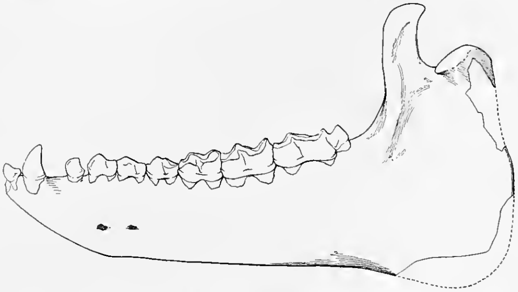

FIGURE 359.—Lower jaw of *Metarhinus*? (*Rhadinorhinus*?) sp. One-fourth natural size. Am. Mus. 1859; White River, Uinta Basin, Utah, Uinta B 1.

The postcranial skeleton has been well described by Peterson and is chiefly interesting as illustrating the highly progressive or caenogenetic character of the skeleton, which foreshadows the adult in the expansion of the scapula, of the proximal end of the humerus, and of the ilia, as well as in the great relative size of the thorax and in the general proportions of the limb bones.

Metarhinus earlei Osborn

Plates LXXVIII–LXXX; text figures 124, 219, 302, 358, 361, 407, 521, 522, 573–575, 577, 647, 745

[For original description and type references see p. 183. For skeletal characters see p. 644]

Type locality and geologic horizon.—North side of Haystack Mountain, Washakie Basin, Wyo.; *Metarhinus* zone (Washakie B 1). Also abundant in Uinta Basin, Utah, at the summit of the *Metarhinus* zone (Uinta B 1), in the "*Metarhinus* sandstones" of Riggs.

Specific characters.—Skull (Am. Mus. 13166, type), length 393 millimeters, breadth 240, or 388:245, or 405:255; cephalic index 60–63. Occipital condyles narrow (78 mm.), premaxillary symphysis elongate, nasals elongate, spreading distally, prominent infraorbital shelf. Type p^1–m^3, 167 millimeters. Molar series broad and low crowned, no hypocone on m^3; canines slender, diastema short.

This animal is readily distinguished from *M. fluviatilis* by its superior size and by the lesser prominence of the orbits.

Geologic distribution and materials.—The type of this species is a skull (Am. Mus. 13166), fortunately discovered by the American Museum expedition of 1906 in Washakie B 1. The nasals and the nasofrontal horn region of the type are broken away. A jaw belonging to another individual (Am. Mus. 13179) was also found in Washakie B 1 and agrees approximately in measurement with this skull. It may prove to belong to the same species.

In the Riggs collection of the Field Museum there are two skulls (Nos. 12169 and 12187), also two lower jaws (Nos. 12178 and 12189). These four specimens are recorded from the uppermost "*Metarhinus* sandstones," or the *Metarhinus* zone (Uinta B 1).

Skull.—The first feature of note in the type skull is the mesaticephalic proportions, the measurement being 240 millimeters across the zygomata and 393 from the condyles to the symphysis—that is, the width is a little less than two-thirds the length, whereas in *Mesatirhinus petersoni* skulls the width is only a trifle more than one-half the length. Correlated with this feature is the relative narrowness of the occipital condyles (78 mm.). The occipital region is also distinctive because of a deep pit on the upper part of the occiput and a pair of hooklike processes turning inward on the borders of the occipital crest (fig. 361); these falciform, incurved, overhanging borders are quite distinctive. The sagittal crest is short. The infraorbital shelf is prominent but slender. There is no hypocone on m^3. We are especially struck by the prolongation of the premaxillary symphysis, as illustrated in Figure 361, and the resemblance to *Dolichorhinus*. The well-preserved basicranial region, which is also of mesaticephalic character, indicates the affinities of this species to *Mesatirhinus megarhinus* and more remotely to *M. petersoni*.

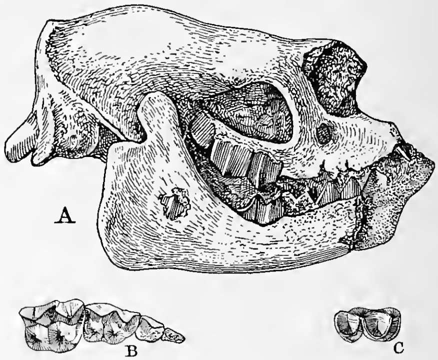

FIGURE 360.—Skull and deciduous teeth of type of *Heterotitanops parvus*

One-half natural size. After Peterson. Carnegie Mus. 2909 (type), White River, Uinta Basin, Utah, Uinta B 1. Possibly a young *Metarhinus*. A, Skull; B, right upper deciduous molars (dp^2, dp^3, dp^4); the anterior tooth is probably the permanent p^1; C, left lower deciduous molar (dp_4).

The fine skull in the Field Museum, No. 12187, illustrates the very peculiar constriction of the nasals in front of the orbits and their distal expansion, also the rudimentary horn bosses and curved nasals in lateral view. Riggs notes that the Uinta Basin representatives of *M. earlei* are somewhat broader headed and more massive than the Washakie Basin type and that in both the Field Museum skulls the hypocone on m^3 is wanting; there is also a slight elongation of the postcanine diastema. (Riggs, 1912.1, p. 30.)

Dentition.—A feature distinguishing this animal from both *M. megarhinus* and *M. fluviatilis* is seen in the double convexities (protocone and tritocone) of the ectolophs of the superior premolars, as in certain skulls of *M. petersoni.* The superior molars exhibit prominent ectolophs and greatly elevated internal cones. The internal cingula of p^3, p^4 are large and progressive, extending completely across the internal base of the protocone. The external cingulum of p^4 also extends nearly across the base of the tritocone. The deuterocone of p^2 is larger than in *M. petersoni.* The crowns as a whole are laterally compressed. This hypsodont character is an advance on the condition observed in *M. petersoni.*

Jaw.—A jaw from Washakie B (Am. Mus. 13179) provisionally referred to this species, as shown in Figure 358; exhibits proportions which are distinctively mesaticephalic, like those of the skull. It is of very superior size, and the ramus is of much greater depth than in the jaw referred to *M. fluviatilis* (fig. 358). The canines are short, rounded, and recurved. The hypoconulid of m_3 is conic and posteriorly cingulate, with a detached cuspule on the base of the inner side.

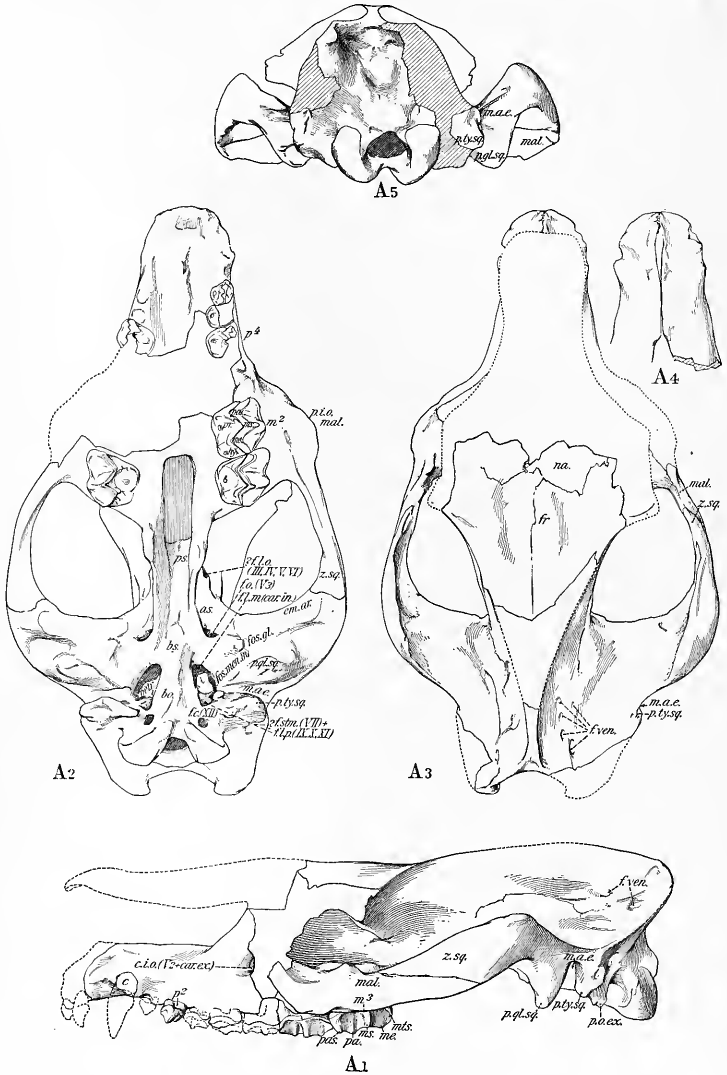

FIGURE 361.—Type skull of *Metarhinus earlei*

One-fourth natural size. Am. Mus. 13166 (type); north side of Haystack Mountain, Washakie Basin, Wyo., Washakie B 1. A_1, Side view; A_2, palatal view; A_3, top view; A_4, maxillo-premaxillary symphysis, dorsal view; A_5, occipital view.

Additional observations on Metarhinus earlei.—An excellent skull in the Carnegie Museum, No. 3098, found 190 feet above the bottom of Uinta B 1, has the dimensions following.

	Millimeters
Basilar length	410
Zygomatic width	243
Cephalic (zygomatic) index	60
P^1–m^3	162
P^1–p^4	63
M^1–m^3	98

The infraorbital shelf is almost as small as it is in *Rhadinorhinus,* but the nasals are broad.

Measurements of Metarhinus fluviatilis, M. cristatus, M. earlei, and Rhadinorhinus diploconus, in millimeters

	M. fluviatilis		M. cristatus, Field Mus. 12194 (type)	M. earlei, Am. Mus. 13166 (type), Washakie B 1	R. diploconus	
	Am. Mus. 1500 (type), Uinta B 1	Am. Mus. 1946, Uinta B 2			Am. Mus. 2055, Uinta B 2	Am. Mus. 1863 (type), Uinta B 2
P^1–m^3	145	140		167		168
P^2–m^3	132	131		156		156
M^{1-3}	85	84	92	102	86	103
P^4, anteroposterior	18			[a] 21	19	20
P^4, transverse	23	23		26		26
Transverse condyles				[a] 76		[a] 76
Pmx to condyles	[a] 355		[a] 385	393		[b] 440
Transverse zygomata			240	240		

[a] Estimated.

[b] Specimen crushed.

This table shows the marked inferiority in size of *M. fluviatilis* as compared with *R. diploconus* and *M. earlei*, as well as the close agreement in most measurements between *M. earlei* and the type of *R. diploconus*. *M. cristatus* is intermediate in size between *M. fluviatilis* and *M. earlei*.

Measurements of species of Metarhinus, in millimeters

	M. fluviatilis, Am. Mus. 1500 (type)	M. riparius		M. cristatus, Field Mus. 12194	M. earlei		
		Field Mus. 12186 (type)	Field Mus. 12183		Am. Mus. 13166 (type)	Field Mus. 12187	Field Mus. 12168
Skull							
Length, incisors to condyles	352	406	406	[a] 385	390	388	[a] 405
Breadth across arches	205	[b] 210	[a] 220	240	237	245	[a] 255
Breadth between orbits	112	[b] 114	107	145	[a] 137	142	[a] 220
Postorbital process to condyles	214	205	212	215	198		[a] 220
Last molar to condyles		189	193	195	182	184	
Length of free nasals	[a] 107	[a] 128	115			120	[a] 130
Greatest breadth of nasals		68	68			74	
Postglenoids to condyles (median line)		87	89			73	
Breadth across condyles		79	82	90	75	79	[a] 80
Greatest depth of arch		55	51			50	
Length of molar-premolar series	145	160	155		169	158	170
Length of molar series	86	93	93	92	104	100	103
Length of crown of canine		24	29			29	30
Diameter of crown of canine	18	18	20			15	16
Length of diastema	9	11	10		11	8	11
Narrowest point in sagittal area		10		4	6	9	17
Breadth of orbitonasal area	39	41	39	43	50	42	50
Mandible		Field Mus. 12195			Am. Mus. 13179	Field Mus. 12189	Field Mus. 12178
Length, condyles to incisors		338	330		330	[a] 315	340
Height, condyles above angle		133	125		157	135	148
Length of molar-premolar series		172	162		171	168	170
Length of molar series		110	102		107	110	105
Length of crown of canine		34	[a] 32				
Diameter of crown of canine		21	19		20		18
Depth of ramus from base of p_3		52	49		45	48	54
Depth of ramus from base of m_3		60	60		82	60	69

[a] Estimated.

[b] Specimen distorted.

Metarhinus cristatus Riggs

[Compare *M. fluviatilis* Osborn]

Plates LXXVIII, LXXIX; text figure 139

[For original description and type references see p. 191]

Type locality and geologic horizon.—Uinta Basin, Utah; *Metarhinus* zone (Uinta B 1), lower levels.

Specific characters.—Skull, estimated length 380 millimeters, breadth 240; molar series 94; frontal region broad; sagittal crest long and high; zygomatic arches relatively heavy. Molars short crowned, no hypocone on m^3.

Materials.—Known only from the type (Field Mus. 12194), a single skull lacking nasals and premaxillaries.

The type (fig. 139) was described by Riggs under the impression that it came from a much higher geologic level than that at which the type of *M. fluviatilis* was found. This geologic record has now been corrected to show that *M. cristatus* was found at nearly the same level as the type of *M. fluviatilis*—the lower half of Uinta B 1, or the *Metarhinus* zone. *M. cristatus* may therefore be the same animal as *M. fluviatilis*. It is true that there is no hypocone on m^3 in *M. cristatus*, but this element is described as a mere "cingulate hypocone" in *M. fluviatilis*. The disparity in size between the two types is not very great, the breadth across the zygomatic arches being 205 millimeters in *M. fluviatilis* and 240 in *M. cristatus*. The character of the sagittal crest and of the orbital region in the two types is quite similar, although it would appear that in the *M. fluviatilis* type the orbits are somewhat more prominent. The difference may be sexual, but the size of the skull of *M. cristatus* is intermediate between that of *M. fluviatilis* and *M. earlei* (see measurements above). Its breadth, or cephalic index, is possibly greater, although its length is merely estimated. It certainly contrasts sharply with the long-headed *M. riparius*.

Metarhinus riparius Riggs

Plates LXXVIII, LXXIX; text figure 138

[For original description and type references see p. 191]

Type locality and geologic horizon.—Uinta Basin, Utah; "*Metarhinus* sandstones" at summit of *Metarhinus* zone (Uinta B 1). Abundant in both lower and upper levels of Uinta B 1.

Specific characters (Riggs).—Skull long and narrow, length 405 millimeters, breadth 210, cephalic index 55, 51; anterior cranial region expanded, sagittal crest short; interorbital region relatively narrow and rounded; rudimentary horn cores above orbits; mandible straight in the ramus; canines large, lower canine long and recurved; molar series relatively short, 88–93 millimeters, hypocone usually present on m^3.

Geologic distribution and materials.—The type of this species (Field Mus. 12186) was found in the "*Metarhinus* sandstones" at the summit of Uinta B 1, but the animal also occurs abundantly in the lower levels, associated with the broad-headed *M. cristatus* and with *Dolichorhinus longiceps* (see table, above). The author describes it as the most common species in this life zone. Four skulls, two associated lower jaws, and one isolated jaw in the Field Museum collections are referred to it—namely, Field Mus. 12174, 12183, 12191, 12195, 12196.

General characters.—The type of these species is a laterally crushed skull, a condition which greatly increases its apparent dolichocephaly; this character, however, seems to rest substantially on other specimens, the cephalic indices ranging from 51 to 53. It is described as the long-headed *Metarhinus riparius* and may possibly be ancestral to the aberrant animal described above, known as *Sphenocoelus*, which it resembles in the following characters: (*a*) Relative dolichocephaly; (*b*) form of the occipital and especially of the temporal crests; (*c*) wide separation of the post-glenoid and post-tympanic processes. It is possible that this represents a branch, *M. riparius-Sphenocoelus* phylum, which may also be represented in the Princeton occiput (Princeton Mus. 10041) from Washakie ?A.

The hypocone on m^3 is not invariably present although seen in the type and in the examples of the species from higher levels. The canines (Riggs, 1912.1, p. 29) are said to be strong, whereas in the broad-headed species, *M. cristatus* and *M. earlei*, they are reduced in size.

Metarhinus? sp.

Text figure 359

A lower jaw (Am. Mus. 1859), from Uinta B 1, is larger than that of any known *Metarhinus* or *Rhadinorhinus* but probably represents a relative of those genera. It differs from the various species of *Dolichorhinus* in being stouter and in having a shorter tooth row. Comparative measurements are given above.

Another lower jaw (Am. Mus. 2355), from "Glover Spring," level Washakie B, apparently represents a large *Metarhinus* of uncertain specific reference. It is probably not referable to *Dolichorhinus vallidens*.

SUBFAMILY RHADINORHININAE (=?MEGACEROPINAE)

Animals of medium size; divergent in structure from members of the *Mesatirhinus* or *Metarhinus* phyla. Skull with nasals contracted and pointed distally; cranial profile concave instead of convex; skull cyptocephalic; facial region—that is, grinding series—somewhat upturned; infraorbital processes not prominent; frontonasal horns wanting or retarded in development; traces of terminal nasal horns in one species. Molars subhypsodont; premolars slightly progressive.

This group of small titanotheres is contemporaneous with *Metarhinus*, *Mesatirhinus* and *Dolichorhinus lon-*

giceps in Uinta B 1. It is a well-defined branch from the more typical Dolichorhininae and, as first observed by Gregory, has the right combination of characters for a remote ancestor of the Megaceropinae. Such an ancestral relationship, however, awaits confirmation by discovery in Uinta C. *Rhadinorhinus* certainly does not lead either into *Diplacodon* or into *Protitanotherium*. Riggs observes (1912.1, p. 41):

> *Rhadinorhinus* apparently represents a side branch from the early *Metarhinus* stem. The facial and cranial regions and the zygomata are similar. The nasals indicate an early specialization in another direction. The dentition is more highly specialized than that of *Dolichorhinus* and in some respects resembles it. The posterior nares open a little farther forward than those of *Metarhinus*. The mere trace of an infraorbital process also removes it somewhat from the long-nosed, low-ground titanotheres.

The grounds for relating this phylum to that of *Megacerops* (=*Symborodon*) are stated fully below.

Dolichorhinine affinities.—Remote relationship to the dolichorhines (*Mesatirhinus-Dolichorhinus*) rather than to *Manteoceras* is indicated by resemblance in the following characters: (*a*) Form of temporal and sagittal crests; (*b*) form of zygomatic arches in top view; (*c*) markéd preorbital concavity and projecting orbits; (*d*) slight projection of infraorbital portions of malar; (*e*) similar conformation of palatal and basicranial region; (*f*) rudiments of a secondary palate; (*g*) incisors somewhat resembling the dolichorhine type; (*h*) premolars and molars in all features dolichorhine with added peculiarities.

These animals differ widely from the typical dolichorhines, however, in the relatively short, pointed nasals and in the concave or saddle-shaped profile of the cranium as seen from the side but even more distinctly in the upbending of the grinding series, which carries with it an upturning of the anterior portion of the face, a feature very distinctive of *Brontotherium* and especially of *Megacerops*, as shown in Figures 401–403.

Rhadinorhinus Riggs, 1912

Plates LXXIV, LXXX, LXXXII; text figures 109, 141, 322, 359, 362–364, 401–403, 405. 647

[For original description and type references see p. 192]

Geologic horizon.—*Metarhinus* zone (Uinta B 1); also *Eobasileus-Dolichorhinus* zone (Uinta B 2).

Generic characters.—Titanotheres with slender subdolichocephalic skulls; cephalic indices 47–52; nares deeply recessed laterally; orbits not prominent; nasals tapering or pointed and abbreviate anteriorly; infraorbital shelves rudimentary or wanting. Molars with elevated hypocones; premolars somewhat progressives; hypocone of m^3 present or rudimentary.

History.—As shown above the first of these animals known was originally described by Osborn in 1895 as "*Telmatotherium diploconum*," but it was subsequently (1908.318) transferred by the same author to *Metarhinus diploconus*. The type lacked the nasal bones. The superior specimen found by Riggs, in 1910, a skull with the nasals preserved, justified his creating the new genus and species *Rhadinorhinus abbotti*, belonging to Uinta B 1, or a lower geologic level than that of *R. diploconus* (Uinta B 2).

The species appear to be distinguished as follows:

Rhadinorhinus abbotti Riggs, Uinta B 1; skulls somewhat more primitive and of smaller size; length 426 millimeters, breadth 224, cephalic index 52; hypocone on m^3 vestigial.

Rhadinorhinus diploconus (Osborn), skulls of somewhat larger size, length 440 millimeters, breadth 210, cephalic index 47; hypocone on m^3 large.

The indices of these species, which are of limited reliance because based on single specimens, are remarkably similar, as follows:

Indices of Rhadinorhinus

	Cephalic	Facio-cephalic	Molar-premolar-cephalic	Molar-cephalic
R. diploconus	47	43	38	23
R. abbotti	[a] 52	44	38	24

[a] Estimated.

Rhadinorhinus abbotti Riggs

Plate LXXX; text figures 141, 403

[For original description and type references see p. 192]

Type locality and geologic horizon.—Uinta Basin, Utah; *Metarhinus* zone (Uinta B 1). Rare.

Specific characters.—Skull mesaticephalic, length 426 millimeters, breadth 224; cephalic index 52. P^1–m^3, 164 millimeters; m^1–m^3 104. Nasals shorter than premaxillaries, thickened at suture, and tapering toward a terminal rugosity; posterior nares opposite m^2; sagittal crest long and narrow. First and second incisors with semiconical crowns; postcanine diastema short.

Materials.—The type of this interesting species (Field Mus. 12179) was discovered by Mr. J. B. Abbott, in whose honor it was named by Riggs. No other specimens are recorded from Uinta B 1.

From the author's original description the following citations may be made: In its general proportions the skull of *R. abbotti* (Pl. LXXX) is similar to that of *Metarhinus riparius;* somewhat longer and more slender in the zygomatic arches; the skull suggests a longer-limbed and more active animal; the skull is slight in construction, the arches more slender; the frontal region is rounded; the postorbital processes elongate; the nasals are convex on the inferior surface owing to the thickening at the sutural line; the facial and palatal aspects differ widely from those of *Metarhinus riparius;* the anterior narial opening is high and the nasals are not infolded at the sides; they terminate above the anterior margins of the canines so that the premaxillaries are exposed when the skull is viewed from above.

There is no antorbital fossa, as in *M. fluviatilis;* the muzzle is broad and the canines evidently elongate. The teeth are longer in the crowns (that is, more hypsodont) throughout than in *Metarhinus.* The author continues (1912.1, p. 37):

> The molar teeth are long in the crown, having inner cones nearly equal in height to the ectoloph. The molar-premolar series is well preserved and unworn in the type specimen. The canines are broken at the alveolus; half of the incisors are preserved. The dentition as a whole is more highly specialized than that of *Metarhinus.* The first and second incisors have short, rounded, semiconical crowns indented by cups on the posterior surface. The third incisor has a more elongate crown (23 mm.), the cup is suggested by a prominent cingulum on the posterior margin. An interval of 6 millimeters separates the third incisor from the canine. The latter is 18 millimeters in diameter and circular at the alveolar section. The elongate third incisor would indicate a long-crowned canine. The first premolar is a simple, blunt cone with an internal cingulum and emplanted by two roots. Premolars $^{2, 3, 4}$ increase steadily in length of ectoloph and deuterocone; strong internal cingula persist. The last three have taken on the subrectangular outline indicating a stage in dental specialization similar to that of *Sthenodectes.* The molars are long-crowned; the protocone increases steadily in height from first to third. The hypocone is more prominent in the second and reduced to a vestige in the cingulum of the third. The entire molar-premolar series is more curved [that is, in a vertical plane] than in any other Uinta titanothere.

Additional observations on Rhadinorhinus abbotti.—A fine skull in the Carnegie Museum (No. 2866, Uinta B 1) has the following measurements, which are very close to those of the type:

Measurements of Rhadinorhinus abbotti, in millimeters

	Field Mus. 12179 (type)	Carnegie Mus. 2866
Pmx to condyles	426	424
Transverse zygomata	224	220
Postorbital process to condyles	240	220
Last molar to condyles	196	200
p^1–m^3	164	168
M^1–m^3	103	101

The infraorbital protuberance is small but distinct; the nasals are not so sharply pointed as in the type. The superior maxillary symphysis is very long. This specimen, together with the type, clearly shows that *Rhadinorhinus* is an early offshoot from the *Metarhinus* stem (W. K. Gregory).

Measurements of skulls of Rhadinorhinus, Mesatirhinus, and Sthenodectes, in millimeters

	R. abbotti, Field Mus. 12179 (type)	R. diploconus, Am. Mus. 1863 (type)	M. petersoni, Am. Mus. 12184 (type)	M. superior, Field Mus. 12188 (type)	S. incisivus, Carnegie Mus. 2398 (type)	S. incisivus, Field Mus. 12168
Length, incisors to condyles	426	440	435	585	488	460
Breadth across arches	224	[a] 210	215	240	305	300
Breadth between orbits	134		115	120	170	160
Postorbital process to condyles	240	262	220	276	261	262
Last molar to condyles	196		210	260	197	190
Length of free nasals	102		95	138		
Greatest breadth of nasals				68	64	
Postglenoids to condyles (median line)	88				74	86
Breadth across condyles	84	[a] 82			89	101
Greatest depth of arch	38			36		
Length of molar-premolar series	164	172	165	184	207	211
Length of molar series	103	110	105	105	130	132
Length of crown of canine				23	56	47
Diameter of crown of canine		15	[a] 20	18	25	27
Length of diastema	7	6	10	15	0	0
Narrowest point in sagittal area	4			26		
Breadth of orbitonasal area	46	47		52	94	

[a] Estimated.

Measurements of lower jaw of Sthenodectes incisivus (Field Mus. 12166)

	Millimeters
Length, condyles to incisors	360
Height, condyles above angle	168
Length of molar-premolar series	215
Length of molar series	130
Length of crown of canine (estimated)	30
Diameter of crown of canine	19
Depth of ramus from base of p_3	60
Depth of ramus from base of m_3	84

Rhadinorhinus diploconus (Osborn)

Plates LXXIV, LXXXII; text figures 109, 362–364, 401, 402, 405, 647

[For original description and type references see p. 173]

Type locality and geologic horizon.—White River, Uinta Basin, Utah; *Eobasileus-Dolichorhinus* zone (Uinta B 2), two specimens.

Specific characters.—Skull mesaticephalic, length 440 millimeters; breadth 210 (estimated); cephalic index 47. Facial region upturned; basicranial region subdolichocephalic; premaxillary symphysis elongate; infraorbital shelf absent; malar rounded; preorbital region relatively abbreviate; occipital condyles relatively narrow. P^1–m^3, 168 millimeters; large hypocone on m^3 (?variable); marked upward flexure (cyptocephaly) of premolar series and of incisive border; superior premolars somewhat progressive, with rudimentary tetartocone rectigradations; molars elevated, with prominent protocones.

Materials.—This peculiar animal, according to O. A. Peterson's record, is geologically more recent than *R. abbotti,* since it occurs in Uinta B 2 in the *Eobasileus-Dolichorhinus* zone. The type skull (Am. Mus. 1863) was discovered by Peterson in Uinta B 2 during the American Museum expedition of 1894. Our knowledge is partly supplemented by another skull (Am. Mus. 2055), also from Uinta B 2.

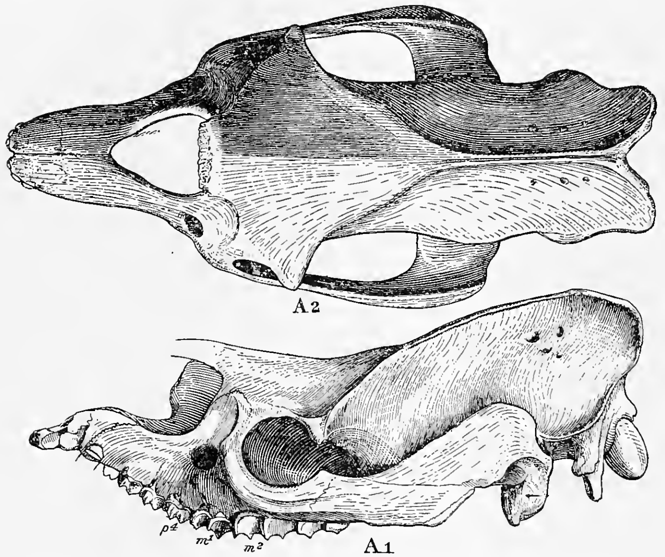

FIGURE 362.—Type skull of *Rhadinorhinus diploconus*

One-fourth natural size. Am. Mus. 1863 (type); White River, Uinta Basin, Utah; Uinta B 2. A_1, Side view, as partly reconstructed in 1895 by H. F. Osborn and R. Weber; drawing reversed. A_2, Top view. Later reconstructions of this skull are shown in Figure 364.

History.—The specific name *R.* (*Telmatotherium*) *diploconus* was assigned by Osborn in reference to the large hypocone on the last superior molar of the type specimen, a character which is lacking in *R. abbotti,* also in the second specimen from Uinta B 2 (Am. Mus. 2055). There is, therefore, some doubt whether the hypocone on m^3 is constant. In the original description it was also stated that the nasofrontals did not possess a horn; there seem to be no certain indications of a horn swelling in the nasofrontal region. The extremities of the nasals are wanting. The small size of the canines in circular section may indicate that the type specimen was a female. The premaxillary symphysis is decidedly longer and more firmly united than in *Mesatirhinus megarhinus.*

Distinctive features.—In contrast with *Mesatirhinus* and *Dolichorhinus* we observe that the frontoparietal profile is concave instead of convex; associated with this is the distinctively upturned facial region of the skull. The mesaticephalic proportions of the skull are indicated by the moderate transverse breadth of the zygomata, with an estimated width of 210 millimeters as compared with the total length of 440 millimeters from the symphysis to the condyles. Correlated with this is the relative narrowness of the occipital condyles as compared with those of *M. megarhinus.* The primitive elongation of the sagittal crest is comparable to that in *M. fluviatilis* and *M. earlei.* The animal also agrees with these species decidedly in the narrowness and abbreviation of the preorbital region. Like these animals, it may be described as narrow-snouted (a characteristic of *Megacerops*). The narial notch is also deeply recessed, so that there is only a short space at the side between the notch and the anterior border of the orbits. The postorbital processes of the frontals are very large. Beneath the orbit is found one of the most distinctive characters—namely, the simple, rounded form of the malars, which is in wide contrast to the oblique shelf of *Manteoceras* or the broadly projecting shelf of all the other species of *Mesatirhinus* and *Metarhinus.*

R. diploconus differs from *Metarhinus fluviatilis* as follows: (1) All the cheek teeth are more elongate anteroposteriorly, hence the internal border of the molars is less oblique than in *M. fluviatilis;* (2) the internal cingulum of p^4 is not complete; (3) the postero-external shoulder on p^4 is more prominent; (4) the skull top in side view is broadly concave (flatter in *M. fluviatilis*); (5) the zygomatic arch in side view curves downward more sharply.

Variations.—Of the two skulls referred to *R. diploconus,* one (Am. Mus. 2055) is smaller and has smaller teeth than the type and lacks the hypocone on m^3.

Cyptocephaly.—The upturned face of *R. diploconus* suggests that of *Megacerops* of the Oligocene. It would seem that the skull in correlation was somewhat saddle-shaped above, with the nasal region more elevated than the frontal.

Features in detail.—The superior view of the type skull (Am. Mus. 1863) lacks the extremities of the nasals; it exhibits the marked backward extension of these bones, the great prominence of the orbital ring, the gentle supratemporal ridges converging from the very prominent postorbital processes into the long, narrow sagittal crest, the gentle outward arching of the zygomata. In the badly distorted palatal view of the same skull a resemblance to *Mesatirhinus* is nevertheless evident. The distorted occiput exhibits an elevation of 97 millimeters and a deep superior concavity. In the lateral view (figs. 362, 364) we are struck by the downward, midcranial curvature of the profile (which appears more marked than in *Mesatirhinus* and *Manteoceras*), by the very prominent conformation of the orbital region above described, by the narrow space, measuring only 45 millimeters, between the orbit and the narial notch. The malar, as in other titanotheres, forms the entire outer portion of the infraorbital bar, the maxillary entering into its anterior rim, as in *Mesatirhinus* and *Manteoceras*. It appears to lack the infraorbital shelf as noted above. The malar passes anteriorly into the narrow and decidedly convex and elevated bridge at the point of union with the lacrimals. It is narrow and flattened below the posterior portion of the orbit as it passes backward; it is thin on the inferior surface. The zygomatic portion of the squamosal is moderately elevated and expanded.

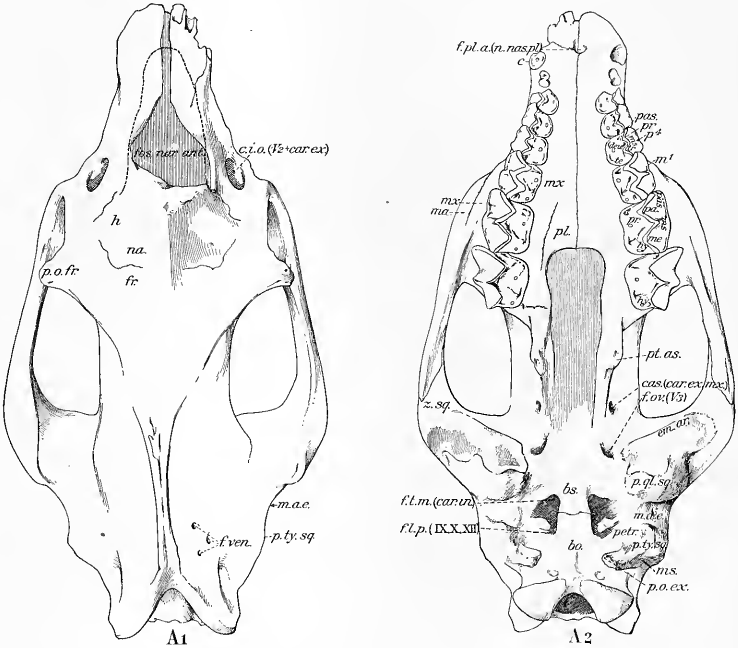

FIGURE 363.—Type skull of *Rhadinorhinus diploconus*

One-fourth natural size. Am. Mus. 1863. White River, Uinta Basin, Utah; Uinta B 2. Partly straightened. The occipital crest bas been narrowed by crushing. A$_1$, Top view; A$_2$, palatal view.

Dentition.—The materials consist of the type skull (Am. Mus. 1863) and of another skull (Am. Mus. 2055) containing alveoli of the cutting teeth and the worn crowns of the grinding teeth.

Incisors: The superior incisor alveoli have the characteristic convergence of the opposite series, and so far as can be judged from the alveoli, which increase regularly from i^1 to i^3, the canine fang (ap. 14 mm., tr. 12) is laterally compressed and is of small dimensions, like those of a female.

The molar-premolar series are of the *Mesatirhinus* type; they measure 169 millimeters in length, as compared with 156 in *M. petersoni*. They are distinguished by several features, among them the very prominent pointed hypocone of m^3, to which the specific name refers but which is lacking in Am. Mus. 2055. P^2, p^3 exhibit the very rudimentary postero-internal or tetartocone ridges which are observed in *T. ultimum* and *Dolichorhinus*. There are other faintly indicated progressive characters, especially the comparatively deep medifossettes and postfossettes on the molars and premolars, correlated with the greater hypsodonty, and the nearly symmetrical protocone and tritocone convexities on the ectoloph of p$^{2-4}$, as in *M. earlei*.

Premolars: More in detail: P^1 is separated from the canine by a narrow diastema (5 mm.) and is a bifanged tooth; p^2 is in a much more progressive stage of evolution than in *M. petersoni*, with its subquadrate form, anteriorly placed deuterocone, subfunctional tetartocone, well developed and slightly convex tritocone, the dimensions (ap. by tr.) being 16 by 19 millimeters; p^3 is of similar pattern (ap. 17 mm., tr. 21), with nearly symmetrical protocones and tritocones, an anterior style, and a rudimentary postero-internal cusp or tetartocone. In the development of the last-named cusp p^2 is slightly more progressive than p^4 (ap. 20 mm., tr. 25); p^4 is of the same pattern but entirely lacks any trace of the tetartocone. An internal cingulum nearly surrounds these teeth except opposite the deuterocone.

Molars: M^1 (ap. 29 mm., tr. 27) is slightly longer than broad and thus like the other molars is of marked dolichocephalic type; the hypococone is very high and prominent. M^2 (ap. 37 mm., tr. 34) exhibits faint external and incomplete internal cingula with a strong antero-internal cingular basin, a progressive feature of all these molars. This basin, or "hypoconid fossa," indicates relatively advanced hypsodonty in the lower molars, which we might infer also from the subhypsodonty of the upper molars.

Peculiar also is the sharp furrow dividing the protocones from the hypocones, and the prominence of the internal cingulum midway between the protocones and hypocones. M^3 has an elevated ectoloph (28 mm.) and is also longer (37 mm.) than broad (35 mm.); its prominent hypocone constitutes a distinctive feature, but from its absence in Am. Mus. 2055 it may not be a valid and constant specific distinction.

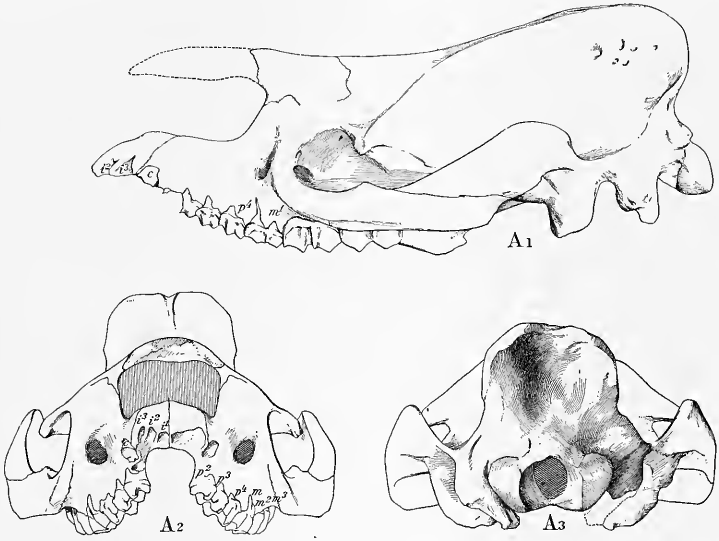

FIGURE 364.—Type skull of *Rhadinorhinus diploconus*

One-fourth natural size. Am. Mus. 1863. White River, Uinta Basin, Utah; Uinta B 2. Straightened and reconstructed, except nasals and condylar region. A1, Side view (reversed); A2, front view, partly straightened, but occiput probably too high and postorbital process of frontal too low; A3, occipital view, straightened.

Is Rhadinorhinus ancestral to Megacerops?—The possible ancestry of *R. diploconus* to *Megacerops* first suggested itself to W. K. Gregory in 1903 and was carefully considered by him and by Osborn in subsequent years. There are, in fact, many features in which *Rhadinorhinus diploconus* appears to foreshadow *Megacerops*, chief among which are the following: (1) Saddle-shaped profile, high nasofacial region, depressed frontoparietal profile; (2) facial region relatively abbreviate, upturned—that is, an upward flexure of maxillaries and premaxillaries; (3) nasals small, pointed anteriorly; (4) malars and antorbital bar rounded, with very short space in front of antorbital bar; (5) orbits small, inset; (6) a deep recession at the sides of the nares, and nasals high set; (7) occiput with a deep concavity; (8) chin weak, concave below, sloping up to a plane higher than that of the grinding teeth; (9) ramus with coronoid process, etc. (see Am. Mus. 2059, *Metarhinus fluviatilis*, a diminutive copy of the Oligocene *Megacerops* type); (10) first and second upper incisors (*R. abbotti* Riggs) with short, rounded subconical crowns; (11) canines of somewhat obtuse form, with swelling posterior cingulum; (12) lower premolars sloping upward anteriorly with strong internal cingulum; (13) upper premolars relatively progressive, well-rounded contours, large tritocones and relatively progressive tetartocone rudiments; (14) tetartocone rudiments in p^2, p^3 (*R. diploconus*) more advanced than in p^4, premolars subquadrate in form; (15) molars elongate or subhypsodont.

Intermediate forms between *R. diploconus* which may be discovered in Uinta B 2 and Uinta C will determine the question whether this relatively primitive form is ancestral to the Megaceropinae.

SUCCESSORS TO THE MANTEOCERAS-DOLICHORHINUS GROUP (EOTITANOTHERIUM, DIPLACODON)

SUBFAMILY DIPLACODONTINAE (=?MENODONTINAE, =?BRONTOTHERIINAE)

[Eocene phylum *Diplacodon*]

Including upper Eocene forerunners of the Oligocene genera *Menodus, Brontotherium*. Primitively dolichocephalic, progressively mesaticephalic. Precocious development of horns. Nasals narrowing anteriorly, curved downward at the tips. Second internal cones on the superior premolars precociously developed. (For progressive characters see Oligocene stages, p. 467.)

The phyletic relations of the two animals now to be described are not certainly determined; they are provisionally placed in a separate subfamily (Diplacodontinae), although it is possible that they belong in one of the Oligocene subfamilies (Menodontinae, Brontotheriinae). They include the *Diplacodon* of Marsh, discovered in 1873, and the *Eotitanotherium* of Peterson, discovered in 1912.

Eotitanotherium Peterson

[*Diploceras* Peterson; cf. *Diplacodon* Marsh]

Plate LXXXI; text figures 148, 149, 365–367, 372, 598–605, 647

[For original description and type references see p. 196. For skeletal characters see p. 656]

Geologic horizon.—Uinta B 2. In 1913 Peterson (1914.1) announced the surprising discovery, in the middle levels of the Uinta Basin, Utah, of a large titanothere having a pair of prominent bony outgrowths above the orbits, which he proposed to name *Diploceras.* Peterson later gave it the name *Eotitanotherium* to replace *Diploceras,* which was preoccupied.

Generic characters.—Large upper Eocene dolichocephalic titanotheres with very long, decurved nasals and well-developed, anteroposteriorly oval horns. Premolars decidedly progressive. P^3, p^4 with large distinct tetartocones and reduced external and internal cingula. The type of *Eotitanotherium osborni* Peterson (Carnegie Mus. 2859), so far as known, conforms with the definition of *Diplacodon* as given below:

> Skull mesaticephalic to dolichocephalic, zygomatic arches slender; superior premolars with flattened ectolophs and double convexities, p^2–p^4 progressive, quadritubercular—that is, with tetartocones; molars of elongate or dolichocephalic type—that is, laterally compressed.

E. osborni Peterson further agrees with *Diplacodon elatus* Marsh in the general small, obtuse form of the canine and in the presence of a wide post canine diastema.

On the other hand, the type of *E. osborni* appears to represent a distinct species or even a different genus from *D. elatus,* for although it comes from a lower geologic level (Uinta B 2) its premolars are decidedly more progressive in character, p^3, p^4 having the tetartocones larger and more separate from the deuterocones, the external and internal cingula reduced, and the whole appearance of the crown more molariform than in *D. elatus.*

Comparative measurements of the two species are given below.

Comparative measurements of Eotitanotherium and Diplacodon, in millimeters

	E. osborni, Carnegie Mus. 2859 (type)	D. elatus, Yale Mus. 10320 (type)
P^1–m^3	246	250
P^1–p^4	97	90
M^1–m^3	146	158
P^4, ap. by tr	29×37	28×34
M^1, ap. by tr.	40×43	41×42
M^2, ap. by tr.	48×50	52×42
M^3, ap. by tr.	60×55	60×57
Canine, vertical	25	----------
Canine, anteroposterior	17	----------
Postcanine diastema	28	24
Nasals, length	119	----------
P_1–m_3	255	----------
P_1–p_4	95	----------
P_2–p_4	79	----------
M_1–m_3	158	----------
Postcanine to hyloid of m_3	283	----------
Postcanine diastema	34	----------
Depth below m_3	93	----------

Whether the paratype skull (Peterson, Carnegie Mus. 2858) belongs with this species is somewhat doubtful. The greater size of the horns and the associated widening of the nasals in the paratype may well be a sexual difference, the paratype being possibly a male, the type a female. On the other hand, the paratype differs radically from the type in having the tetartocone of p^4 feebly developed, thus approaching *D. elatus.*

Although *Eotitanotherium,* from Uinta B 2, is probably allied to the somewhat later *Diplacodon* (Uinta C 1), it seems best to let it stand provisionally as a distinct genus, especially in view of the progressive character of p^3 and p^4 in this older stage.

Eotitanotherium osborni Peterson

[*Diploceras osborni* Peterson]

[For original description and type reference see p. 195. For skeletal characters see p. 656]

Type locality and geologic horizon.—Duchesne River, near Myton, Uinta County, Utah; *Eobasileus-Dolichorinus* zone (Uinta B 2).

Specific characters.—P^1–m^3, 240 millimeters; m^1–m^3, 145. Median and lateral incisors small and "round-topped," approaching Oligocene type, with heavy posterior cingulum; lateral incisors more massive. Canines short, subconic, without cingula, postcanine diastema 28 millimeters. Premolars and molars with little or no external cingula; internal cingula reduced; p^3, p^4 highly progressive, submolariform, with large tetartocones (type) and two well-marked external convexities; dimensions of p^4 (ap. by tr.) 29 by 37 millimeters. Upper molars wider than in *D. elatus,* m^3 with incipient tetartocones. Nasals long, tapering, decurved. Horn swellings low, elongate, oval in basal section. Lower jaw with deep ramus and deep symphysis.

The type and paratype skulls of *Eotitanotherium* (*Diploceras*) *osborni* were thus described by Peterson (1914.1, pp. 30–37):

SKULL

[Fig. 365]

> In comparing the recently discovered material with the best preserved remains of *Protitanotherium* (*P. emarginatum* Hatcher) a number of important differences are at once observed. The

nasals of the new species are longer, thinner, somewhat narrower (especially in specimen No. 2859); furthermore the lateral borders of the nasals are much less thickened, and instead of the broadly emarginated area at the free end of the nasals in *P. emarginatum*, the termination of the nasal of the present form has an abrupt downward turn resembling that of *Megacerops coloradensis* Leidy, and its anterior margin is very convex transversely, instead of concave, as is the case in *P. emarginatum*. Upon the whole the nasals of the species we are describing extend further forward. There seems to be a considerable variation in the development fo the horn cores; thus, in skull No. 2858 this protuberance appears to have a development comparable to that of some of the titanotheres found in the Oligocene, while in specimen No. 2859 these osseous bosses are very much smaller, more conical, and in proportion more like those of *P. emarginatum*, in spite of the fact that the skull we are considering pertains to an old individual. (See Pl. VII [=fig. 365].) This varied development of the horn cores is no doubt due to sexual differences, or possibly to individual variation. The premaxillaries extend well in front of the maxillaries and are separated in front, forming a deep median notch, as in *P. emarginatum*, so that the median pair of incisors are wide apart, while farther back they are firmly coossified and also solidly fused with the maxillaries. The infraorbital foramen is also of large size as in *P. emarginatum* and located above p^4 as in the latter species. The maxillary is on the whole very robust and shows that it had advanced well toward the condition found in *Diplacodon* and *Titanotherium*. This is also true of the jugal, the prominent lower border of which has the downward and backward sweep in front of and under the orbit, which is characteristic of *Titanotherium*. The zygomatic arch, though widely expanded behind, is, however, less robust than in the Oligocene genus and agrees better with the type of *Diplacodon elatum* described by Marsh. The postorbital processes on the frontal and jugal are of large size, in this respect unlike *Titanotherium*. The postorbital process on the frontal of the latter genus is usually located farther back and is much smaller in proportion. The external portion of the glenoid cavity is preserved in No. 2858 and is somewhat less convex in the anteroposterior direction than in the latter genus. As in *Titanotherium* the anterior palatine foramina are small round openings, which in the present genus are situated farther back from the alveolar border of the incisors. The palate is of the deep concave form usually met with in the titanotheres, and the posterior narial opening extends approximately as far forward as in the Oligocene genus, reaching to the posterior portion of m^2.

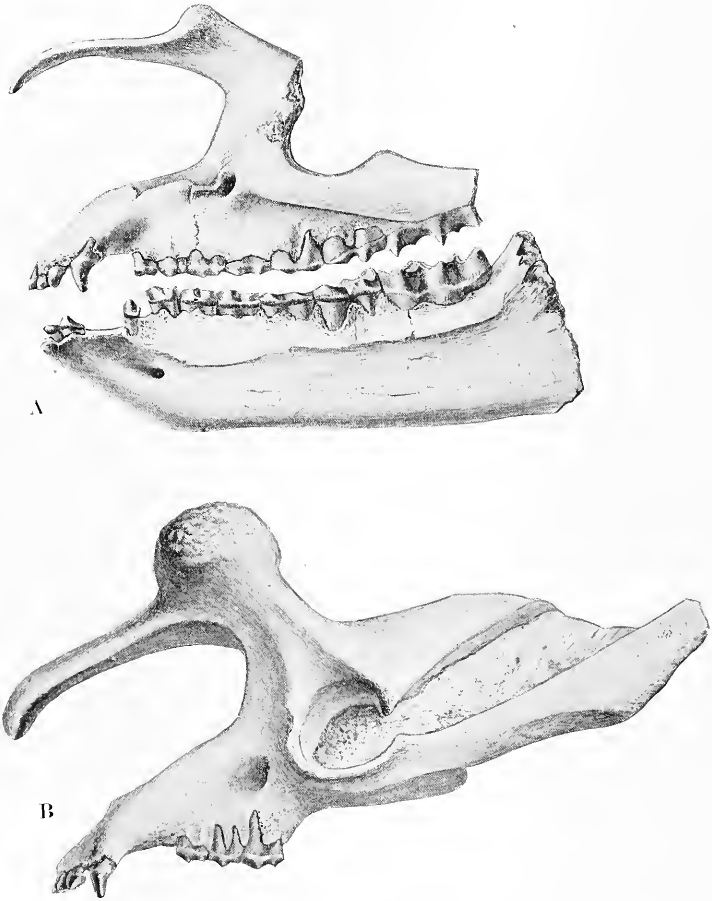

FIGURE 365.—Skulls of *Eotitanotherium osborni*

After Peterson. One-fourth natural size. A, Type skull, with associated lower jaw, ♀, Carnegie Mus. 2859, Duchesne River near Myton, Uinta County, Utah, Uinta B 2; B, paratype skull, ♂, Carnegie Mus. 2858 (reversed), same locality and level as A.

That the type of the skull was saddle-shaped is very evident from the material under study, but whether or not the characteristically broad superior aspect of the parietals and the heavy and broad occiput seen in *Titanotherium* had been attained to the same degree as the similarity of the anterior region in the two genera suggests might have been the case will not be completely known until the posterior region of the skull of the Uinta representatives of this phylum is found. It is highly probable that the similarity presented by the anterior region will be preserved throughout the cranium, which will then reveal more exactly the features of a true titanothere than was anticipated. From the type of *Protitanotherium emarginatum* at Princeton University, Hatcher[29] was apparently able to determine that the sagittal crest is absent and that the dorsal surface of the skull is probably slightly concave anteroposteriorly.

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[29] Am. Naturalist, vol. 29, p. 1085, 1895.

Measurements in millimeters

	No. 2858	No. 2859
Skull		
Diameter from incisors to posterior border of glenoid cavity	470	
Diameter from incisors to anterior border of orbit	[a] 180	[a] 179
Anteroposterior diameter of orbit	67	[a] 67
Vertical diameter of orbit	55	
Diameter from incisors to anterior border of posterior nares	260	256
Transverse diameter at the canines	[a] 93	86
Transverse diameter at diastema between the canines and the premolars	[a] 67	67
Transverse diameter across the horn cores	[a] 290	136
Lower jaw		
Total length of jaw fragment		380
Diameter from incisor to p_1		67
Vertical diameter of ramus at p_1		[a] 70
Vertical diameter of ramus at m_2		[a] 80
Vertical diameter of ramus at m_3		92

[a] Approximate measurements.

MANDIBLE

[Fig. 365]

The lower jaw is somewhat depressed by crushing, but allowing for this fact, it appears that the horizontal ramus of *Diploceras osborni* is shallower than in *P. emarginatum.* Characteristics which may further be noted are the more rounded under surface of the symphysis and the constriction of the lower jaws in the area between the canine and the premolars, which is greater than in *P. emarginatum.* As in the latter, the symphysis is strong and the mental foramen is large, located well down on the ramus, directly below p_2. The lower jaw is broken off back of m_3.

DENTITION

[Fig. 365]

The upper incisors and canines are well preserved, though much worn in the two crania under description. The molar-premolar series is less completely preserved in No. 2858, while in 2859 the superior dentition is completely represented. The lateral incisor and the canine of the right mandible and the complete molar-premolar series of the left ramus are also present in the latter individual.

As stated above, the median upper incisors are widely separated by the deeply excavated median notch of the premaxillaries. As seen in the illustration, the incisor series is placed well in front of the canine and the arc of the circle, which their arrangement represents, is more convex than in *P. emarginatum.* Their crowns are nearly circular in outline, covered with a heavy coat of enamel, bluntly conical, with a prominent cingulum at their posterior bases. They perhaps increase in size more gradually from i^1 to i^3 than in *P. emarginatum.* The canine is relatively smaller than in the latter genus, which imparts a much lighter looking aspect not only to this region of the dentition but also to the entire outline of the anterior portion of the muzzle in the paratype, No. 2858, as well as in the type, No. 2859. Furthermore the crown of the canine (especially in No. 2859) is shorter, blunter, and the lateral ridges are less developed in the present species than in either *P. emarginatum* or *Diplacodon elatum. D. elatum* has the canine more nearly of the same proportion as in *P. emarginatum.* The diastema back of the canine is relatively longer and its border much thinner than in *P. emurginatum,* in which respect it is more nearly like *Diplacodon elatum.*

The crown of p^1 is so much worn that its characters can not be made out. It is, however, of greater anteroposterior than transverse diameter and undoubtedly had a simple structure like that of *P. emarginatum.* P^2 is also much worn, especially along the external portion. The external face of the ectoloph is subdivided by a deep vertical groove and is much convex both anteroposteriorly and supero-inferiorly. This deep groove adds greatly to the anteroposterior convexity of the proto- and tritocones. The general outlines of the tooth are less quadrate than in *Titanotherium,* which is apparently due to the lack of devel-

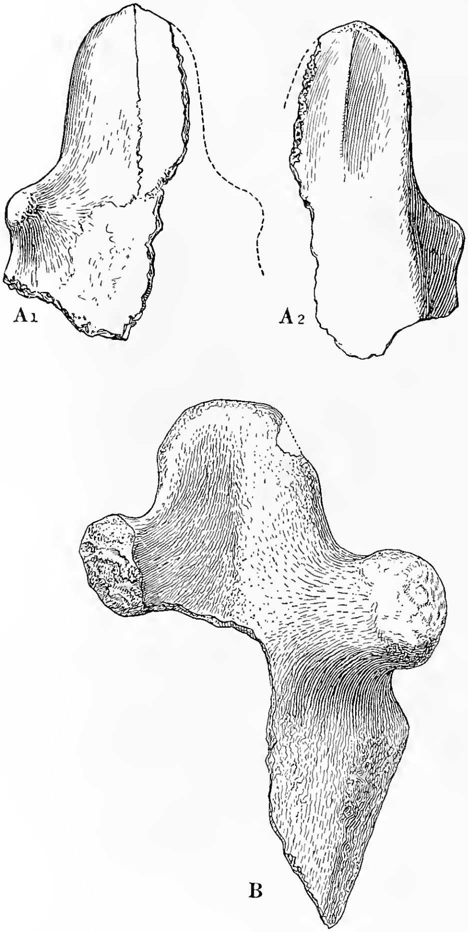

FIGURE 366.—Nasals and horn swellings of *Eotitanotherium osborni*

One-fourth natural size. A_1, Carnegie Mus. 2859 (type), Duchesne River near Myton, Uinta County, Utah, Uinta B 2, top view; A_2, same, basal view; B, Carnegie Mus. 2858 (paratype), locality and level same as A, top view.

opment of the antero-internal angle in the species under consideration. In the type of *Diplacodon elatum* p^1 is lost, while the external portion of p^2 is broken off. In the present species the deuterocone of p^2 is less ridgelike than in *D. elatum,* the two interal tubercles being somewhat better indicated and the ridge between them distinctly less developed. P^3 is more quadrate in outline than the preceding tooth and has two distinct internal tubercles on the crown, which are separated by a shallow groove, while in *Diplacodon elatum* these tubercles are united into a solid internal ridge, revealing a distinct differentiation from what is seen in the present species [compare Pl. LXXXI]. On the other hand, p^4 both in the type we are describing and in *D. elatum* are similar, there being two internal tubercles, deutero- and tetartocones, the former considerably the larger.[30] The more important differences in the dentition of the two forms, so far as they can now be compared, seem to be in the proportion of the canines, the difference in the length of the premolar series, and the detailed structure of p^3. The greater length of the premolar series is naturally to be expected in a form from a lower geological level.

The detailed characters of the molar series of the genera here compared present no differences of importance. The two Uinta forms agree in the obscure or feeble development of the cusplike elevations on the anterior face of the molars near the inner angle, more conspicuously developed in *Titanotherium.* At the postero-internal angle of the cingulum of m^3 in the Oligocene forms there is sometimes a distinct tubercle, which is indicated in the Uinta forms by only a slight swelling of the cingulum.

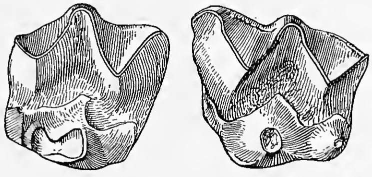

FIGURE 367.—Two upper molars of *Eotitanotherium* (*"Diploceras"*) *osborni* Peterson

Crown view. One-half natural size. Carnegie Mus. 2860a. These isolated teeth were found with the paratype, Carnegie Mus. 2860; Duchesne River near Myton, Uinta County, Utah.; Uinta B 2.

In proportion the inferior incisor dentition is further in advance of the canine than in *P. emarginatum.* I_1 and i_2 are represented only by a portion of their roots buried in the symphysis. I_3 has a very prominent cingulum posteriorly. Notwithstanding the much smaller size of the specimen, its crown has very nearly the same diameter as in *P. emarginatum,* which would indicate that the inferior incisors were possibly larger in proportion and more nearly equal in size. The crown of the canine is injured, but its diameters appear to be equal to those in the superior series, though relatively smaller than in *P. emarginatum.* P_1 has a single root and a simple conical crown, which has not received any wear, due to its somewhat inferior position. P_2 is submolariform and in its general characters does not differ from the same tooth in *P. emarginatum.* P_3 is quite molariform, while P_4 has a complete molar pattern.

There is no difference in the general features of the lower molars in the two genera here compared, and in turn the molars of *Diplacodon* are on the whole quite similar in their detailed structure to those of the Oligocene genus.

The proportion of the alveolar border occupied by the lower premolars of this species is in accord with the upper series—that is, of a greater anteroposterior diameter than in *P. emarginatum* and *D. elatum.*[31] Judging from the type (lower jaw) of *Protitanotherium superbum* Osborn, recently described,[32] that species also has the same proportion of the molar-premolar series as the two latter, while *Telmatherium? altidens* of the same publication has a longer premolar series and more nearly agrees with the present genus.

Measurements, in millimeters

	No. 2859	No. 2858
Length of superior incisor series	34	33
I^1, anteroposterior diameter	11	11
I^1, transverse diameter	10	10
I^2, anteroposterior diameter	12	12
I^2, transverse diameter	12	12
I^3, anteroposterior diameter	15	15
I^3, transverse diameter	14	14
Canine, anteroposterior diameter at the base	19	20
Canine, transverse diameter at the base	18	18
Length of molar-premolar series	246	--------
Length of superior premolar series	101	--------
P^1, anteroposterior diameter	19	--------
P^1, transverse diameter	12	--------
P^2, anteroposterior diameter	22	23
P^2, transverse diameter	25	26
P^3, anteroposterior diameter	30	--------
P^3, transverse diameter	31	--------
P^4, anteroposterior diameter	33	31
P^4, transverse diameter	38	36
Extent of superior molar series	[a] 146	--------
M^1, anteroposterior diameter	38	--------
M^1, transverse diameter	45	--------
M^2, anteroposterior diameter	52	--------
M^2, transverse diameter	54	--------
M^3, anteroposterior diameter	57	--------
M^3, transverse diameter	51	--------
I_3, anteroposterior diameter	14	--------
I_3, transverse diameter	12	--------
Canine, anteroposterior diameter, approximately	17	--------
Canine, transverse diameter, approximately	14	--------
Length of inferior molar-premolar series	255	--------
Length of inferior premolar series	94	--------
Length of inferior molar series	160	--------
P_1, anteroposterior diameter	14	--------
P_1, transverse diameter	10	--------
P_2, anteroposterior diameter	24	--------
P_2, transverse diameter	14	--------
P_3, anteroposterior diameter	28	--------
P_3, transverse diameter	18	--------
P_4, anteroposterior diameter	29	--------
P_4, transverse diameter	20	--------
M_1, anteroposterior diameter	38	--------
M_1, transverse diameter	26	--------
M_2, anteroposterior diameter	49	--------
M_2, transverse diameter	30	--------
M_3, anteroposterior diameter	78	--------
M_3, transverse diameter	32	--------

[a] Professor Marsh's measurement of the molar series of the type of *D. elatum* is an error.

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[30] In No. 2858, the paratype, there is only one internal tubercle, the deuterocone which may by some be regarded as of sufficient importance to constitute a specific difference. For the present I prefer to regard this character as possibly representing a reversion.

[31] In remeasuring the molar series of Prof. Marsh's type of *Diplacodon elatum* it would seem that he was in error in regard to the measurement, which should read 167 instead of 152 millimeters.

[32] Osborn, H. F., New and little-known titanotheres from the Eocene and Oligocene: Am. Mus. Bull., vol. 24, p. 615, 1908.

Diplacodon Marsh

Plates LXXXI, LXXXII; text figures 99, 368–371, 406, 594, 595, 597, 723

[For original description and type references see p. 166]

Geologic horizon.—True Uinta formation (Uinta C).

History.—The original and only known remains of *Diplacodon elatus,* an animal that has played a very large part in titanothere literature, consist of a crushed palate with a full series of grinding teeth, found by the well-known prospector Samuel Smith on White River, Utah, August 24, 1874. The geologic level is now known to be the lower part of Uinta C, a level higher than that of the species *Eotitanotherium osborni,* which we have just been considering. The specimen was described by Marsh in February, 1875, as representing a new genus, which he named *Diplacodon* in reference to the double internal cones on the superior premolar teeth. Marsh immediately recognized the importance of this animal as a structural connecting link between "*Palaeosyops*" and "*Brontotherium.*" He subsequently observed: "In the upper Eocene, both [*Limnohyops* and *Palaeosyops*] have left the field, and the genus *Diplacodon,* a very near relative, holds the supremacy." (Marsh, 1877.1, p. 31.) This animal was also regarded by Earle, Scott, and Osborn as a direct connecting link between the Eocene and Oligocene titanotheres.

Generic characters.—Skull mesaticephalic to dolichocephalic; zygomatic arches slender. Superior premolars with flattened ectolophs and double convexities; p^{2-4} progressive, quadritubercular—that is, with tetartocones; molars of elongate or dolichocephalic type—that is, laterally compressed.

Horns.—In his original description Marsh stated that this animal was distinguished from the Oligocene titanotheres "by the absence of horns." As the skull in the type and only known specimen of *D. elatus* is badly crushed it is difficult to determine whether or not the type animal possessed rudimentary horns; if it had they were certainly not so large as those of the Oligocene titanotheres. In the related type of *Eotitanotherium* (*Diploceras*) *osborni* Peterson there are well-developed horns with elongate oval bases.

Progressive molar characters.—The type skull is too imperfectly known for us to distinguish all its conservative and progressive characters. In the dentition the following progressive characters are observed: (1) Premolars with well-developed tetartocones; (2) complete internal cingula; (3) rudimentary fossettes on the crown surface; (4) premolar tritocones large and subequal with protocones; (5) p^2 much more progressive than in *Telmatherium ultimum* or *Manteoceras uintensis,* with large, centrally placed deuterocones and subquadrate rather than triangular contour; (6) molars with very distinct fossettes or pits on the crown surface near the ectoloph.

All these molar teeth characters point toward the Oligocene stages of the teeth of *Menodus* rather than of *Brontotherium*; on the other hand, the structure of the canines and incisors points rather toward *Brontotherium* than *Menodus.*

Diplacodon elatus Marsh

Plates LXXXI, LXXXII; text figures 99, 368–371, 406, 597

[For original description and type references see p. 166]

Type locality and geologic horizon.—Uinta Basin, Utah; *Diplacodon-Protitanotherium-Epihippus* zone, Uinta C 1, the true Uinta formation.

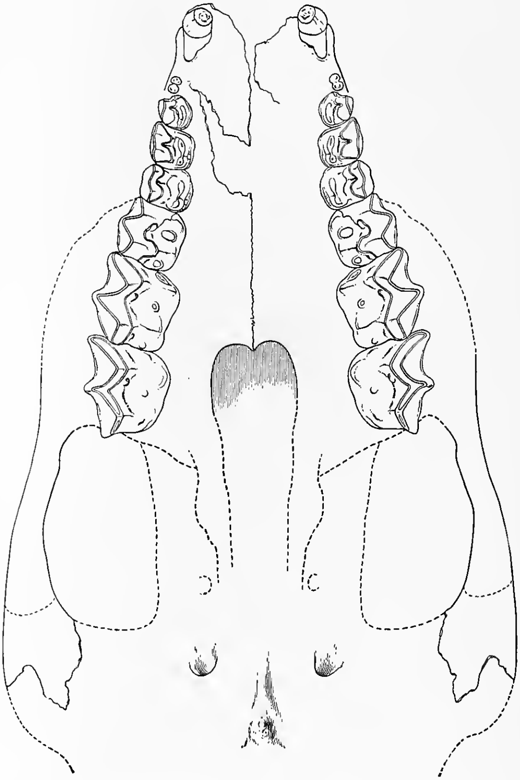


FIGURE 368.—Type skull of *Diplacodon elatus*

Palatal view. One-fourth natural size. Yale Mus. 10320; Uinta C 1. Partial reconstruction of the under surface of the skull based on the type materials.

Specific characters.—Skull mesaticephalic to dolichocephalic. P^1–m^3, 242 millimeters; molars elongate anteroposteriorly and subhypsodont; premolars short and broad; tetartocone rudiment on p^2, tetartocones increasing in distinctness on p^3 and p^4; m^3 without hypocone; canines small in females.

The type specimen (Yale Mus. 10320) is a female, as indicated by its small, rounded, recurved canines. The postcanine diastema is considerable, measuring 24 millimeters. The grinding teeth are laterally compressed, and the zygoma is slender and decidedly feeble, indicating that the skull was dolichocephalic.

The total dimensions of the grinding series are, premolars, 89 millimeters; molars, 152; premolar-molar series, 242. This is of smaller size as compared with the inferior grinding series of *Protitanotherium emarginatum* (304 mm.), of *P. superbum* (318), and of *Telmatherium altidens* (313).

Progressive characters.—Among the details of progressive character may be mentioned: (1) The cingulum is continued on the inner sides of the crowns of the premolar teeth; (2) the premolar teeth are rendered quadrate internally by the expansion of the tetartocone shelf, and p^2–p^4 exhibit the progressive development of the tetartocone from before backward by constriction or budding from the deuterocone crest; (3) the fossette of the crown is seen in a rudimentary form in the premolars and very distinctly in the molars, a feature characteristic of all Oligocene titanotheres and clearly foreshadowed in *Rhadinorhinus diploconus* of the upper Eocene.

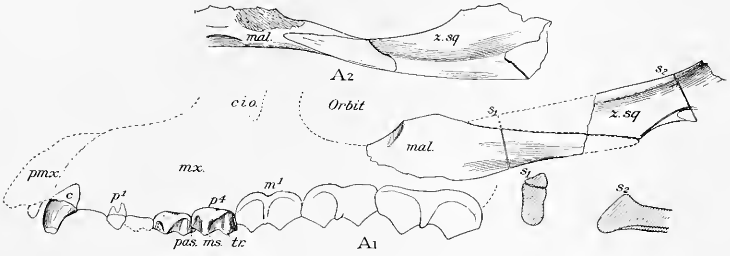


FIGURE 369.—Type skull of *Diplacodon elatus* (female)

Upper jaw and zygoma. One-fourth natural size. Yale Mus. 10320; Uinta C 1. A_1, Upper jaw and teeth, with zygoma partly reconstructed; s_1, s_2, sections; A_2, top view of zygoma, partly reconstructed.

Canines.—The canines are small, laterally compressed, and slightly recurved, but too much worn and fractured to clearly represent their form.

Premolars.—As noted above, the deuterocone crest is convex on the median or lingual side and flat or concave on the outer or buccal side, as in *Telmatherium.* Another distinctive character is seen in the ectolophs, which are decidedly flattened, especially the outer surfaces of the tritocones, reminding us of the condition in *Dolichorhinus;* the external cingulum arises and festoons the protocones. The detailed proportions of the teeth (ap. by tr.) are, p^2, 21 by 23 millimeters; p^3, 25 by 29; p^4, 28 by 35. In p^4 the deuterocone is large and elevated (17 mm.) and the worn tetartocone is low (13 mm.) but almost entirely distinct.

Molars.—In the molars the external cingula are faint, but the internal cingula are wanting. A characteristic feature is the antero-internal expansion of the cingulum, which makes the entire anterior border angular and prominent, especially as seen in m^2. This cingulum ridge bounds the fossa for the metaconid and is clearly foreshadowed in *Rhadinorhinus diploconus.* The fossettes are nearly worn out in m^1 and m^2; both anterior and posterior fossettes appear, and in m^3 the anterior fossette is a deep, narrow pit. The proportions of the teeth (ap. by tr.) are, m^1, 41 by 44 millimeters; m^2, 55 by 55; m^3, 60 by 55. These proportions are decidedly different from those in *Protitanotherium.* (Fig. 371.) The posterior cingulum of m^3 is elevated, and a low, distinct hypocone swelling appears. The ectolophs exhibit compressed mesostyles. The ectolophs are moderately hypsodont; the posterior view of m^3 shows that the mesostyle terminates in a horizontal ridge, as in many little-worn or unworn titanothere molars; it is especially strong in *Rhadinorhinus diploconus.*

Comparison of Diplacodon elatus with middle Eocene titanotheres.—*Diplacodon* combines characters of *Telmatherium* and of *Dolichorhinus* but does not agree with either in all respects.

Comparison with *Telmatherium: Diplacodon* shares with *Telmatherium* the tendencies toward dolichocephaly and toward the development of tetartocones, but it far outstrips *Telmatherium* in both features and differs very radically in others, as follows: The canines are small; p^2 in *Diplacodon* is much more advanced and of different type; the tritocones of the superior premolars are flattened instead of rounded; the molars are much more elongate and have flattened ectolophs; the zygomata are much more slender.

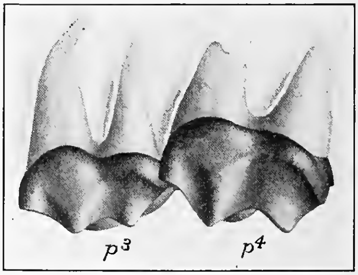


FIGURE 370.—Third and fourth upper premolars of *Diplacodon elatus*

Natural size. Yale Mus. 10320 (type, reversed). Uinta C 1. Outer side view.

Comparison with *Protitanotherium:* These animals are readily distinguished from the mesaticephalic *Protitanotherium* in all the dolichocephalic proportions of the teeth; and from the radical differences in the teeth it is safe to infer that the proportions of the skull also differed widely.

Comparison with *Dolichorhinus:* Resemblances to members of this genus are observed in the flattening of the premolar ectolophs, especially of the tritocones; in the slenderness of the zygomatic arches posteriorly; in the elongate or dolichocephalic type of the grinding teeth; and in the small size of the canines. The most important progressive or divergent differences from *Dolichorhinus* are the great development of the tetartocones, especially on p^4; the great breadth of p^4; the absence of a broad infraorbital shelf on the malars; the apparent retardation of the horn rudiments.

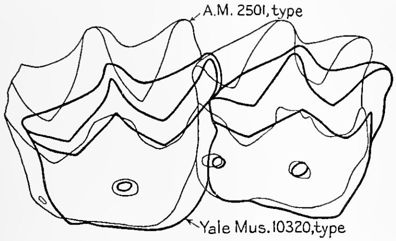


FIGURE 371.—Upper molars of *Diplacodon* and *Protitanotherium* compared

One-half natural size. Superimposed contours of the first and second upper molars of the dolichocephalic *D. elatus* (heavy line) (Yale Mus. 10320, type) and the brachycephalic *P. superbum* (light line) (Am. Mus. 2501, type).

Comparison with *Rhadinorhinus:* Some resemblances between *Rhadinorhinus* and *Diplacodon elatus* led to the doubtful view that the two were related. These resemblances are seen especially in the proportions of the molars, which are of dolichocephalic type, and of the premolars, which are relatively broad. Among other characters common to the two species are the following: Molars subhypsodont; m^2 of elongate, compressed form; parastyles and mesostyles sharp and delicate; hypocones of m^1, m^2 set well in on crown; external cingula delicate; deep fossettes median and posterior. In the premolars we observe that the crowns are relatively broad; the tetartocones of p^2, p^3 are somewhat progressive in *R. diploconus*; the tritocone is very large on p^2–p^4; and the medifossettes on p^2–p^4 are deep.

Type skull of Diplacodon elatus.—The fractured skull affords only a few characteristic features. The main indications are of a dolichocephalic type, with slender zygomatic arches. The premaxillary symphysis is apparently deep, measuring 92 millimeters from the incisive border to the lower border of the nasal notch. The extent of the palatines upon the hard palate was apparently rather narrow, the posterior nares opening directly opposite the interval between the second and third molars. There is the characteristic rugosity at the junction of the basisphenoid and basioccipital. As above noted, there is no conclusive evidence regarding the horn rudiments except that if present at all they appear to have been not very prominent.

The most important feature by far is the slender and simple structure of the zygomatic arch (fig. 369). The malars give no evidence of the existence of an infraorbital shelf; on the contrary, this region was smooth, flattened, and not very prominent. Similarly, the squamosal portion of the arch is shown, giving a maximum depth of 30 millimeters and a width of 37. The very slender zygoma was apparently nearly parallel with the sides of the skull, as in *Dolichorhinus*, but as in *Rhadinorhinus diploconus* it lacked the infraorbital shelf; it also lacks the deep vertical expansion seen in *Telmatherium*.

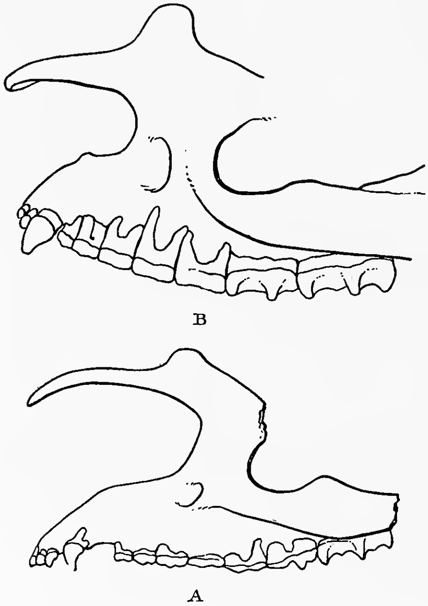


FIGURE 372.—Facial region of *Eotitanotherium osborni* and *Brontotherium leidyi*

One-fifth natural size. A, *E. osborni*, Carnegie Mus. 2859 (type), Uinta B; B, *B. leidyi*, Nat. Mus. 4249 (type), Chadron A.

CHAPTER VI

EVOLUTION OF THE SKULL AND DENTITION OF OLIGOCENE TITANOTHERES

SECTION 1. REVIEW OF THE ENVIRONMENT, GEOLOGIC SUCCESSION, AND GEOGRAPHIC DISTRIBUTION OF THE LOWER OLIGOCENE TITANOTHERES

In order to facilitate an understanding of the evolution of the skull and dentition of the Oligocene titanotheres, a brief résumé of the matter presented in Chapter II is here given. The environment of the lower Oligocene titanotheres, described in Chapter II, was different from that of their Eocene ancestors. It consisted mainly of the broad flood-plain region east of the Rocky Mountains. The geographic range, however, extended westward into the broad upland plateaus west of the Rockies and northward over British Columbia into Asia as far west as the eastern part of Europe.

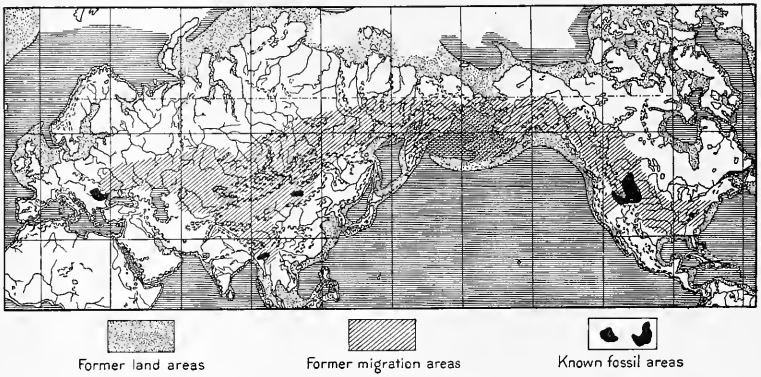


FIGURE 373.—Map showing the areas in which remains of titanotheres have been found (solid black) and areas in which, during Eocene and Oligocene time (oblique lines) titanotheres were probably in migration

The general regions in which titanotheres have been found are the northwestern United States, the Gobi Desert (Mongolia), Burma, and southeastern Europe.

The conditions in the Great Plains region appear to have been eminently favorable to the existence of the titanotheres, because the members of all the numerous branches into which this great family was divided show an increase in size, which is especially conspicuous in the males.

Our ideas regarding the geologic levels of the species and the mutations of the members of the four subfamilies are founded upon the original observations of Hatcher, who very carefully recorded the vertical distribution of the types and other specimens in his great collection for the National Museum, which are fully enumerated elsewhere in this monograph. To the records of these specimens have been added records obtained from other museum collections.

The faunistic subdivisions of the *Titanotherium* zone, which forms part of the White River deposits and is of Chadron age (lower Oligocene), range in thickness from 150 to 200 feet, as follows:

	Feet
Chadron C (upper or *Brontops robustus* zone)	30–50
Chadron B (middle or *Brontops dispar* zone)	70–90
Chadron A (lower or *Brontops brachycephalus* zone)	50–60

The lower Oligocene deposits of the Chadron formation of the Great Plains were laid down on the irregularly worn surface of the Pierre shale (Upper Cretaceous), which had been exposed to erosion for a long time. Consequently the deposition of the *Titanotherium*-bearing beds was not uniform: it began at some points earlier than at others, and the total thickness of the *Titanotherium* zone accordingly ranges from 150 to 200 feet. There are also some discrepancies in the records, which are doubtless due to irregularities of deposition in the overflow and stream channel deposits.

The known areas where deposits of the *Titanotherium* zone are exposed and where fossils occur are shown on the accompanying map (fig. 373).

The change of form of the lower Oligocene titanotheres was almost as great while this 200 feet of sediment was being deposited as that of the Eocene titanotheres while 2,000 feet of sediment was being deposited. We infer that the average deposit of 200 feet of sediment in so many localities entirely deceives us as to the length of lower Oligocene time. These sediments were being laid down probably not for hundreds but for thousands of years. During this long period the titanotheres were certainly very abundant over the entire western plains.

Without exception all the animals whose remains are found at the base of the *Titanotherium* zone were relatively small, and all had short and superficially similar horns. The great increase in size observed between the animals of the beds of Chadron A and those of Chadron C is made evident by a comparison of the outlines of the skulls (figs. 389–393) and lower jaws (figs. 395–397).

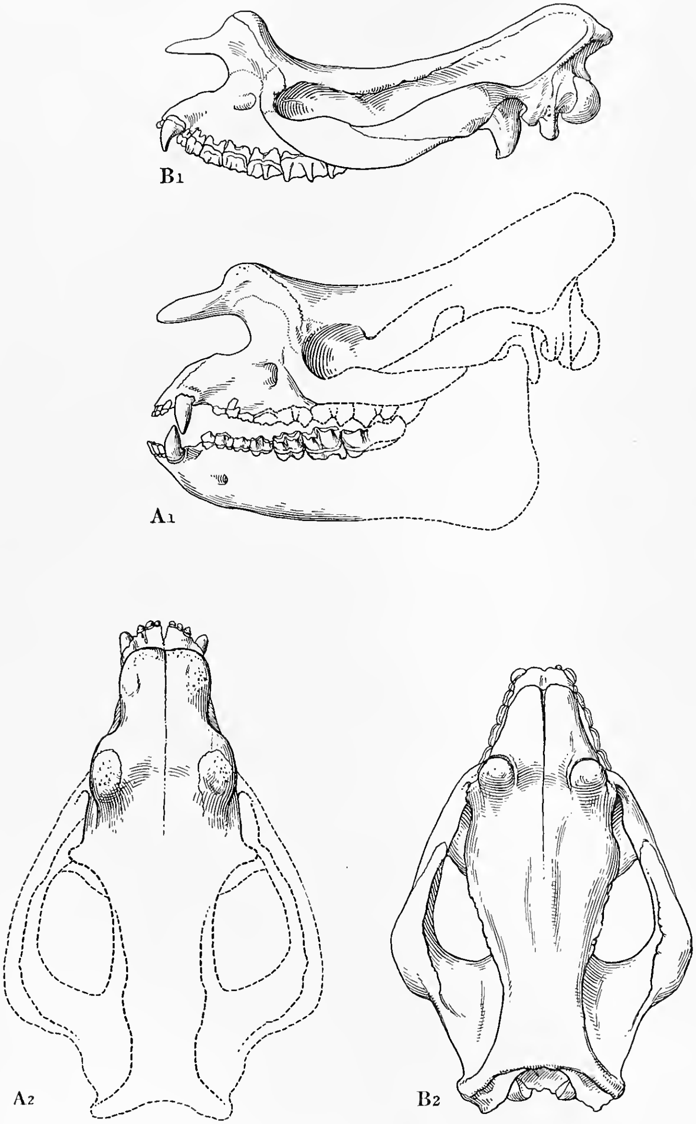


FIGURE 374.—Comparison of upper Eocene and lower Oligocene titanotheres, showing similar early stages in the evolution of the horns

A_1, A_2, Reconstruction of the skull and jaw of an adult *Protitanotherium emarginatum*, Princeton Mus. 11242; upper Eocene. B_1, B_2, Partly reconstructed skull of a young *Brontops brachycephalus*, Nat. Mus. 4258; lower Oligocene. One-eighth natural size.

In order to comprehend the extraordinary number and the extremely varied forms of the titanotheres that inhabited South Dakota in early Oligocene time we must first imagine the existence of a vast continental region as the theater of evolution of these migrating animals, a region far larger than any of the comparatively small areas in which the fossil remains have been collected and which are shown by the black areas on Figure 373.

A vast level or undulating country, consisting of great flat plains traversed by slow meandering streams, bounded on the west by mountain ranges, valleys, and plateaus interspersed with active volcanic peaks but allowing free migration to the east, north, and south—such was the environment of the Oligocene titanotheres.

SECTION 2. INTRODUCTION TO THE ANATOMY OF THE SKULL AND THE DENTITION OF THE OLIGOCENE TITANOTHERES

HORNS: TRANSFORMATION, ELONGATION

Length of the horns.—The gradual evolution of the horns in the Eocene titanotheres was followed by their more rapid evolution in the Oligocene titanotheres, until they became the dominant and central feature of the skull, conditioning its entire architecture. With the development of the horns as powerful weapons are correlated changes in the structure of the nasals, of the zygomatic arches, of the cranial vertex, of the occiput, of the vertebral spines and in the entire anatomy of the anterior portion of the body. The primary divisions of the Oligocene titanotheres as determined by length of horn are as follows:

Menodontine group (short-horned): *Teleodus*, *Brontops*, *Diploclonus*, *Allops*, *Menodus*.
Brontotheriine group (long-horned): *Megacerops* ("*Symborodon*"), *Brontotherium*.

First stage of development.—The horns in the Oligocene titanotheres, as in the Eocene *Dolichorhinus* and *Protitanotherium*, arise at the junction of the frontonasal suture, slightly in front of the orbits, overhanging the sides of the face (fig. 374). The primitive horn section is an anteroposterior oval. The longest diameter of all the earliest horn tips is parallel with the long axis of the skull. The anterior edge of the oval extends into the sides of the nasals (*N*); the posterior edge of the oval subsides laterally toward the frontals, lacrimals, and maxillaries (*M*).

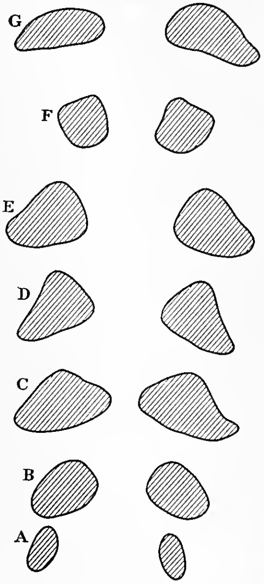


FIGURE 375.—Sections at base of horn in the six chief generic types of Oligocene titanotheres (B–G) and in the upper Eocene *Protitanotherium emarginatum* (A)

A, *Protitanotherium emarginatum*, Princeton Mus. 11242; anteroposteriorly oval. B, *Brontops dispar*, Nat. Mus. 4290; rounded, obliquely oval. C, *Diploclonus amplus*, Yale Mus. 12015a (type); rounded, transversely widened, trihedral. D, *Allops serotinus*, Yale Mus. 4251 (type); angulate, trihedral. E, *Menodus giganteus*, Am. Mus. 505 (neotype); rounded, trihedral. F, *Megacerops acer*, Am. Mus. 6348 (type); rounded, quadrate. G, *Brontotherium platyceras*, Harvard Mus. (type); transversely oval. All one-fifth natural size.

Second stage of development.—A low transverse "connecting crest" arises at the median bases of the hornsand gives them a more or less distinct trilateral section consisting of an antero-internal face, an antero-external face, and a posterior face. These three faces are especially distinct in species of *Menodus*, such as *M. trigonoceras*. In *Megacerops*, however, the connecting crest is not typically developed, so that no internal angle (*C*) appears (*Megacerops acer*, p. 545).

Sections of the horn.—Each phylum takes on a characteristic horn section, which may be reproduced by bending a copper or lead wire in the manner shown in Figure 376. The horn section is always cut at right angles to the perpendicular axis of the horn and as near the base of the horn as practicable. Each horn develops progressively a characteristic section at the base (fig. 399) and at the tip. The four chief types of horn sections are as follows:

Short-horned:
  Anteroposterior oval, subtriangular, oblique oval, subtransverse oval: *Brontops*, *Diploclonus*.
  Subtriangular oblique, subtriangular transverse: *Menodus*, *Allops*.
Long-horned:
  Subtriangular, suboval, transverse oval: *Brontotherium*.
  Rounded, anteroposterior oval, flattened anteriorly, rounded posteriorly: *Megacerops*.

Forward shifting of horns.—The horns tend to shift forward and absorb the nasals. Thus the general correlation of horns and nasals is as follows:

Short, triangular, oval horns, elongated nasals: *Brontops*, *Menodus*.
Long, oval or rounded horns, abbreviated nasals: *Brontotherium*, *Megacerops*.

In the extremely long-horned types, such as *Brontotherium*, the horns shift forward until they overhang the anterior nares and finally the symphysis; they thus absorb the nasals but retain their base of support on the greatly shortened maxillaries. Thus the nasal angle (*N*) disappears, and the horns acquire a transverse oval section.

Horns in females.—In skulls from the higher geologic levels of the Oligocene the difference between the horns of the two sexes is rather marked; in skulls from the lower Oligocene and from the Eocene the difference is less. There is reason to believe that the horns were at first alike in both sexes. In females the horns exhibit an arrested stage of development. This fact is most clearly shown by a comparison of two female skulls of *Brontotherium* (Am. Mus. 1005, 1006) with two male skulls (Am. Mus. 492, 1070). (See fig. 377.) In many females the horns are imperfectly ossified at the tips; in some they are pointed. In species of *Menodus* the "connecting crest" is more constant and more pronounced in males than in females, but in females of *Brontotherium* the connecting crest appears to rise almost to the summit of the horn, as in the female skull selected by Cope as the type of *Menodus peltoceras* (=*Brontotherium curtum*) (fig. 478). The

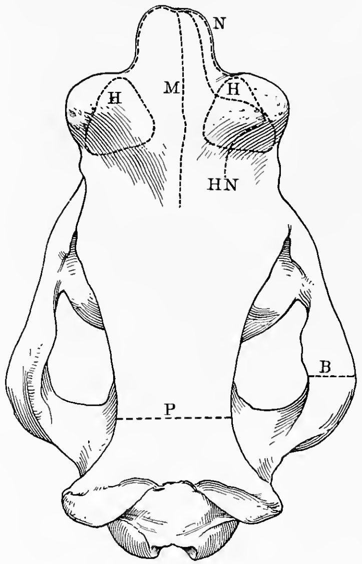


FIGURE 376.—Position of the standard sections and contours of Oligocene titanothere skulls

N, Nasal contour; M, median section of nasals and connecting crest; H, basal horn section; HN, oblique-longitudinal section, nasals to horn tip; P, section across parietal vertex; B, buccal section of zygoma.

male skull of *M. giganteus* (Am. Mus. 505, 1066, 1067; fig. 444) has stout triangular horns, whereas the female skull (Am. Mus. 506; fig. 445), although a very large specimen, has more slender horns, which are rounded in section, and has very slender canines. Similar sexual differences are observed in specimens of *M. trigonoceras.*

Sport variations in the horns.—It is difficult to determine whether the internal "hornlet," or branch horn, which appears on the inner side of the main horn in specimens belonging to at least three different phyla (*Diploclonus, Menodus, Brontotherium*) is a veritable progressive character—that is, a rectigradation—or merely a sport. This branching horn is believed to be a generic character of the animal called *Diploclonus amplus* by Marsh. Another example of internal branching is that shown by a female of *Brontotherium gigas elatum* (Am. Mus. 1006).

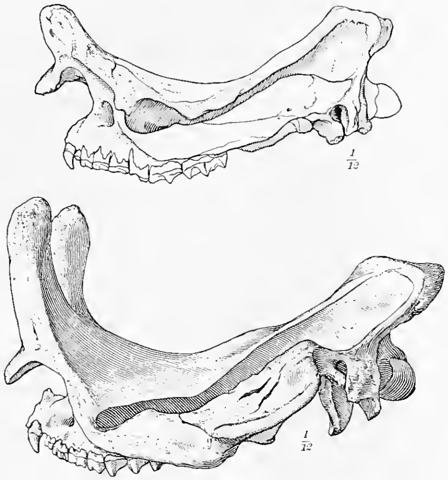


FIGURE 377.—Male and female skulls of *Brontotherium gigas*

A, Am. Mus. 1006, ♀; B, Am. Mus. 492, ♂. One-twelfth natural size.

Effects of geologic crushing.—Vertical or lateral crushing not only profoundly influences the entire proportions of the skull but totally alters the shape and angulation of the horns, as illustrated in two examples of *Menodus trigonoceras* and *Megacerops copei* (figs. 439, 394, G), one of which is crushed vertically, the other horizontally.

NASALS: EXPANSION, ABBREVIATION

The hypertrophy of the horns and the compensating atrophy of the nasals were pointed out by the writer in 1887. Primitive nasals are invariably elongate, but they show a fundamentally characteristic form, which again distinguishes two groups. In the menodontine group they are distally broad and truncate, as in *Menodus,* primitively narrow and broadening distally, as in *Brontops,* and moderately broad and laterally decurved, as in *Diploclonus;* in the brontotheriine group they are distally tapering and decurved, as in *Megacerops,* and progressively abbreviate and pointed, as in *Megacerops* and *Brontotherium.*

The shape of the nasals, however, does not sharply distinguish all members of the two groups, as there is more or less convergence between the members of different phyla. In members of both groups the tendency to shorten the nasals appears to be progressive; it is less marked in *Menodus* and is carried to the greatest extreme in *Brontotherium.*

In the *Menodus* group an age character is the distal broadening, expansion of the nasals, as seen in the comparison of young and old specimens of different species of *Brontops.*

ZYGOMATIC ARCHES: EXPANSION, BUCCAL PLATES

Expansion of the arches.—The progressive spreading of the posterior portion of the zygomatic arches (figs. 391–393) is a highly characteristic feature of members of both the menodontine and brontotheriine groups. The more primitive titanotheres in both groups exhibit moderately expanded zygomata without any rugose areas. The rugose development of the zygomatic arch takes place pari passu with the massive development of the horns. Thus the highest degree of zygomatic expansion characterizes the great brontotheres (figs. 392, 394) in which the horns reach their maximum development. This becomes a sexual character; the extremely robust and widely spreading zygomatic arches of the more progressive species of males present a contrast with the moderately expanded arches that are associated with the feeble or imperfect horns and small canines of the less progressive females. In males and females of *Menodus* the same differences are observed, but in a less marked degree than in *Brontotherium.* The less expanded zygomata of the female skulls give them a less brachycephalic and more primitive character throughout the phylum. Thus in the nasals, in the horns, and in the zygomatic arches the males always appear more progressive and the females more primitive.

Zygomatic cephalic indices.—The expansion of the zygomatic arches is so much more rapid than the elongation of the skull as a whole that the breadth across the zygomata nearly if not quite equals the basilar length; thus a skull which is really elongated, like that of *Brontotherium platyceras,* presents a high zygomatic index, whereas the brachycephalic general character is less marked in the grinding teeth and in the parietal vertex of the skull (compare fig. 390, B, D, F).

OCCIPITAL PILLARS; AUDITORY MEATUS

The occiput.—Correlated with the progressive evolution of the horns is the progressive transformation of the occiput from the transversely convex contour of the vertex to the deeply concave contour, correlated with the development of the enormous lateral pillars and supraoccipital rugosities to which are attached the powerful muscles and tendons of the neck. Figure 378 illustrates these extremes of structure. In general the massiveness of the occiput is directly correlated with the size, location, and function of the horns. Thus in *Megacerops acer* (fig. 378, B) the occiput is narrow, slender, and slightly indented, in keeping with the relatively slender horns, and presents a very wide contrast to the broad, rugose,

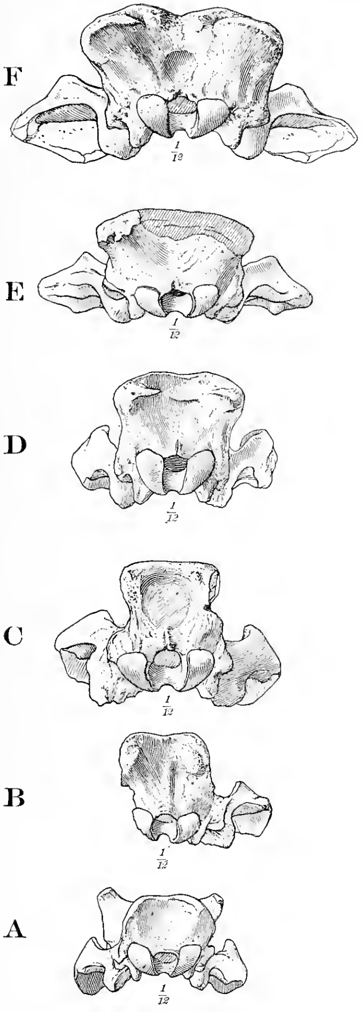


FIGURE 378.—Occipital view of skulls in different phyla of Oligocene titanotheres, showing widening of the occiput and development of its lateral pillars and superior crests in the final stages

After Osborn. A, *Menodus heloceras*, Am. Mus. 6360 (type); Chadron A. B, *Megacerops acer*, Am. Mus. 6348 (type); ?Chadron C. C, *Allops marshi*, Harvard Mus.; ?Chadron B. D, *Menodus trigonoceras*, Am. Mus. 1067, ♀; Chadron C. E, *Megacerops bucco*, Am. Mus. 6345a, ♂ (type); Chadron C. F, *Brontotherium gigas*, Am. Mus. 492, ♂; Chadron C.

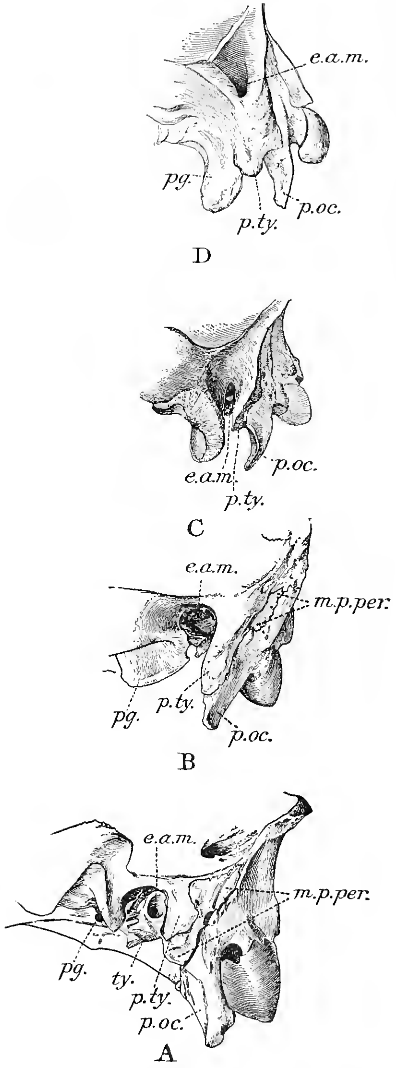


FIGURE 379.—Influence of progressive brachycephaly on the auditory region of perissodactyls

A, Dolichocephalic, *Equus caballus;* B, mesaticephalic, *Tapirus;* C, mesaticephalic, *Dicerorhinus sumatrensis;* D, brachycephalic, *Rhinoceros sondaicus*. Note disappearance of mastoid portion of periotic (*m. p. per.*) and inclosure of auditory meatus (*e. a.m.*) inferiorly. Parallel changes occur in the titanotheres.

deeply indented occiput of *Brontotherium gigas elatum* (fig. 378, F).

Inclosed auditory meatus.—The progressive union of the postglenoid and post-tympanic processes in the titanotheres parallels that which we observe in a comparison of the rhinoceroses, tapirs, and horses (fig. 379). For example, in the skull of the primitive *Menodus heloceras* (fig. 378, A) the external auditory meatus is widely open below, paralleling the condition which we observe in the Sumatran rhinoceros, *R.* (*Dicerorhinus*) *sumatrensis* (fig. 379, C). In *Brontotherium platyceras* the auditory meatus is reduced to a small foramen inclosed by a solid wall of bone, paralleling the condition observed in the Javan rhinoceros, *R. sondaicus* (fig. 379, D).

SEXUAL CHARACTERS COMMON TO ALL PHYLA

The following sexual characters, though common to all phyla, are most conspicuous in titanotheres from the higher geologic levels:

Male	Female
1. Skulls larger.	1. Skulls smaller.
2. Canines larger and more robust.	2. Canines smaller, more pointed.
3. Incisors larger, more constant.	3. Incisors smaller and more variable.
4. Nasals broader, more robust at tips.	4. Nasals narrower, less robust at tips.
5. Horns more powerful and robust.	5. Horns shorter, more pointed, less completely ossified at tips.
6. Connecting crest very prominent.	6. Connecting crest less prominent.
7. Arches more widely expanded.	7. Zygomatic arches less widely expanded.
8. Zygomatic-cephalic indices higher, more brachycephalic.	8. Zygomatic-cephalic indices lower, more mesaticephalic.
9. Occiput more robust, expanding, and rugose.	9. Occiput less robust.
10. Closure of cranial sutures accelerated.	10. Closure of cranial sutures retarded.

The incisors are apparently more variable and are more likely to drop out of place in the females than in the males, especially in individuals of *Brontotherium* (Pl. XIX). The smaller canines are among the most persistent characteristics of the female (Pl. XX). Our observations do not confirm Hatcher's remark that "a feeble internal cingulum" upon the premolars is a female character. The entire grinding series appears to be relatively as large and as vigorously developed in females as in males. Between the females and the males in the ascending series of *Brontotherium* there is a very marked and rather puzzling disparity in the size of the skull.

TEETH: DISTINCTIVE FEATURES AND EVOLUTION

Incisors, superior and inferior, considered as phyletic characters.—The strong or the feeble development of the incisors and the presence or the absence of certain members of the incisor series are two characters that are distinctive of the phyla, genera, and species.

In contrast to the Eocene titanotheres, all the known Oligocene titanotheres, except *Teleodus*, had only two pairs of incisor teeth. As early as upper Eocene time the reduction and the loss of incisors is foreshadowed in *Protitanotherium* and *Diplacodon* by the hypertrophy of certain pairs of incisors and the atrophy of others. This hypertrophy, atrophy, and disappearance of the incisors is graphically presented below:

$$\textit{Megacerops}:\ \frac{0.\ 0.\ 0}{0.\ 0.\ 0}$$

$$\textit{Menodus}:\ \frac{0.\ i^2.\ i^3}{i_1.\ i_2}\ \text{to}\ \frac{0.\ 0.\ 0}{?}$$

$$\textit{Brontotherium}:\ \frac{0.\ i^2.\ i^3}{i_1.\ i_2.\ 0}\ \text{to}\ \frac{0.\ 0.\ i^3}{0.\ i_2.\ 0}$$

$$\textit{Brontops brachycephalus}:\ \frac{0.\ i^2.\ i^3}{i_1.\ i_2.\ 0}\ \text{to}\ \frac{0.\ 0.\ i^3}{0.\ i_2.\ 0}$$

$$\textit{Teleodus avus}:\ \frac{?i^1.\ i^2.\ i^3}{i_1.\ i_2.\ i_3}$$

$$\textit{Protitanotherium}:\ \frac{i^1.\ i^2.\ i^3}{i_1.\ i_2.\ i_3}$$

In the *Brontops* phylum the third lower incisor (i_3) is apparently the first to disappear in the lower jaw, and the third upper incisor (i^3) the first to disappear in the upper jaw. The jaw of *Teleodus avus* (Pl. XIX, D) contains six incisors. The outermost pair (i_3) have very short roots and insecure tenure, so that further evolution in the same direction would probably result in the crowding out of i_3. By far the largest teeth with the longest roots are the second incisors (i_2). Intermediate in size are the first incisors (i_1).

In the upper jaw of *Brontotherium* (Pl. XIX, A) the median pair (i^1) have apparently been lost; the persistent teeth represent the second incisors (i^2) and the greatly enlarged third incisors (i^3). In the lower jaws of *Brontotherium* a third pair of incisors (i_3) have apparently been lost. The first pair (i_1) have spread apart, leaving a diastema in the midline; the second pair (i_2) remain large and usurp the position of the third (i_3).

The form of the crown of the incisor teeth is also highly distinctive. In members of the menodontine group the incisor crowns are smoothly rounded or conic, often laterally compressed, as in *Teleodus* (Pl. XIX, D). In members of the brontotheriine group the incisors are cingulate posteriorly.

Canines, superior and inferior, considered as sexual characters.—The canines (Pl. XX) are highly distinctive of each phylum and of each genus, as they differ widely in form and in function. The shape is the same in both sexes, but those of the male are always larger and much more powerful than those of the female. For example, in *Menodus giganteus* (Am. Mus. 505) the male tusks measure 62 by 34 millimeters, whereas the female tusks (Am. Mus. 506) measure 40 by 21 millimeters. In *Brontotherium elatum* also, as shown by a comparison of five skulls, the female tusks are about two-thirds the size of the male tusks.

All primitive members of the menodontine group (such as *Menodus* or *Brontops*) have long, pointed canines, whereas all primitive members of the brontotheriine group (such as *Brontotherium leidyi*) have short, obtuse canines. Secondarily some progressive members of the menodontine group (such as *Brontops robustus*) develop short, obtuse canines that are not readily distinguished from the short, obtuse canines of the late members of the brontotheriine group (such as *Brontotherium gigas*). This is an example of convergence.

Within each of these two groups the canines are differentiated. The extremely elongate and powerful canines of *Menodus* are readily distinguished from the smaller canines of *Brontops*, as well as from the anteroposteriorly compressed canines of *Allops*. Again, in the brontotheriine group the robust canines of *Brontotherium* are readily distinguished from the diminutive canines of *Megacerops*.

Premolar evolution; retrogression, abbreviation.—In correlation with the abbreviation of the face (brachyopy) seen in the titanotheres the premolars are sacrificed to the evolution of the molars. This is observed in the variability or loss of $p\frac{1}{1}$, in the arrested molarization of the premolars (or their failure to acquire the complete molar pattern), and in the relative abbreviation of the premolar series as compared with the molar series and as expressed in the premolar-molar index. This evolution is just the reverse of that in the dolichopic Equidae, in which the premolars evolve more rapidly than the molars.

In the *Menodus* phylum the face is relatively elongate (dolichopic) and the premolar index (50–53) remains more constant. In the *Megacerops* and *Brontotherium* phyla the face is relatively abbreviate and the premolar-molar index (42–46) is low and retrogressive, although the premolars increase greatly in width.

Premolar-molar indices $\left(\frac{p^2-p^4}{m^1-m^3}\right)$

	Menodontine group (Menodus phylum)		Brontotheriine group (Brontotherium phylum)	
Upper Titanotherium zone (lower Oligocene).	Menodus giganteus	50–53	Brontotherium curtum Brontotherium gigas	42–46 47
Lower Titanotherium zone (uppermost Eocene).	Menodus proutii	49	Brontotherium leidyi	47
Uinta C (upper Eocene)	Telmatherium ultimum	51		
Upper Bridger (middle Eocene)	Telmatherium cultridens	61		
Upper Wind River (lower Eocene)	Eotitanops borealis	63		

Arrested molarization of premolars.—In all Oligocene titanotheres arrested molarization is seen, first, in the entire absence of a mesostyle on the ectoloph of the permanent superior premolars, although the mesostyle is present on the milk premolars; second, in the retarded development of the tetartocones, especially on p^4. The retarded development of the tetartocone of p^4 may be adaptively correlated with the fact that this tooth erupts much later than p^3 or p^2 (Pl. XXI, figs. 405, 406; Carnegie Mus. 116). Nevertheless, p^4 is nearly as broad as m^1, whereas in Eocene titanotheres, except those of the very highest levels, p^4 is much narrower than m^1.

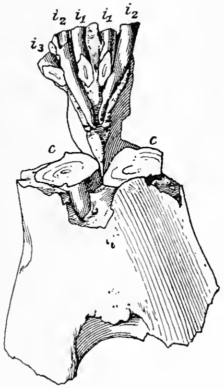


FIGURE 380.—Inferior aspect of chin in *Manteoceras*

A fragment from the upper Bridger, Am. Mus. 1746, probably *Manteoceras manteoceras*, showing large size of canine roots, length of roots of i_2, and shortness of roots of i_1 and i_3. One-half natural size.

The differential rate of molarization of the premolars is one of the most characteristic distinctions between phyla. Each phylum has its own rate of molarization. In *Brontops* the premolars transform very slowly. In *Diploclonus*, *Allops*, and *Menodus*, respectively, they transform with increasing rapidity. In *Megacerops* and *Brontotherium* the premolars transform very rapidly. Thus in the two extremes the retarded premolars of *Brontops brachycephalus* with incipient tetartocones are readily distinguished from the progressive premolars of *Brontotherium leidyi* with strongly developed tetartocones, although both animals belong to the same geologic level.

Loss of $p\frac{1}{1}$ *with age.*—The presence or absence of $p\frac{1}{1}$, which was much cited as a specific character by Marsh, is rather an age character. This tooth is present in many young skulls and absent in many old skulls, as has been observed in specimens of *B. brachycephalus*, *B. dispar*, *B. robustus*, *Allops crassicornis*, *Menodus giganteus*, *Brontotherium gigas*. It lacks a firm hold in its socket, and its root impinges against the obliquely placed roots of the canines. This tooth comes into use very early in *Brontops*, *Menodus*, and *Brontotherium* and tends to drop out early because all the teeth protrude from their sockets as wear on them advances, and the roots of p^1 soon lose their firm hold in the alveolus. P^1 is always a smaller and simpler tooth than p^2, which tends to crowd it out of place.

Molar evolution.—The Oligocene grinding tooth evolves out of the primitive Eocene grinder and takes its proportions from the skull. Thus we compare the elongate, dolichocephalic grinding tooth of *Menodus* with the abbreviated, brachycephalic, transversely spreading grinder of *Brontotherium* (fig. 382.)

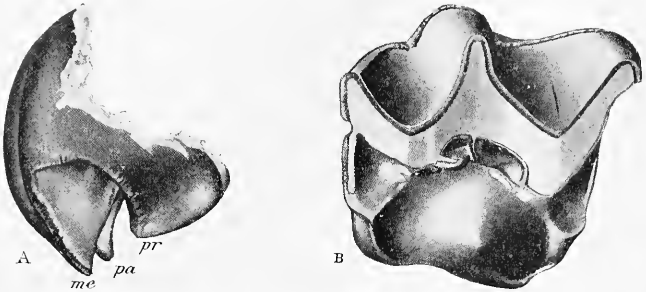


FIGURE 381.—Upper molars of *Menodus giganteus* and *Allops marshi*

A, *Menodus giganteus*, Am. Mus. 496. First left upper molar, posterior view. This tooth was beginning its eruption at the time of the animal's death; in life the tips of the cusps would soon have come into use. The internal cusps (*pr*) are low; the outer wall of the tooth is produced into a long arc. This outer wall wears down much faster than the inner cusps, and the tooth as a whole slowly rotates downward and inward, the outer side moving faster than the inner side, so that in old animals the outer roots are widely protruded and the surface of the crown is tilted inward.

B, *Allops marshi*, Am. Mus. 499. Second right upper molar, crown view. From the base of the metacone a small projection, the "crochet," runs forward into the deep medifossette; from the middle of the crown opposite the mesostyle a second small projection, the "crista," runs inward and forward; from the base of the paracone a third ridge, the "antecrochet," runs back toward the crochet and crista. Crochet, antecrochet, and crista appear in both the deciduous premolars and the permanent molars of Oligocene titanotheres along with the deepening medifossette. They are barely foreshadowed in the upper Eocene *Diplacodon* and *Rhadinorhinus*.

Two-thirds natural size.

Special characters.—The most exceptional character is the vertical elongation of the ectoloph (figs. 227, 228, 381) which attains twice the height of the protocone; thus a disharmonic crown is produced, hypsodont on the outer side and brachyodont on the inner side; this elongation of the ectoloph leaves a deep pit (medifossette) in the central valley of the crown, which is bounded by three secondary foldings of enamel—anterior, median, and posterior—which are comparable to but not homologous with the crochet, antecrochet, and crista of the rhinoceros molar tooth. These secondary folds are rectigradations which are also slightly developed in certain upper Eocene titanotheres. The medifossette is distinctly foreshadowed in the upper Eocene *Diplacodon*. A shallow postfossette appears internal to the hypocone. On the antero-internal border of the crown appears a prominent cuspule which is comparable to the protostyle; it never detaches itself from the protocone; in the center of the crown are sometimes observed vestigial or reversional traces of the protoconule and of the metaloph. The terminology of the molars, as compared with that in other perissodactyls, is set forth in Chapter V (p. 263).

The correlation of dolichocephaly and brachycephaly with tooth proportions is illustrated in the comparative measurements of the brachycephalic *Brontops robustus*, the dolichocephalic *Menodus giganteus*, and the brachycephalic *Brontotherium gigas elatum*. (See p. 451.)

Upper molars; hypocone and cingulum.—The hypocone of m^3 appears as a low cusp on the posterior cingulum in *Brontops dispar* and as a prominent cingulum cone in *Menodus* (*Diconodon*, *Anisacodon montanus*). In some specimens of *Menodus* the hypocone of m^3 is separate and is surrounded by a cingulum; in others it is small but distinct or is confluent with the cingulum. Thus the separation of the hypocone would not appear to be a valid specific, much less a valid and constant generic character.

Cope observed that the strong or feeble development of the cingulum divides the titanotheres into two parallel groups (Cope, 1891.2, p. 9), which are now recognized as follows:

Menodontine group (*Menodus, Brontops*, etc.): Cingulum strongly or distinctly developed.

Brontotheriine group (*Brontotherium*, *Megacerops*, etc.): Cingulum retrogressive, feebly developed, or wanting.

In *Menodus* the cingulum is especially strong; in *Megacerops* it is especially feeble. The cingulum is thus a distinct phyletic or group character. It is not a sex character, as Hatcher suggested (1893.1, p. 216). For example, in the female skull of *Menodus giganteus* (Am. Mus. 506) the cingulum is quite as strongly marked as in the male skulls (Am. Mus. 505, 1066, 1067). The cingulum is less strong in *Brontops* and *Diploclonus* than in *Menodus* and is almost obsolete in *Megacerops acer* and *Brontotherium platyceras*.

FIGURE 382.—Extreme dolichocephalic (A) and brachycephalic (B) types of upper premolar-molar series in Oligocene titanotheres

A, *Menodus trigonoceras*, Carnegie Mus. 3068, one-fourth natural size; B, *Brontotherium gigas elatum*, Am. Mus. 492, tooth row reduced to the same absolute length as in A.

Correlation of dolichocephaly and brachycephaly with proportions of teeth

[Measurements in millimeters]

	Brontops robustus, Yale Mus. 12048 (type)	Menodus giganteus, Field Mus. P 5927	Brontotherium gigas, Am. Mus. 492
Pmx to condyles	765	825	830
Width of skull across zygomatic arches	667	515	740
Zygomatic index	87	62	89
P^1–m^3	350	425	353
Dental index	45	51	42
P^1–p^4	137	150	130
M^1–m^3	220	270	241
P^4, ap. by tr	40 × 65	[a] 50 × 68	47 × 72
Sum of anteroposterior measurements of m^1–m^3 compared with sum of transverse measurements	220 × 255	[a] 249 × 246	241 × 277

[a] Measurement taken from Am. Mus. 505.

Lower molars.—The lower grinding teeth also indicate either the brachycephalic or the dolichocephalic proportions of the skull. This is especially witnessed in the third lower molar (Pl. XXII), in which, for example, the relatively long, narrow form in *Menodus* contrasts with the relatively broad, robust form in *Brontotherium.* M_3 is further distinguished clearly in the different phyla by the form of the hypoconulid, or third lobe, which is more lophoid in the *Menodus* group, more crescentic in the *Brontotherium* group. Similarly the main crescents are somewhat more open in dolichocephalic molars and more closed or acute in brachycephalic molars.

The cingulum is strongly developed on the lower grinders in members of the menodontine group and feebly developed or obsolete in members of the brontotheriine group.

The molarization of the lower premolars proceeds step by step with the molarization of the upper premolars. Thus the premolars acquire the molar pattern slowly in the menodontine group and more rapidly in the brontotheriine group.

The internal wall, especially of the third lower molars, develops sharp crests (metacristid, entocristid, fig. 383), which are similar in form and position to those of certain other early perissodactyls, especially the paleotheres and chalicotheres; but, with the exception of *Lambdotherium,* the titanotheres do not develop the metastylid and entostylid, cusps which in other perissodactyls arise by fissure of the metaconid and entoconid respectively.

DEVELOPMENT OF THE SKULL AND DENTITION

Stage 1.—The earliest known stage (Pl. XXIII) is represented by a specimen in the Yale Museum, which is a lower jaw containing the deciduous teeth of a newly born animal. Three alveoli of deciduous incisors and two deciduous premolars (dp_2, dp_3) are in place; the latter are unworn. The third and last deciduous premolar had not yet erupted and much of it is buried in the jaw. The titanotheres, like many other ungulates, apparently had but three deciduous premolars on each side in the upper and the lower jaws.

The position of the incisor alveoli was the same as in *Teleodus avus* (Pl. XIX, D) and suggests their identification as di_1, di_2, di_3. The opposite incisors were separated in the midline, and di_1 lies much below the plane of di_2. Perhaps this indicates a protrusile tongue. The first permanent premolar, p_1, is just emerging. Possibly the deciduous canine had been shed at an earlier stage. The deciduous premolars (dp_2, dp_3) have heavy external cingula. The horizontal ramus of the jaw is very shallow; the ascending ramus relatively very heavy.

Stage 2.—Stage 2 is represented by a "calf" jaw with alveoli for three deciduous incisors and for the deciduous canines (Am. Mus. 510; Pl. XXIV, A), which is provisionally referred to *Menodus giganteus.* It includes the alveolus of permanent p_1 of the left side. The deciduous premolars (dp_2–dp_4) are in place and slightly worn. They are more molariform than the permanent premolars that succeed them.

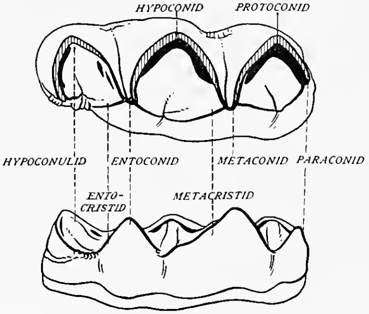


FIGURE 383.—Third left lower molar of *Brontotherium leidyi*, showing the metacristid and entocristid

Carnegie Mus. 93. One-half natural size

Stage 3.—Stage 3 is represented by a "calf" jaw of *Menodus giganteus* (Am. Mus. 509; Pl. XXIV, B). The root of i_2 (?) is in place; the remaining front teeth are not preserved; the tip of the permanent canine is embedded in the jaw, and behind it is a root that may belong to p_1; dp_2–dp_4 are in place; dp_2 and dp_3 are considerably worn, but not dp_4. Permanent p_1 is in horizontal line with dp_2, and although it is a very small tooth it is probably the one that is present in adult titanotheres. M_1 lies nearly ready to cut the gum.

Stage 4.—One of the youngest known titanothere skulls (fig. 384) is in the Museum of the University of Wyoming (No. 4). It was collected by Mr. W. H. Reed in Hell's Half Acre, Natrona County, Wyo., from a low level in the *Titanotherium* zone.

The large size of the first true molar (ectoloph ap. 57 mm.) indicates a larger animal than *B. brachycephalus;* it is of a size equaled in *B. dispar* (Nat. Mus. 4290). The horn swellings are small knobs, not much larger than those of very old individuals of *Manteoceras manteoceras.* The horn swelling on each side consists of a protuberance on the anterior tip of the frontals, which is embraced in a corresponding excavation of the expanded posterior border of the nasals. The free portions of the nasals are short and rounded distally, with sharply decurved lateral borders. The sutures in the region of the horn—that is, the nasofrontal, lacrimal, and maxillary sutures—conform to the plan exhibited in the National Museum skull 4258 and in skulls of other young titanotheres.

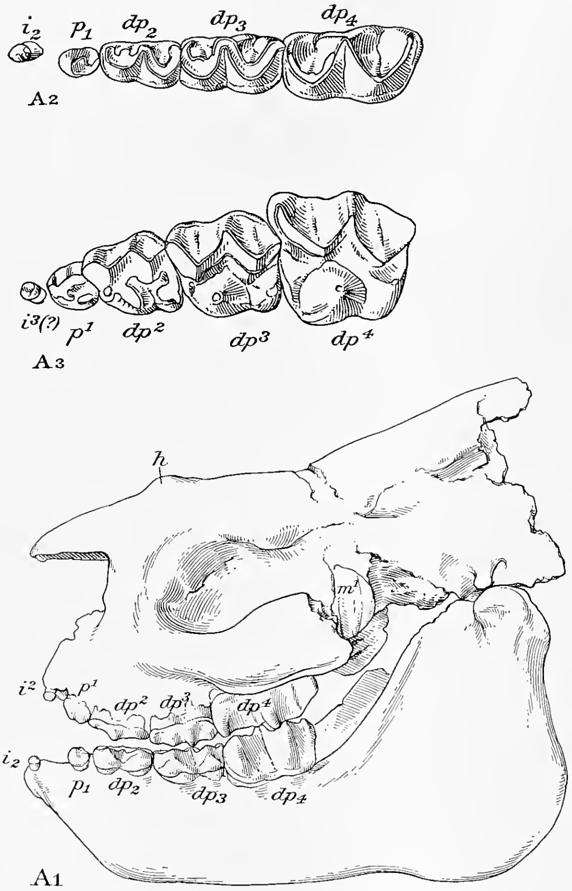


FIGURE 384.—Development of jaws and teeth, stage 4

Skull and teeth of female calf, Univ. Wyoming Mus. 4, referred to *Brontops dispar.* A_1, Skull and lower jaw, one-third natural size; A_2, upper teeth, one-half natural size; A_3, lower teeth, one-half natural size.

The upper jaw shows the permanent incisor i^3 (which is exposed in the specimen but was possibly beneath the gum in life); a tooth is just coming into place which is apparently p^1 of the adult; three deciduous premolars (dp^2, dp^3, dp^4) are in place. The lower jaw shows i_2, (?) p_1, and dp_2, dp_3, dp_4. M^1 and m_1 are buried in the jaws. Measurements of this specimen are as follows:

Measurements of deciduous teeth of Brontops dispar (*Univ. Wyoming Mus. 4*)

Upper jaw	Millimeters
P^1–dp^4	132
P^1, ap. by tr.	18×18
Dp^2, ap. by tr.	29×25
Dp^3, ap. by tr.	37×32
Dp^4, ap. by tr.	44×33
Dp^4, tr. (across mesostyle)	40
Permanent m^1, ectoloph, anteroposterior	57
Permanent m^1, ectoloph, height of metacone	45+
Nasals to middle of horn	75
Nasals, free breadth (estimated)	55
Pmx to condyles (rough estimate)	305
Lower jaw	
Front edge of symphysis to angle	284
Height condyle to angle	145
P_1–dp_4	128
Dp_1, ap. by tr. (trigonid)	11×10
Dp_2, ap. by tr. (trigonid)	31×15
Dp_3, ap. by tr. (trigonid)	37×20
Dp_4, ap. by tr. (trigonid)	49×25

Stage 5.—A more advanced stage is shown in a young jaw (Carnegie Mus. 124; Pl. XXIV, *C*) referred provisionally to *Brontops dispar.* The permanent incisors i_1 and i_2 are just coming in, while the deciduous incisors and canines have probably been shed. The permanent canine lies just below the surface. The tooth designated ? dp_1 although associated with milk teeth, appears to be the permanent p_1. The milk molars dp_2–dp_4 are worn. M_1 is just protruding. M_2 lies buried in the ascending ramus, below the coronocondylar sinus.

Stage 6.—A later ontogenetic stage is illustrated in a remarkably complete skull and jaw in the Carnegie Museum (No. 116), which were described by Hatcher in 1901 (1901.1; figs. 385, 386). The specimen was found on Warbonnet Creek, Sioux County, Nebr., near the base of the *Titanotherium* zone. The reference to *Brontops brachycephalus* is provisional.

In the side and top views (fig. 385) it is seen that the horns are formed by the overgrowth of the frontals upon the nasals, as in the Eocene *Manteoceras.* The lacrimal is expanded, and its outer ridge is continuous with the external ridge of the horn. The parietals extend forward upon the frontals. The interparietal is apparently distinct. The occiput is shown in Figure 386.

The construction of the skull conforms in its underlying plan to that of Eocene titanotheres, differing chiefly in the shortening of the face, the lengthening of the midcranium, and the widening of the skull top.

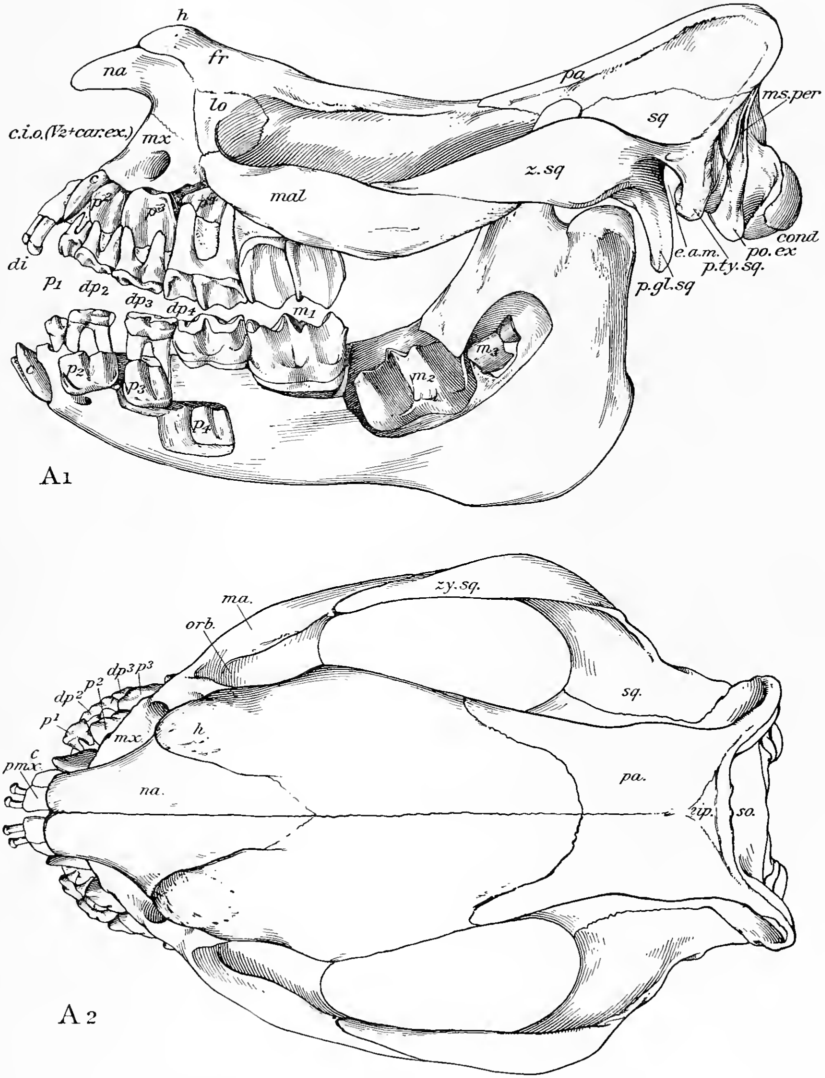


FIGURE 385.—Development of jaws and teeth, stage 6

Brontops? brachycephalus?, Carnegie Mus. 116: young skull and jaw. One-fourth natural size. After Hatcher. Level near the base of the Chadron formation (*Titanotherium* zone). A_1, Side view; A_2, top view.

Dentition.—The deciduous teeth were about to be shed, and their roots protrude widely. In the upper dentition the deciduous incisors, di^2(?), di^3(?), are small and round topped. Behind them the permanent canine lies buried. The deciduous canine has been shed. The deciduous premolars (dp^2, dp^3, dp^4) are well worn. M^1 is fully in place. P^2, p^3, p^4 lie embedded; permanent $p\frac{1}{1}$ are apparently represented in the well-worn teeth immediately in front of $dp\frac{2}{2}$. In the lower jaw the milk incisors were probably in the gums; at least their alveoli must have been shallow. The permanent canine is beginning to come in. The milk molars are well worn, and m_1 is in place. P_2, p_3, p_4 lie on descending levels in the jaw, the first nearing eruption. M_2 also lies embedded, and m_3 is beginning to form.

Hatcher's original description of the skull is as follows:

> When viewed from above the frontals are much the more conspicuous elements. They are bluntly rounded posteriorly and are projected far backward beneath and between the lateral anterior projections of the parietals. Anteriorly the frontals are continued into two long lateral projections which extend beyond the orbits, overlie the posterior and lateral margins of the nasals, and give rise to the pair of horn cores that form such characteristic features in the Titanotheridae. The nasals are arched superiorly, concave inferiorly, with rather long posterior extensions interposed between the frontal horns. In the present specimen the nasals are very thin along their inner margins but much thickened externally and posteriorly, where they give the chief support to the horns. They are slightly shorter than the premaxillaries and somewhat emarginate anteriorly.
>
> The parietals are not so broad as the frontals. They are deeply emarginate anteriorly and posteriorly, where they are separated by the interparietal portion of the supraoccipital much as in *Equus*. From the above description it will be seen that the anterior border of the parietals overlies and incloses laterally the posterior border of the frontals, while the anterior border of the latter has a like articulation with the nasals, the relative position of these bones being similar to that of the shingles of a roof.

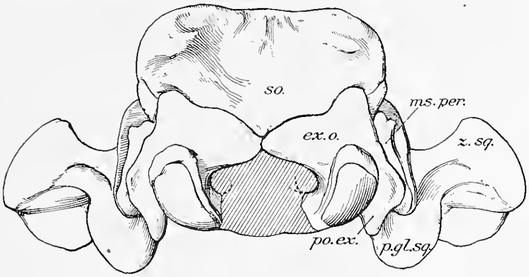


FIGURE 386.—Occiput of young skull of *Brontops? brachycephalus?*

Carnegie Mus. 116. One-fourth natural size. The exoccipitals meet above the foramen magnum. The wide supraoccipital affords attachment to the powerful ligamentum nuchae, the recti capitis lateralis, complexus, and other neck muscles.

> The zygomata are rather broadly expanded and are composed about equally of the malars and squamosals.
>
> When seen from the side the skull appears somewhat low, with an abbreviated facial region and a rather long posterior portion. The occipital crest and anterior frontal regions are each somewhat elevated. The nasals appear rather deep and send down the inferior and posterior projection, which articulates by suture with the superior border of the maxillary. The infraorbital foramen lies wholly within the maxillary. The maxillonasal suture is opposite the middle of the orbit. The lacrimal is rather large. The malar is long and thin; anteriorly it has an extended contact with the maxillary and posteriorly with the squamosal portion of the zygoma. The squamosal rises high above the external auditory opening and overlaps the side of the parietal throughout most of its length. There is a long, thin, transversely expanded postglenoid process and a shorter and proportionately stronger post-tympanic process of the squamosal. The tympanic is absent, having been lost from the present specimen. The periotic is present, and its paramastoid portion appears externally between the post-tympanic and paroccipital process. Just above this there is another small bone which is continued into a long pointed process inserted between the exoccipital and the squamosal and parietal; it probably became coossified later with the periotic, but in the present specimen it is seen as a separate bone, as shown in Figure 1 and in Plate VII. [See figs. 385, 386.] The exoccipitals are rather large and support the paroccipital process and the occipital condyles. The latter are ossified from two distinct centers, the articular portions bearing distinct epiphyses, as shown in the accompanying figures.
>
> Seen from behind the occiput is low and broad. The condyles are widely separated by the foramen magnum, which is much broader than deep. The condyles are entirely supported by the exoccipitals, which rise and meet in the middle line above the foramen magnum, entirely excluding the supraoccipital from any part in the formation of the superior border of that opening. The supraoccipital is very broad and low. The occipital crest is nearly flat above but broadly emarginate posteriorly. (See fig. 1 of the text, and Pl. VIII.)
>
> Inferiorly the palate is seen to be formed anteriorly by the very short premaxillaries, for the most part broken away in the present specimen, and by the maxillaries, between the posterior lateral extremities of which are inserted the palatines. These form the posterior median portion of the roof of the palate and send backward on either side a lateral projection along the inner sides of the maxillaries and pterygoids, which are continued nearly to the posterior end of the basisphenoid.
>
> The vomers are continued far back as a thin plate resting upon the pre- and basisphenoids and sending downward a thin, knifelike median bony septum. The basisphenoid in the present specimen is entirely free from the basioccipital, the suture being open, and the basioccipital had dropped out and was lost before the specimen was found. The absence of the basisphenoid and tympanic bones makes it impossible to describe and locate the various foramina of this region of the skull.

Stage 7.—Still more advanced is the stage shown in Am. Mus. 497 (Pl. XXV, *A*), deciduous and permanent upper teeth of *Menodus giganteus*. The first tooth of the series is the permanent p^1, as shown by its exact agreement in measurements and in characters with the first premolar in adult skulls of *M. giganteus* (Am. Mus. 505, 506). Phylogenetically this tooth may have been forced into association with the deciduous premolars dp^2, dp^3 through the abbreviation of the muzzle region and the consequent crowding backward of the permanent canine. In this specimen the permanent canine, which is still buried in the jaw, lies closely appressed against the second permanent premolar. The serial homology of this tooth as p^2 is also established by its measurements, as compared with the adult *Menodus giganteus*. In this as in many other mammals there was probably no deciduous predecessor of p^1.

In the specimen here figured m^1 is coming into place. The identity of these teeth is also established by comparison with the adult *M. giganteus*, so that there is no doubt that dp^4, dp^3, dp^2 are correctly identified.

Comparative measurements, in millimeters, of deciduous and permanent dentition of species of Menodus and Brontops

[The measurements given in the first five columns were made on the ectoloph]

	P^1	P^2	P^3	M^1	Dp^2	Dp^3	Dp^4	Dp_4	M_1	P^1–dp^4	P_1–dp_4
M. giganteus, Am. Mus. 505, ♂	22	32	45	72	------	------	------	------	------	------	------
M. giganteus, Am. Mus. 506, ♀	23	35	46	71	------	------	------	------	63	------	------
M. giganteus, Am. Mus. 496	------	------	------	77	------	[a] 47	67	------	------	------	------
M. giganteus, Am. Mus. 497	26	40	46	76	45	47	65	------	------	174	------
M. giganteus, Am. Mus. 494	21	------	------	------	46	51	66	------	------	------	------
M. giganteus, Am. Mus. 509	------	------	------	------	------	------	------	58	62	------	160
B.? brachycephalus?, Carnegie Mus. 113	------	------	40	68	------	------	------	------	62	136	138
B. dispar, Carnegie Mus. 124	------	------	------	------	------	------	------	48	56	------	130
B. sp.?, ?Yale Mus	------	------	------	------	------	------	------	------	------	------	[a] 135
B. sp.?, Univ. Wyo. 4	18	------	------	57	29	39	47	49	57	132	128

[a] Estimated.

SUMMARY OF THE REPLACEMENT OF THE TEETH IN OLIGOCENE TITANOTHERES

The following is a summary of the order of succession of the upper and lower teeth as observed in the six juvenile stages represented in Plates XXIII and XXIV and in Figures 384 and 385.

1. The three deciduous incisors (di$\frac{1}{1}$, $\frac{2}{2}$, $\frac{3}{3}$) have the same relative position as the permanent incisors (i$\frac{1}{1}$, $\frac{2}{2}$, $\frac{3}{3}$) in *Teleodus avus.* They were shed very early.
2. The deciduous canines, known only from their alveoli in one specimen (Pl. XXIV, A), were shed perhaps even earlier than the deciduous incisors (Pl. XXIII, XXIV).
3. No evidence of deciduous predecessors of p^1 and p_1 has been observed either in Eocene or in Oligocene titanotheres, and in these, as in other ungulates, there were probably only three and not four deciduous premolars.
4. The permanent p$\frac{1}{1}$ came into place soon after the deciduous dp$\frac{2}{2}$, $\frac{3}{3}$ and functioned with the deciduous series.
5. The first true molars (m$\frac{1}{1}$) came into place before the deciduous premolars had been replaced. At later periods m$\frac{2}{2}$ and m$\frac{3}{3}$ came into place successively, so that in old animals m$\frac{1}{1}$ is greatly worn, whereas m$\frac{3}{3}$ is but little worn.
6. The fourth premolar (p$\frac{4}{4}$) follows the general mammalian rule of coming in late.

In the Oligocene titanotheres, as in many other mammals, the second, third, and fourth deciduous premolars (dp$\frac{2}{2}$, $\frac{3}{3}$, $\frac{4}{4}$) are much more molariform than the permanent premolars (p$\frac{2}{2}$, $\frac{3}{3}$, $\frac{4}{4}$) which replace them. Thus molarization of the deciduous premolars is observed even in the middle and lower Eocene titanotheres (*Lambdotherium*, *Palaeosyops*) and is equally characteristic of the Oligocene titanotheres. In *Menodus giganteus* (Am. Mus. 497, Pl. XXV, *A*) the third deciduous premolars (dp$\frac{3}{3}$) are like molars, dp^3 and dp^4 having prominent mesostyles and large, distinct tetartocones.

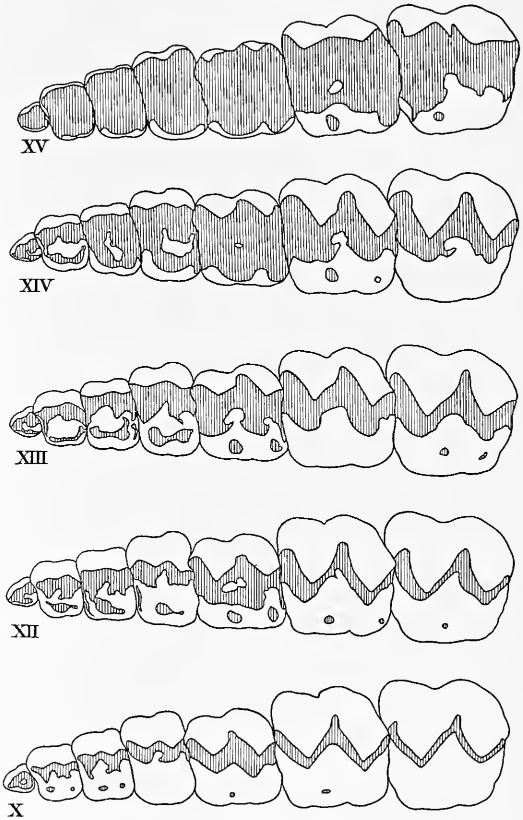


FIGURE 387.—Stages of wear in the adult upper grinding teeth of Oligocene titanotheres

The following specimens, all drawn to the same length, show the progressive degrees of wear from the young adult (X) to the very aged (XV) ontogenetic stage of the dentition: X, *Allops crassicornis*, Nat. Mus. 4289 (type); XII, *Brontops robustus*, (type), Yale Mus. 12048; XIII, *Menodus giganteus*, Am. Mus. 505; XIV, *Allops serotinus*, Am. Mus. 520; XV, *Brontops brachycephalus*, Nat. Mus. 4947. (See p. 456)

STAGES OF WEAR OF THE ADULT GRINDING TEETH

Seven early and adolescent stages in the ontogeny of the dentition have been described above. In the eighth and ninth stages (adolescent) the deciduous premolars (dp^2, dp^3, dp^4) are gradually replaced by the permanent premolars p^2, p^3, p^4. In the tenth ontogenetic stage (X) of the young adult the internal cusps of the second and third but not the fourth premolars are beginning to show the dentine through the enamel surface; the last molar is but little worn. In the very aged fifteenth ontogenetic stage (XV) nearly the whole enamel surface of the crowns of p^1–m^1 inclusive has been worn away, so that the dentine is very widely exposed; in m^2 both the protocones and hypocones are much worn. The intervening stages show intermediate conditions, as follows (fig. 387):

XV. Fifteenth ontogenetic stage: *Brontops brachycephalus*, Nat. Mus. 4947.

XIV. Fourteenth ontogenetic stage: *Allops serotinus*, Am. Mus. 520.

XIII. Thirteenth ontogenetic stage: *Menodus giganteus*, Am. Mus. 505.

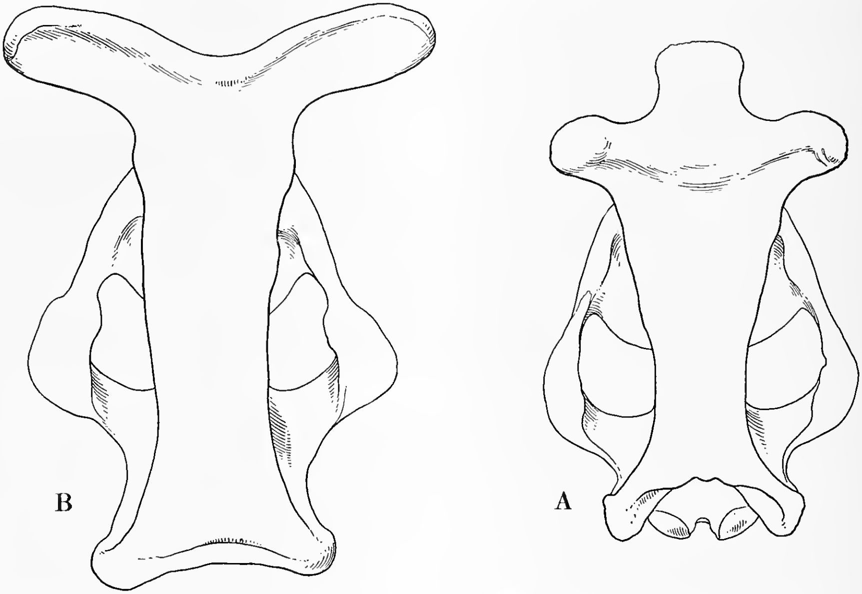


FIGURE 388.—Skull contours showing extreme divergence between *Menodus giganteus* (A), a final term of the menodontine series, and *Brontotherium platyceras* (B), a final term of the brontotheriine series

In *Menodus* the opposite borders of the cranial roof diverge anteriorly, the horns are short and trihedral, the zygomata but little expanded, and the occiput not greatly produced backward. In *Brontotherium* the opposite borders of the cranial roof are nearly parallel, the horns very long and flattened, the zygomata widely expanded, and the occiput greatly produced backward. One-tenth natural size.

XII. Twelfth ontogenetic stage: *Brontops robustus* Yale Mus. 12048 (type).

X. Tenth ontogenetic stage: *Allops crassicornis*, Nat. Mus. 4289 (type).

AGE AND OTHER CHARACTERS COMMON TO BOTH SEXES OF TITANOTHERES OF ALL STRATIGRAPHIC LEVELS

Age characters.—The age characters are naturally much more conspicuous in males than in females. In both sexes the adults of one geologic generation follow the general law of anticipating the advanced mutations or specific stages reached by adults of higher geologic levels. Thus the variability of a tooth on a lower geologic level is prophetic of its absence on a higher geologic level. This variability is especially displayed in retrogressive structures such as the degenerate incisor teeth in the *Brontops* series, as is shown by the following formulas:

Juvenile incisors, $I\frac{1-2}{1-2}$.
Adult incisors, $I\frac{2-1}{2-1}$.

The incisive teeth tend to drop out in the adults, as observed in the type of *Diploclonus tyleri* Lull.

Thus among the age characters are the following: (1) Increasing size and rugosity of the skull, arches, horns, and nasals; (2) distal expansion and rugosity of the tips of the nasals; (3) loss of variable and vestigial teeth, incisors and premolars, in old age; (4) union of the anterior caudal vertebra with the sacrum to form four sacrals (Hatcher, 1893.1, p. 217).

In general, growth is in a high degree differential—that is, proportions constantly change, as, for example, in the gain of width over length, in the rapid increase of the horns in length, and in the relative gain in the length of the nasals, although only in a few specimens have we sufficient material to measure these differentials in growth.

Abnormal sport and reversional characters.—Among the abnormal characters may be observed the following: (1) Reversional or abortive protoloph and metaloph on the superior premolar teeth; (2) abnormal reduplication of tetartocones on superior premolar teeth observed in specimens of *Brontops dispar, Allops crassicornis, Menodus varians;* (3) progressive rectigradational or anomalous reduplication of horns as observed in specimens of *Diploclonus, Menodus, Brontotherium.*

SECTION 3. DIVISION OF THE OLIGOCENE TITANOTHERES INTO GROUPS AND SUBFAMILIES

CHARACTERS OF THE SKULL AND TEETH OF THE MENODONTINE AND BRONTOTHERIINE GROUPS

The following study of the characters of the skull and teeth enables us to divide all the highly varied forms of Oligocene titanotheres into two great groups, the menodontine and the brontotheriine, which separated from each other in Eocene time. (See p. 467.) These characters, which are much more pronounced in male than in female skulls, are seen to be the direct and indirect results of one or other of the opposing principles of skull and tooth transformation described on pages 254–262, 450, namely:

1. Dolichocephaly and dolichopy versus brachycephaly and brachyopy; cyptocephaly.
2. Differential transformation of canines (p. 448), premolars, and molars. (See figs. 405, 406.)
3. Differential development of horns, nasals, orbits, zygomata, etc. (See figs. 389–394.)

Primary groups of the Oligocene titanotheres

	Menodontine group (Teleodus, Brontops, Diploclonus, Allops, Menodus)	Brontotheriine group (Megacerops ("Symborodon"), Brontotherium)
Canines	Primitively pointed, recurved, not closely approximated toward median line.	Primitively short, bulbous, with swelling posterior cingulum, closely approximated.
Opposite grinding series as seen in palate view.	Not strongly arched anteriorly toward median line.	Strongly to very strongly arched toward median line.
Upward flexure of premolars as seen in side view.	Slight to moderate	Very pronounced.
Antorbital region of skull	Relatively elongate	Abbreviated (Brontotherium) to very abbreviated (Megacerops).
Premolar series (length)	Relatively longer	Relatively shorter.
Internal cusps of upper premolars	Steep-sided (Menodus); moderately so (Brontops).	Very low, robust, subcircular.
Ectolophs of grinding teeth	Somewhat more vertical	Sharply depressed to crown.
Hypocone of m^3	Often surrounded by cingulum	Very heavy, triradiate, continuous with cingulum.
Internal cingula	Sharp on premolar teeth	Often less developed and rounder.
External cingula	Usually pronounced	Reduced or absent.
Zygomata	Slight to heavy, often deep	Broad to extremely expanded and flattened.
Horns	Short, diverging obliquely outward and forward.	Long, usually more erect.
Malar-lacrimal bridge over infraorbital foramen.	Usually very broad	Usually very narrow.
Anterior narial cavity	Broad and open	Becoming very high and narrow.
Backward prolongation of occiput behind zygomata.	Moderate	Moderate to extreme.
Jaw	Angle sharply produced backward	Angle less produced backward, more slender.
P^1	Somewhat more elongate	Somewhat abbreviate.
Convexity, top of parietals	Absent	Pronounced.
Orbit	Medium to large	Medium to small.
Skull vertex	Divergent anteriorly, convergent posteriorly.	More or less parallel.
Skull vertex, side view	More concave	More convex.
Proportions of molar teeth	More elongate	More expanded transversely.

Features of the jaws.—As most of the jaws found were entirely dissociated from the skulls, it is difficult to determine the generic and even more so the specific references of many separate jaws. Observation should be directed first to the prevailing dolichocephalic or brachycephalic proportions, to the shallowness or depth of the ramus, to the slenderness or massiveness of the angular region, and especially to the depth or shallowness of the chin region. In general, members of the menodontine group have a deep symphyseal or chin region, whereas members of the brontotheriine group have a shallow chin.

The generic diagnosis of remains that include a full series of teeth is relatively simple. Specific diagnosis is partly dependent on size. In order to associate a lower jaw with a skull the measurement should be taken from the glenoid cavity to the front of the superior canine and from the mandibular condyle to the posterior face of the inferior canine. If all the other characters are properly determined and the progressive stages of the superior and inferior premolars correspond, this method of associating the jaws with the skulls is reliable. This method, however, can be used to advantage only on skulls and jaws that are not distorted by crushing. Usually the most practicable measurements are the following:

Upper: Front face of canine to middle of posterior fossa of m^3 (for hypoconulid of m_3).
Lower: Rear face of canine to tip of hypoconulid of m_3.

The following table shows the chief characters of the jaw that distinguish the members of the two groups:

Characters of the jaw that distinguish members of the menodontine group from members of the brontotheriine group

Character	Menodontine group					Brontotheriine group	
	Teleodus	Brontops	Diploclonus	Allops	Menodus	Megacerops	Brontotherium
Horizontal ramus	Deep	Shallow	Shallow	Intermediate	Deep	Short, massive	Massive, deep posteriorly.
Symphyseal region in side view below mental foramen.	Convex	Very shallow	Shallow	Intermediate to convex.	Fuller	Shallow	Very shallow.
Region of angle	Barely produced.	Usually produced downward.	?Produced, truncate.	Intermediate	Produced backward and downward into a convex elbow. Posterior border oblique.	Broad, posterior border vertical.	Broad, posterior border often vertical.
Incisors	I_3	I_{2-1}	I_{2-1}	I_{2-1}	I_0 (typically)	? I_0	I_{2-1}.
P_1 in fully adult jaws	Present	Usually present	Present	Present or absent	Present or absent	?Absent	Present or absent.
Diastema in front of p_1	Present	Present, wide	Present	Absent	Absent	?Absent	Absent.
Canines	Slender	Slender to short, stout	Slender to short, stout.	Conic to compressed anteroposteriorly.	Conic	(?)	Swollen at base with massive posterior cingulum.
External cingulum of canines, premolars, molars.	Not sharply defined.	Present in early types; lost in B. robustus.	Intermediate.	Present	Strongly marked		Absent.
Upward flexure of premolar series.	Moderate	Slight or moderate	Slight or moderate.	Very slight	Absent	Pronounced	Typically pronounced.

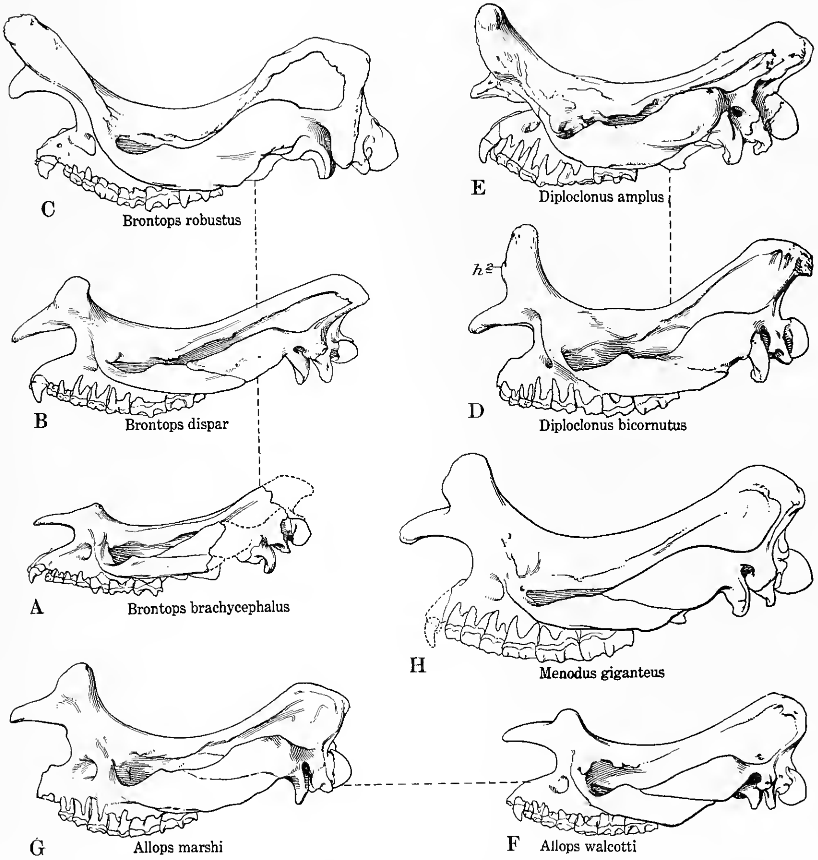


FIGURE 389.—Skulls of the menodontine group

Side view. One-twelfth natural size.

Subfamily Brontopinae: A, *Brontops brachycephalus*, ♀, a very small and primitive member of the *Brontops* phylum, with incipient horn swellings, long nasals, and slender canines; Chadron A. B, *Brontops dispar*, an intermediate stage with moderately developed horns; Chadron B. C, *Brontops robustus*, final stage of this phylum; a very massive brachycephalic skull with stout forward directed horns, short, thick nasals, short, heavy occiput, and expanded zygomata; canines short and thick; Chadron C. D, *Diploclonus bicornutus*, referred to this genus partly because of the accessory horn swelling (h^2). The skull contour suggests that of *Menodus*. E, *Diploclonus amplus*, a massive short skull recalling *Brontops robustus* but possessing an accessory horn swelling and very short nasals. Occiput long.

Subfamily Menodontinae: F, *Allops walcotti*, a primitive dolichocephalic form, supposed to be ancestral to the *Allops* phylum; Chadron A. G, *Allops marshi*, in general contour intermediate between *Brontops dispar* (B) and *Menodus* (H), thought to be related to *Allops serotinus* and *Allops crassicornis*. H, *Menodus giganteus*, latest stage of the *Menodus* phylum; dolichocephalic, horns trihedral in basal section, nasals long, zygomata not expanded, canine long, cheek teeth with sharp external cingula; Chadron C.

In all members of this group the skull top in side view is deeply concave. The cheek teeth almost always have sharp external cingula.

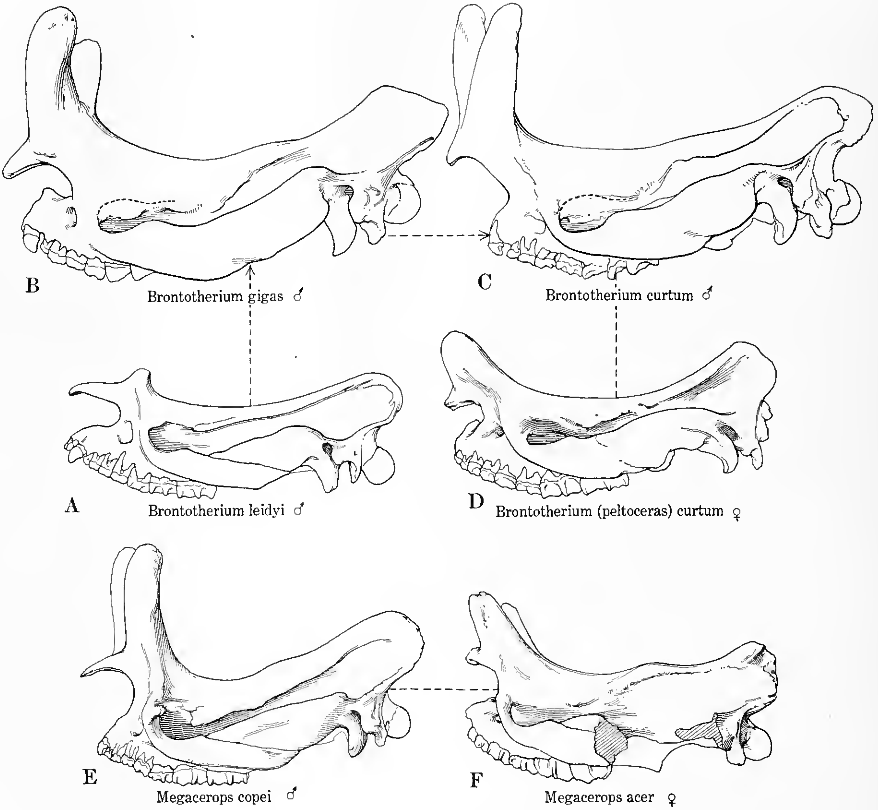


FIGURE 390.—Skulls of the brontotheriine group

Side view. One-twelfth natural size.

Subfamily Brontotheriinae: A, *Brontotherium leidyi*, a primitive member of the *Brontotherium* phylum with short horns transversely oval in section, long nasals tapering and decurved, canines short and swollen, two stout incisors, and cheek teeth with but little external cingulum; Chadron A. B, *Brontotherium gigas*, a progressive brontothere with long erect horns transversely oval in basal section, nasals of intermediate length, zygomata widely expanded, occiput long, and a marked parietal convexity; Chadron C. C, *Brontotherium curtum*, a highly advanced brontothere with very long horns far in front of the orbits and much flattened anteroposteriorly, nasals short, skull top long, and zygomata much expanded; Chadron C. D, *Brontotherium (peltoceras) curtum*, a female brontothere with skull short and massive, horns very thick, high connecting crest, and nasals short.

Subfamily Megaceropinae: E, *Megacerops copei*, long horns thick at the base, nasals long and thin, canines very short and swollen, premolar series upturned, and zygomata massive. F, *Megacerops acer*, horns of moderate length but very thick at the base, nasals short and thick, premolar series upturned, zygomata heavy, midparietal swelling prominent.

Compared with the Menodontinae, members of this group usually have the skull top less deeply concave, and many have a parietal swelling, The horns are commonly transversely oval in section, the premolar series upturned anteriorly, and the canines in males short and swollen.

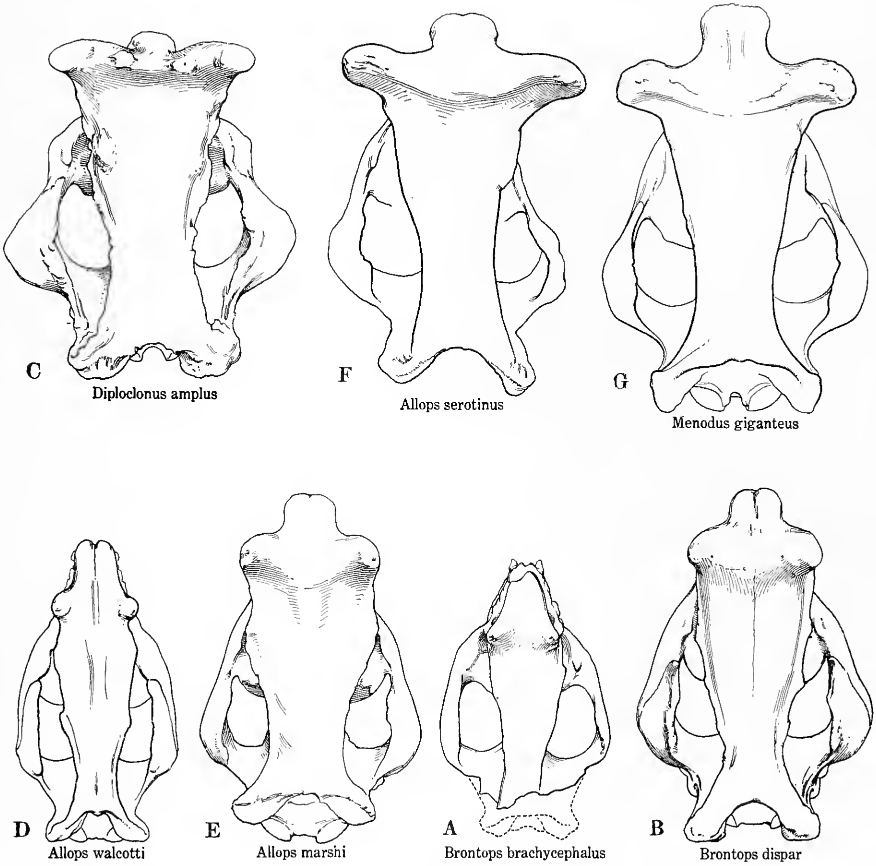


FIGURE 391.—Skulls of the menodontine group

Top view. One-twelfth natural size.

Subfamily Brontopinae: A, *Brontops brachycephalus*, a primitive stage with horns very short and nasals long and tapering. The specimen is a female, and the zygomata are not much expanded; the skull top is rather slender, although the skull as a whole is broad. B, *Brontops dispar*, an intermediate stage with short horns rounded in section, nasals and frontals broad, and zygomata expanded. The midparietal crest is constricted, as in many other members of this family. C, *Diploclonus amplus*, a highly specialized brachycephalic stage, resembling *Brontops robustus* in general proportions. The horns are wide and flattened at the base and pointed at the tips and bear accessory hornlets on the antero-internal portion. The nasals are wide and short.

Subfamily Menodontinae: D, *Allops walcotti*, a primitive dolichocephalic type (thought to be ancestral to the *Allops* phylum) with small horns elongate oval in section, nasals long and tapering, zygomata slender, and skull top narrow. E, *Allops marshi*, horns widely trihedral in basal section and directed outward and upward, skull top fairly broad, zygomata gently expanded. F, *Allops serotinus*, a specialized stage with long outward-directed horns, wide, short nasals, wide frontals, and moderately stout zygomata. G, *Menodus giganteus*, the terminal stage of the *Menodus* phylum, with skull dolichocephalic, skull top long, zygomatic expansion moderate, nasals long and distally wide, horns sharply trihedral in basal section, the connecting crest lying in the plane of the posterior face of the horns.

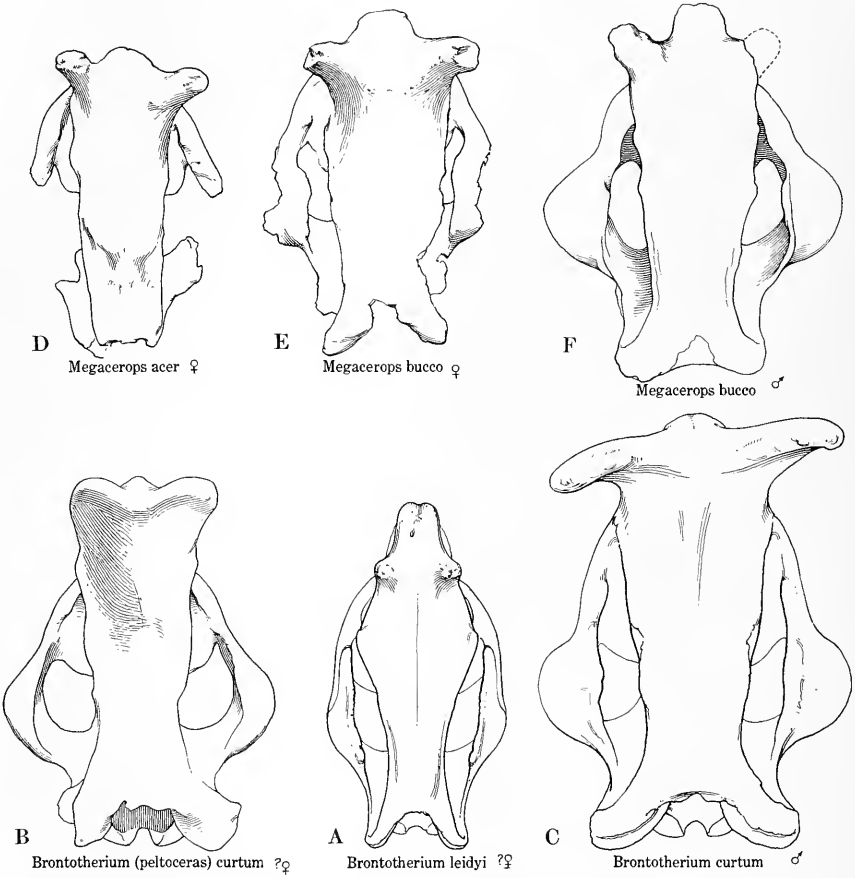
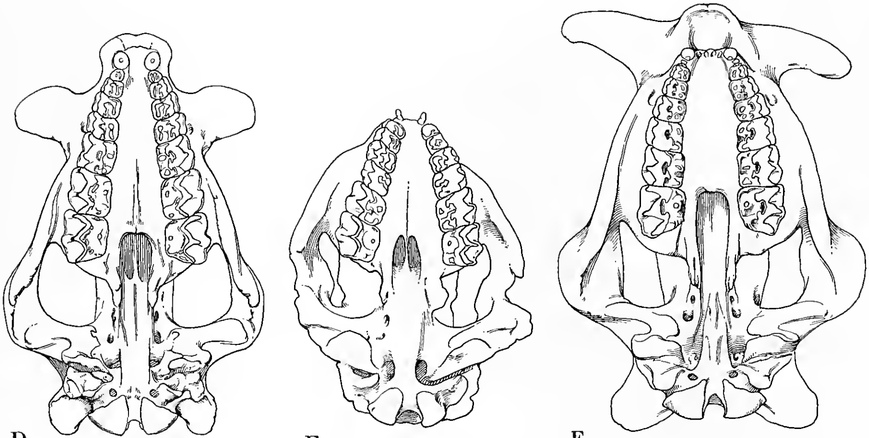


FIGURE 392.—Skulls of the brontotheriine group

Top view. One-twelfth natural size.

Subfamily Brontotheriinae: A, *Brontotherium leidyi*, a primitive stage with skull top long, small horns transversely oval at the tips, nasals long and tapering, frontal region wide, zygomata not expanded; Chadron A. B, *Brontotherium (peltoceras) curtum*, skull top long but zygomata arching widely, short massive horns confluent with the high connecting crest and pointed at the tips, nasals reduced and pointed. C, *Brontotherium curtum*, a very large male skull with widely expanded zygomata, widely flaring flat-oval horns, very short nasals, wide frontal region, occipital pillars widely expanded transversely.

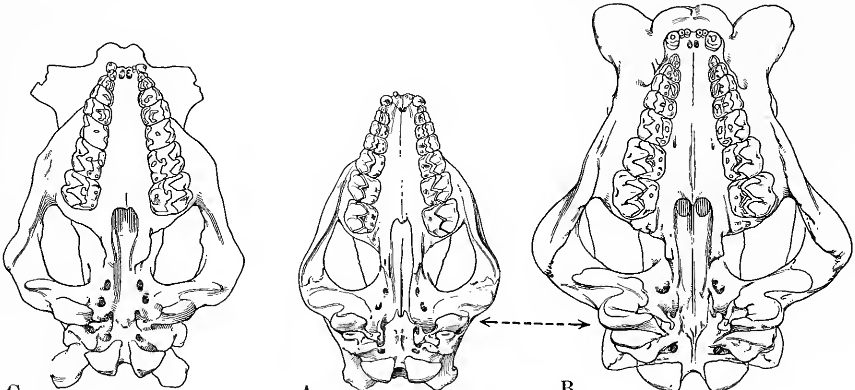
Subfamily Megaceropinae: D, *Megacerops acer*, skull short with widely expanded zygomata, horns cylindrical with but little connecting crest, nasals short and wide, skull top wide with parallel edges. E, *Megacerops bucco*, ♀; resembles in general the preceding type but has larger horns. F, *Megacerops bucco*, ♂, a large animal with greatly expanded zygomata and rather feeble cylindrical horns.



D Menodus giganteus

E Megacerops bucco

F Brontotherium curtum



C Allops serotinus

A Brontops brachycephalus

B Brontops robustus

FIGURE 393.—Skulls of the menodontine and brontotheriine groups

Palatal view. One-twelfth natural size

Menodontine group: A, *Brontops brachycephalus*, brachycephalic, grinding teeth of moderate width. B, *Brontops robustus*, skull very large and brachycephalic, grinding teeth wide, incisors and canines massive. C, *Allops serotinus*, skull more elongate, grinding teeth of intermediate proportions. D, *Menodus giganteus*, dolichocephalic, grinding teeth elongate, tooth rows rectilinear.

Brontotheriine group: E, *Megacerops bucco*, skull base very brachycephalic, grinding teeth broad, tooth rows curvilinear, fourth premolar submolariform, canines small. F, *Brontotherium curtum*, skull very large, skull base long but tooth rows curvilinear, grinding teeth wide, fourth premolar submolariform.

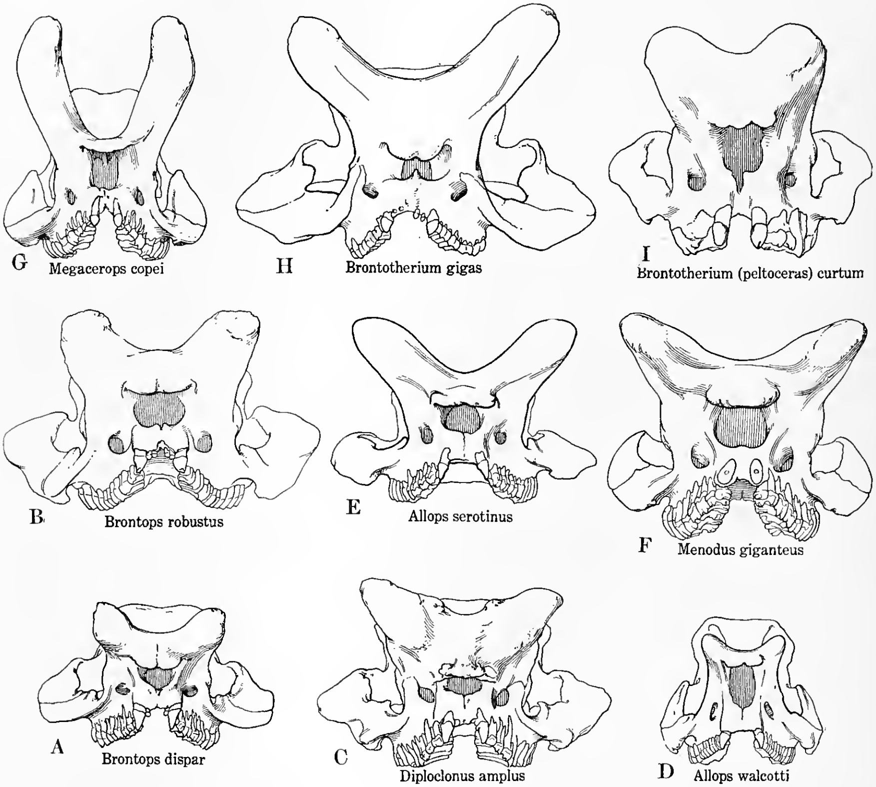


FIGURE 394.—Skulls of the menodontine and brontotheriine groups

Front view. One-twelfth natural size.

Menodontine group: A, *Brontops dispar*, horns short and thick, subcircular in section and pointed, nasals of moderate size, zygomata moderately expanded, lateral incisors present, canines relatively long and conical. B, *Brontops robustus*, skull massive, horns comparatively short and transversely expanded, with thick rugose tips, nasals short and robust, zygomata heavy, two large incisors, canines short, thick, and conical. C, *Diploclonus amplus*, horns divergent, very wide at base and rapidly narrowing to the pointed tips, an accessory hornlet, nasals small, zygomata expanded. D, *Allops walcotti*, skull small and slender, horns very small, nasals broad, zygomata deep and slender. E, *Allops serotinus*, long divergent horns narrowing but little toward the tip, zygomata of moderate size, canines slender and pointed. F, *Menodus giganteus*, long divergent horns narrowing rapidly to pointed tips and trihedral in section, nasals expanded distally, zygomata relatively small and deep, canines (not shown) elongate pointed, incisive border edentulous.

Brontotheriine group: G, *Megacerops copei*, ♂, horns long, erect, and cylindrical, with no connecting crest, nasals thin, zygomata not widely expanded (diminished by crushing), canines small, rounded, and close together, premolars upturned anteriorly. H, *Brontotherium gigas*, ♂, skull very wide, zygomata enormous, horns long and wide, nasals of intermediate length, two incisors on each side, canines short and swollen. I, *Brontotherium curtum*, ♀?, horns short but very broad and massive, with high connecting crest, nasals short and narrow, zygomata not widely expanded, canines swollen.

CHARACTERS AND RELATIONS OF THE SUBFAMILIES

Each of the major groups described above divides into two separate branches to which Osborn gives the rank of subfamilies, as follows:

- Menodontine group (short-horned):
  - Brontopinae: Mesaticephalic (in females) to brachycephalic. Incisor teeth persistent.
  - Menodontinae: Mesaticephalic, stenocephalic. Incisor teeth reduced or wanting.
- Brontotheriine group (long-horned):
  - Megaceropinae: Brachycephalic. Incisor teeth reduced or wanting.
  - Brontotheriinae: Mesaticephalic to brachycephalic. Incisor teeth persistent.

Each of these subfamilies includes one or more phyla, which in turn may embrace one or more genera.

Polyphyly.—The fact that the Oligocene titanotheres separated into four subfamilies before the beginning of the Oligocene epoch has been shown both by the distinct connection of two of these subfamilies with different Eocene ancestors and by the marked differences between titanothere remains that are found at the very lowest levels of the *Titanotherium* zone. Here the ancestors of the Menodontinae, of the Brontopinae, and of the Brontotheriinae are found to be quite separate and distinct. No Megaceropinae have yet been found at these low geologic levels of the Oligocene.

Summary of distinctions.—The means of distinguishing the numerous branches and sub-branches of the great family differ somewhat from those employed to distinguish the Eocene branches from one another. The proportions of the head and of the zygomatic arch, whether dolichocephalic or brachycephalic, still remain a distinguishing characteristic. Owing to the buccal expansion of the zygomatic arches the males of *Menodus* are technically mesaticephalic or even sub-brachycephalic rather than "dolichocephalic," in spite of the fact that the skull in general appearance and in form of the teeth is long and narrow, especially in contrast with the wide skull and grinding teeth of *Brontops*, *Megacerops*, and *Brontotherium*. The narrower Oligocene skulls may therefore be described as stenocephalic.

As the horns become the dominant feature of the skull the main line of division first arises between the short-horned and long-horned titanotheres. The typical shape of the horns, whether triangular, rounded, oval, or flattened, also becomes of very great value. With these weapons of offense are developed the gigantic swellings of the zygomatic arches by which the breadth of the skull as a whole is measured and cephalic indices are determined. A further differentiation is found in the presence or absence of incisor teeth and in the shape, size, and offensive character of the canine tusks. Wide divergence is seen also in the process begun in upper Eocene time—namely, the molarization of the premolars, or their transformation into the molar pattern. In some lines of descent this process is accelerated, and in others it is retarded. Another distinction is in the development of the cingulum on the grinders.

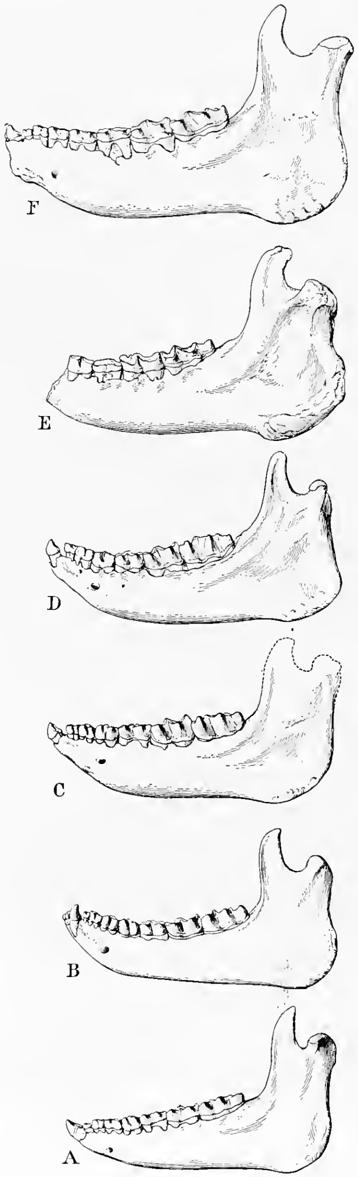


Figure 395.—Lower jaws of the *Brontotherium* phylum

A, *Brontotherium leidyi*, Carnegie Mus. 93 (paratype); B, *B. leidyi*, Am. Mus. 516; C, *B. hatcheri*, Am. Mus. 1070; D, *B. gigas*, Yale Mus. 12009 (type); E, *B. gigas elatum*, Yale Mus. 12061 (type of *Titanops elatus*); F, *B. medium*, Am. Mus. 1051. All one-twelfth natural size.

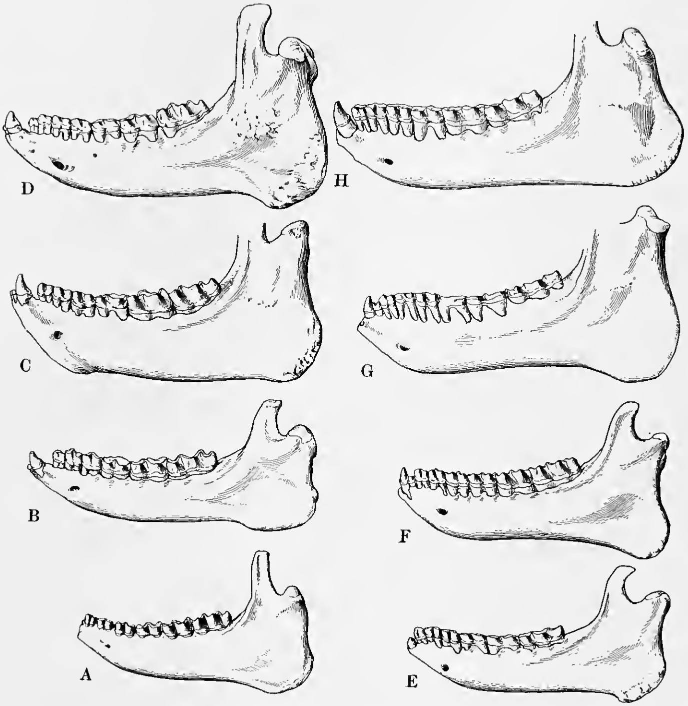


FIGURE 396.—Lower jaws of the *Brontops* and *Menodus* phyla

A, *Brontops brachycephalus*, Am. Mus. 1495; B, *B. dispar*, Nat. Mus. 4941 (type); C, *B. robustus*, Princeton Mus. 10061; D, *B. robustus*, Yale Mus. 12048 (type); E, *Menodus torvus*, Am. Mus. 6365 (type); F, *M. trigonoceras*, Nat. Mus. 4745; G, *M. giganteus*, Am. Mus. 506; H, *M. giganteus*, Field Mus. P 5927. All one-twelfth natural size.

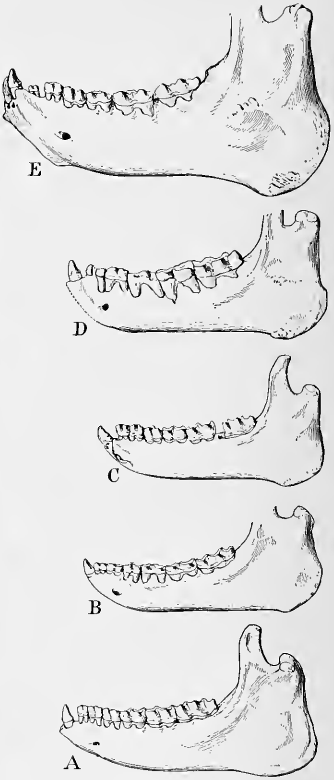


FIGURE 397.—Lower jaws of the *Diploclonus* and *Allops* phyla

A, *Allops walcotti* (?), Nat. Mus. 4247; B, *A. marshi*, Field Mus. P 6900; C, *A. angustigenis*, Ottawa Mus. (cotype); D, *Diploclonus bicornutus*, Am. Mus. 1476 (type); E, *D. tyleri*, Amherst Mus. 327 (type). All one-twelfth natural size.

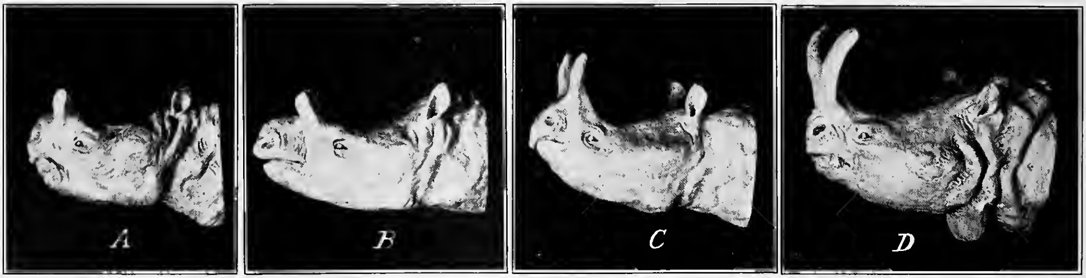


FIGURE 398.—Heads of Oligocene titanotheres, showing proportions, lip structure, and horns

Modeled by Charles R. Knight. *A, Brontops* (brachycephalic); *B, Menodus* (dolichocephalic); *C, Megacerops* (hyperbrachycephalic); *D, Brontotherium* (brachycephalic).

Groups and subfamilies of Oligocene titanotheres

[See fig. 697, p. 769]

Menodontine group: Persistently short-horned titanotheres; nasals broad; grinding teeth with persistent cingula	Brontotheriine group: Originally short-horned, progressively long-horned titanotheres; nasals pointed, reduced; grinding teeth with cingula reduced
SUBFAMILY BRONTOPINAE	SUBFAMILY MEGACEROPINAE
Descendants of the Eocene Manteoceras and Protitanotherium.	Descendants of unknown Eocene forms, possibly of Rhadinorhinus.
Subbrachycephalic to hyperbrachycephalic.	Brachycephalic to hyperbrachycephalic.
Horns suboval, subcircular, transversely oval.	Horns rounded and without connecting crest.
One to two pairs of persistent incisor teeth.	Incisor teeth reduced or vestigial.
Premolar transformation retarded.	Premolar transformation accelerated.
Genera: Teleodus, Brontops, Diploclonus.	Genus: Megacerops.
SUBFAMILY MENODONTINAE	SUBFAMILY BRONTOTHERIINAE
Descendants of unknown Eocene ancestors, possibly related to Telmatherium.	Descendants of unknown Eocene forms.
Mesaticephalic to dolichocephalic and to brachycephalic.	Mesaticephalic to brachycephalic.
Horns typically subtriangular.	Horns transversely oval and progressively flattened.
Incisor teeth vestigial or reduced to one pair.	Incisor teeth persistent.
Premolar transformation not retarded.	Premolar transformation accelerated.
Genera: Allops, Menodus.	Genus: Brontotherium.

The members of these subfamilies are more or less clearly connected with ancestral forms in the Eocene, as shown in Figures 402–409. Further exploration, however, is needed to bridge over securely these lines of descent. Our present knowledge is about as follows:

Genetic relations of Oligocene to Eocene titanotheres

Eocene titanotheres	Oligocene titanotheres
Subfamily Palaeosyopinae. Becoming entirely extinct in middle Eocene time.	No known descendants of the Palaeosyopinae.
Subfamily Telmatheriinae. Exhibiting some resemblances to the Oligocene Menodontinae but differing widely in the presence of large incisor teeth.	Subfamily Menodontinae. Exhibiting some resemblances to the Eocene Telmatheriinae; no known connecting forms.
Subfamily Manteoceratinae. Including two stages, Manteoceras and Protitanotherium, which exhibit many resemblances to the Brontopinae but differ in the possession of very broad nasal bones.	Subfamily Brontopinae. Including Teleodus, Brontops, and Diploclonus, which show many resemblances to the Eocene Manteoceratinae.
Subfamily Dolichorhininae. Composed chiefly of generic forms that became extinct in the upper Eocene but early gave off one branch.	
Subfamily Rhadinorhininae, which shows some resemblance to Megacerops.	Subfamily Megaceropinae. Including Megacerops, the "Symborodon" of Cope, which shows certain resemblances to Rhadinorhinus and other very strong resemblances to Brontotherium.
Subfamily Diplacodontinae. Including the genera Diplacodon and Eotitanotherium, of uncertain relationships with the lower Oligocene Menodontinae and Brontotheriinae.	Subfamily Brontotheriinae. Showing resemblances to the Eocene Diplacodon, Eotitanotherium, Rhadinorhinus. Direct Eocene ancestors unknown.

Brontopinae.—The more heavily built titanotheres of the genus *Brontops* exhibit close resemblances to the Eocene *Manteoceras* and *Protitanotherium.* They pass through the lower Oligocene species of *Teleodus* and exhibit a wide adaptive radiation into the genera *Brontops* and *Diploclonus*. In general they have short, robust limbs, very broad skulls, and short, rounded or pointed horns and are provided with one or two pairs of cropping teeth. The incisors have rounded crowns; the canines are roundly pointed; the premolars are very slow in developing the second internal cones. Short limbs and broad, spreading feet give them a singularly graviportal and brachypodal character, which is analogous to what is known of the limb structure of *Manteoceras*, of the Eocene.

Menodontinae.—The long-limbed relatively cursorial animals typified by the genus *Menodus* agree with the Telmatheriinae in the very robust development of the canines and of the grinding teeth but differ in the marked degeneration of the incisor teeth. In the loss of incisors they parallel the Megaceropinae. In contrast to the *Brontops* series the limbs and arches are slender, the bones of the girdles are relatively high and narrow, and the feet are of the elongate, dolichopodal type. Thus the menodonts are relatively cursorial in contrast with the typically graviportal brontopines.

Brontotheriinae.—The gigantic titanotheres of the subfamily Brontotheriinae appear to be related either to the *Diplacodon* or to the *Rhadinorhinus* phylum of the upper Eocene.[33] They are distinguished by the precocious development of the horns, the rapid transformation of the premolar teeth, the stout, obtuse canines, the retention of two pairs of upper and lower incisor teeth that have cingulate crowns in contrast to the smooth, rounded crowns in the Brontopinae. The horns early acquire at their extremities a transversely oval shape, which finally extends down to the base of the horn. The cranial vertex is extremely long and narrow, but the great buccal processes at the sides of the head develop pari passu with the elongation of the horns. The cheek teeth are less elongate than in *Menodus* and have more rounded crowns and nearly obsolete cingula, well fitted for cutting and crushing coarse vegetation.

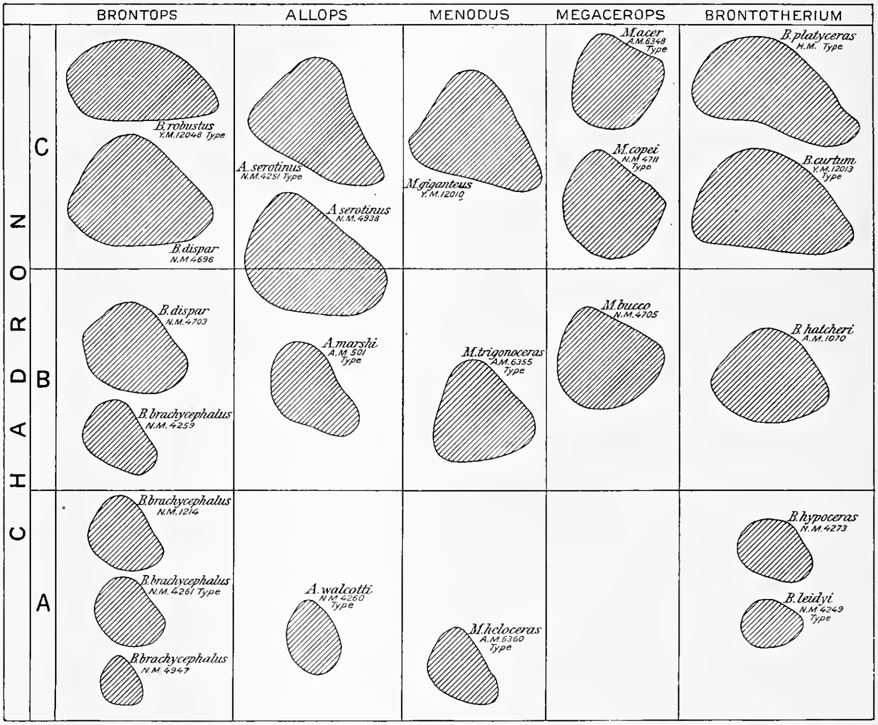


Figure 399.—Sections at base of horn in five principal lower Oligocene phyla of titanotheres, arranged according to ascending geologic levels

Drawn to the same scale.

Megaceropinae.—The Megaceropinae are much smaller animals than the brontotheres, distinguished by skulls of intermediate proportions, with tall, rather slender and cylindrical horns placed well forward above the eyes. The incisors are absent. It appears probable that the snout was narrow and terminated in a pointed lip like that of the black rhinoceros of Africa. The face was very short, narrow, and upturned, bringing the mouth almost up to the level of the eye. The small obtuse canines were brought close together toward the median line. The cusps and cutting edges of the cheek teeth were even more rounded than in *Brontotherium* and entirely devoid of cingulum.

POSSIBLE EOCENE ANCESTORS OF THE BRONTOTHERIINE GROUP

We may again consider the evidence and theories as to the transitions between Eocene and Oligocene titanotheres. (Compare *Diplacodon*, *Rhadinorhinus*, pp. 439, 441, 470–474.)

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[33] See pp. 434, 441, 469, 550.

Diplacodon theory.—The imperfectly known skull of *Diplacodon elatus* from the base of Uinta C exhibits several resemblances to *B. leidyi* from Chadron A, and Osborn was at first disposed (1915) to regard *Diplacodon* as containing the ancestors of *Brontotherium.* (See pp. 439, 441.)

Gregory at first regarded *Diplacodon* as intermediate between the *Rhadinorhinus-Metarhinus* group on the one hand and *Brontotherium* on the other, but later he was inclined to regard *Diplacodon* as possibly related rather to the ancestors of the menodontine group, on account of the resemblances in the premolar-molar series between *Diplacodon* and the early members of the *Brontops* and *Menodus* phyla. (See fig. 406.)

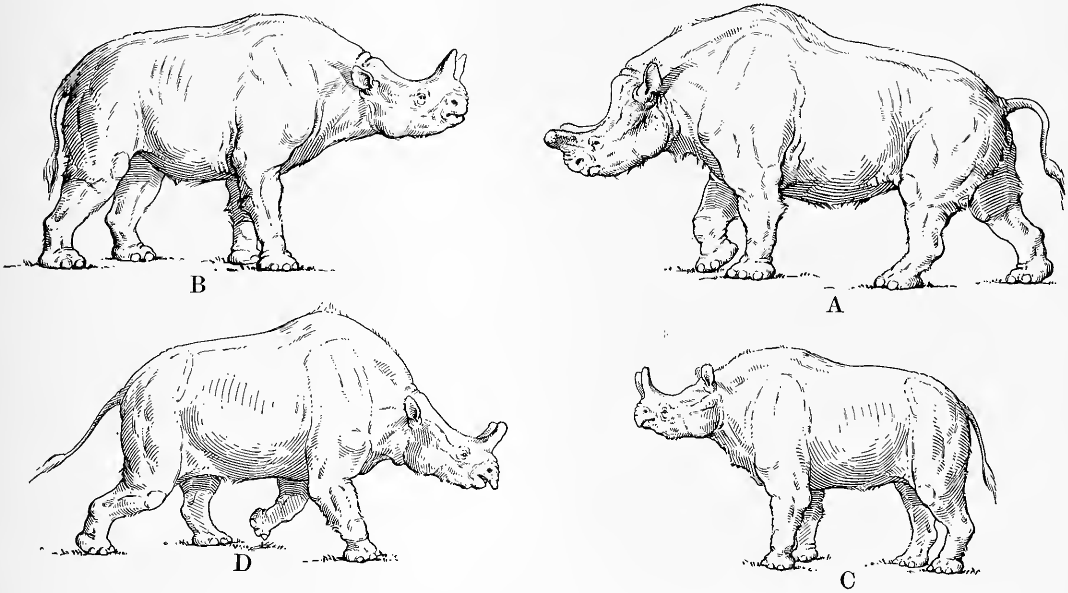


FIGURE 400.—Restorations of lower Oligocene titanotheres of the four principal genera

A, *Brontops robustus;* B, *Menodus giganteus;* C, *Megacerops acer;* D, *Brontotherium hatcheri.* One-fiftieth natural size.

Rhadinorhinus theory.—In 1902 Gregory observed that *Metarhinus fluviatilis* and *Rhadinorhinus diploconus* of the middle Eocene foreshadow *Megacerops* and *Brontotherium* in the following characters: (1) Anterior nares very deep, nasals becoming shorter; (2) bridge over infraorbital foramen very rounded; (3) upward flexure of premolar series in side view and "curvilinear" effect in palate view; (4) canines small and sometimes swollen at base, lower canines set near each other; (5) premolars relatively advanced, tetartocones set well in toward center of crown; (6) lower jaw with spoutlike incisive region (cf. *R. diploconus, M. earlei, M. fluviatilis*).

SECTION 4. OLIGOCENE GENERA ACCEPTED AS VALID IN THIS MONOGRAPH

Valid generic name and type species	Generic name used by Osborn in 1902
Menodus Pomel (M. giganteus), 1849	Titanotherium.
Megacerops Leidy (M. coloradensis), 1870	Megacerops.
Brontotherium Marsh (B. gigas, jaw), 1873	Brontotherium.
Brontops Marsh (B. robustus), 1887	Megacerops.
Allops Marsh (A. serotinus), 1887	Allops.
Diploclonus Marsh (D. amplus), 1890	Megacerops.
Teleodus Marsh (T. avus), 1890	Megacerops.

Menodus.—As is fully explained on pages 204–205, Pomel's name *Menodus giganteus* (1849) was based upon the first specimen of a titanothere made known to the scientific world, a fragment of a lower jaw, originally described by Prout in 1847. A comparison of a carefully drawn figure of this specimen given by Leidy (1854.1, pl. 16, fig. 1) with more complete material now available indicates that *Menodus giganteus* is the same form as that which was later named by Marsh *Brontotherium ingens.* Accordingly, *Menodus giganteus* Pomel has priority over Marsh's name and has therefore been adopted in this work. *Titanotherium* Leidy, although formerly used by the present author instead of *Menodus* Pomel, is now regarded as a synonym of that name, for reasons given on pages 205–206.

Megacerops.—Leidy's *Megacerops coloradensis* was founded upon a fragment of a skull (including the coossified nasals and "horns"; see p. 208) of a titanothere that now appears to be congeneric with the skulls subsequently named by Cope *Symborodon bucco.* The present author formerly used the name *Megacerops* for the generic group called *Brontops* by Marsh, but a reexamination of Leidy's above-mentioned type of *Megacerops coloradensis* has convinced him that this was an error. In the present monograph the name *Megacerops* includes the forms called by Cope "*Symborodon bucco*" and "*S. altirostris.*" (See pp. 212, 215.)

Brontotherium.—Marsh's *Brontotherium gigas*, the genotype of *Brontotherium*, rested upon a certain lower jaw in the Yale Museum (see p. 210), which the present author regards as congeneric with the flat-horned skulls that were later named by Marsh *Titanops elatus*, *Titanops medius*, *Titanops curtus.* Marsh, however, erroneously referred his type skull of "*Brontotherium*" *ingens* to the genus *Brontotherium.* "*B. ingens*" proves rather to be a synonym of Pomel's *Menodus giganteus.*

Symborodon Cope is unfortunately a synonym of *Menodus* Pomel, for the reason that the type species *Symborodon torvus* (see p. 211) was founded upon lower jaws that appear to be congeneric with the type jaw of *Menodus giganteus* Pomel.

Brontops, *Allops*, *Diploclonus*, and *Teleodus* are all now treated as distinct genera, although they were formerly regarded by the author as referable to *Megacerops.*

SECTION 5. THE MENODONTINE GROUP

SUBFAMILY BRONTOPINAE, INCLUDING THE PHYLA MANTEOCERAS, PROTITANOTHERIUM, TELEODUS, BRONTOPS, AND DIPLOCLONUS

STRATIGRAPHIC LEVEL AND DISTINGUISHING FEATURES

The menodontine group consists of titanotheres of upper Eocene to lower Oligocene age that reached a climax in the upper levels of the upper *Titanotherium* zone. Related to the Eocene *Manteoceras.* Distinguished by progressively broad heads (brachycephaly), short-crowned teeth (brachyodonty), and short or moderately proportioned feet (mesatipody). Horns short, progressively shifting forward, of primitive trihedral section at the base, rounded to oval at the summits, progressively transverse oval. Nasals progressively reduced in length and broadening at the extremities. Incisor teeth with rounded crowns; one or two pairs persistent above and below. Canine teeth pointed, of medium length, progressively obtuse. Premolar evolution retarded. Zygomata,

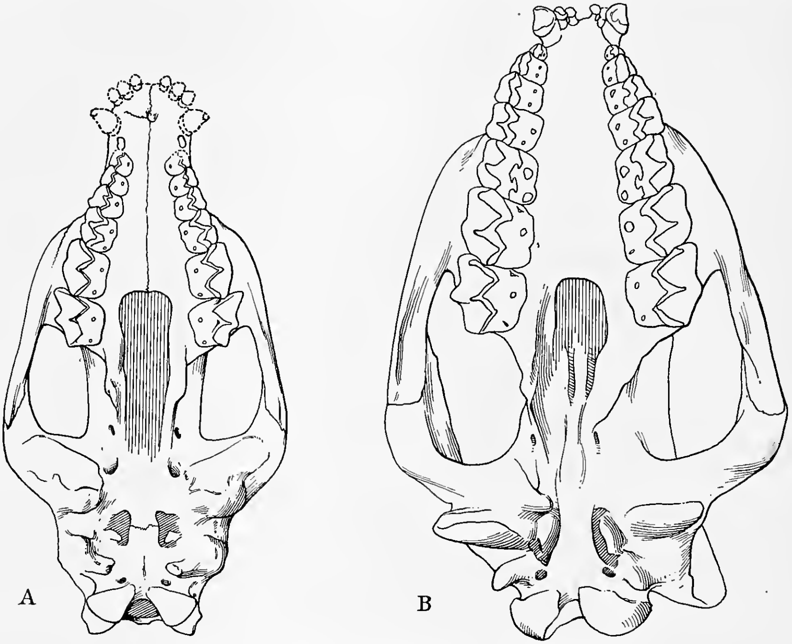


FIGURE 401.—Skulls of *Rhadinorhinus* and *Brontotherium*

Palatal view. A, *Rhadinorhinus diploconus*, Am. Mus. 1863 (type); White River, Uinta Basin, Utah, Uinta B 1; two-ninths natural size. B, *Brontotherium leidyi*, Carnegie Mus. 93 (paratype); Chadron formation; one-sixth natural size.

especially in males, progressively expanding into convex buccal processes. Includes original contemporaneous phyla known as *Teleodus*, *Brontops*, and *Diploclonus*.

These short-horned, broad-headed titanotheres, which have persistent incisor teeth, are very abundant in the lower, middle, and upper levels of the upper *Titanotherium* zone. They present certain characteristics which seem to be shared most nearly by the animal that Marsh called *Brontops dispar*. This animal is represented by a large number of specimens, which grade below into other specifically distinct forms, such as *Brontops brachycephalus*, and above into larger forms, such as *Brontops robustus*. It appears wise to retain as generic or subgeneric names the names proposed by Marsh to distinguish members of the two chief phyla—namely, *Brontops robustus* and *Diploclonus amplus*.

SUBFAMILY CHARACTERS OF TELEODUS, BRONTOPS, AND DIPLOCLONUS

COMPARISONS AND CONTRASTS

Very precise observation of the animals ranged under the phyla *Teleodus*, *Brontops*, and *Diploclonus* shows that they possess a large number of characters in common which distinguish them more or less clearly from the members of the far more readily defined phyla *Menodus*, *Brontotherium*, and *Megacerops*.

The horns attain no very great length and are usually circular in section at the summit. At the base they are trihedral, rounded, or transversely oval in section. The nasals, unlike those of *Menodus* and *Protitanotherium*, are rounded anteriorly, progressively shortened in ascending mutations, and in most old individuals they expand at the extremities.

At the very base of the *Titanotherium* zone Hatcher found a number of small, broad-skulled titanotheres that certainly belong to the *Brontops* phylum and that have been termed *Brontops brachycephalus* by Osborn, because they are surprisingly broad-skulled. Although they are perhaps not directly descended from any known upper Eocene form, such as *Protitanotherium emarginatum*, they have one striking feature in common—the short or rudimentary horns are placed directly above or slightly in front of the orbits and exhibit an elongate oval section at the base, precisely like those of *P. emarginatum*. Such horns were adapted to a lateral butting motion of the head, and it is notable that they are always blunt, or have elongate oval tips.

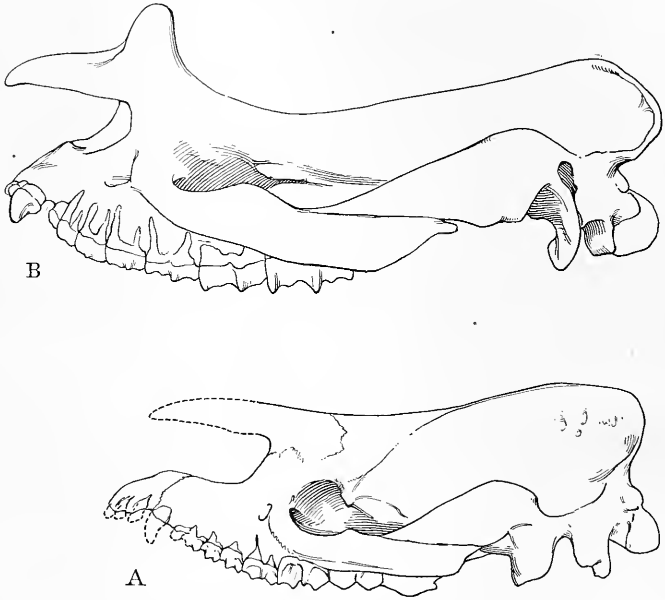


FIGURE 402.—Skulls of *Rhadinorhinus* and *Brontotherium*

Side view. A, *Rhadinorhinus diploconus*, Am. Mus. 1863 (type); White River, Uinta Basin, Utah; Uinta B 1; two-ninths natural size. B, *Brontotherium leidyi*, Carnegie Mus. 93 (paratype); Chadron formation; one-sixth natural size.

On the same low geologic level was also found a lower jaw containing three incisor teeth (an Eocene character), described by Marsh as *Teleodus avus*, which may belong to the same group as *B. brachycephalus*.

Features of the horns.—Horns that are transversely oval at the tips belong to members of the *Bronto-*

therium phylum. The free portion of the nasal bones is correspondingly elongate; the nasals contract in width anteriorly. The canine tusks, especially in males, are elongate, pointed, and slightly recurved. It appears that all lower Oligocene titanotheres also have elongate nasals. The extremely primitive character of the nasals and of the horns in the *Teleodus-Brontops-Diploclonus* group is correlated with a retarded stage in the evolution of the premolar teeth, a very characteristic feature which sharply distinguishes members of this group from members of the *Megacerops* and *Brontotherium* phyla. The premolars (fig. 406) are even more retarded or simpler than those of *Diplacodon elatus* from the upper Eocene Uinta formation, a proof that *D. elatus* was certainly not the ancestor of *Brontops*. On the inner side of the superior premolar crowns we see a large anterior cusp (deuterocone) followed by a low posterior ridge or small rudimentary posterior cusp (tetartocone). The mutations of *B. brachycephalus* in the lower beds were therefore very characteristic and clearly separable both from the upper Eocene forms and from succeeding Oligocene forms.

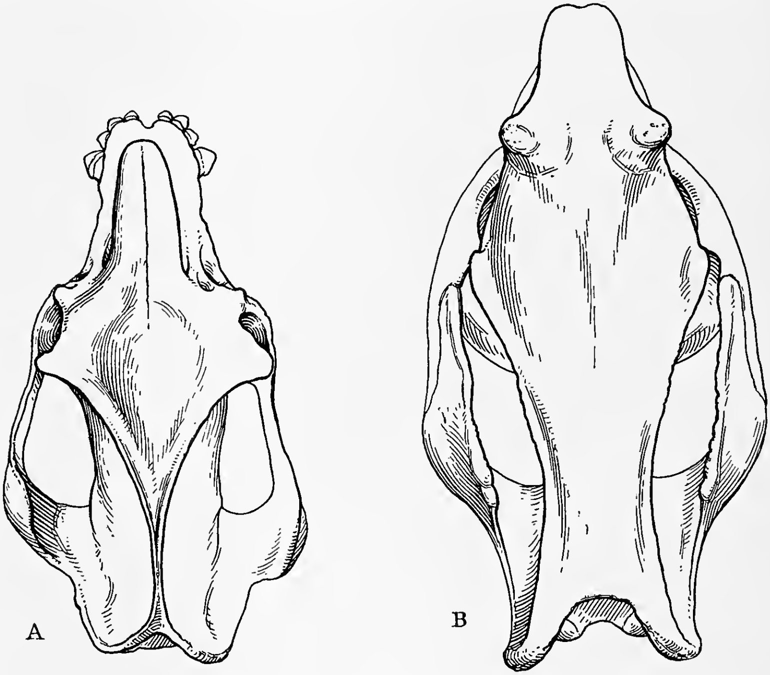


FIGURE 403.—Skulls of *Rhadinorhinus* and *Brontotherium*

Top view. A, *Rhadinorhinus abbotti*, Field Mus. 12179 (type); Uinta B 1; two-ninths natural size. B, *Brontotherium leidyi*, Nat. Mus. 4249 (type); Chadron formation; one-sixth natural size.

Ascending mutations.—As we pass upward into the middle A and upper A levels of the lower *Titanotherium* zone we note that the skulls referred to *B. brachycephalus* progress in size and in general evolution. The horns shift forward somewhat on the face and become elongate; the base of the horn becomes longer in transverse diameter rather than in anteroposterior diameter. The free portion of the nasals becomes shorter and spreads out distally. The premolar grinding teeth gradually become somewhat more complex in these stages of mutation, of change of proportion, and of rectigradation, which are prophetic of the next higher phase of evolution. It must be remembered that many of these skulls are crushed and distorted and represent differences in age and sex as well as a number of progressive stages of evolution. Among the animals specifically classed as *B. brachycephalus* it is quite possible that ancestors of more than one subsequent phylum may be found, such as that leading to *Diploclonus*.

Prophetic characters among the aged individuals of *B. brachycephalus* point toward the much more robust titanotheres of the middle beds to which Marsh gave the names *Brontops dispar* and *Brontops validus*, the former name having the priority. As the following tables show, the Hatcher collection in the National Museum is so rich in forms that it includes a series of transition stages, almost unique in mammalian paleontology, which connect the diminutive *B. brachycephalus* from level A, the base of the *Titanotherium* zone, with the large animals of level B known as *B. dispar*, a form distinguished not only by its larger size throughout but by rounded horns, shorter nasal bones, more robust buccal processes of the zygomatic arches, and somewhat more complicated premolar grinding teeth. It appears that *B. dispar* is highly characteristic and distinctive of the B levels, or middle beds, but that a form of *B. dispar* passes up into the base of the upper *Titanotherium* zone.

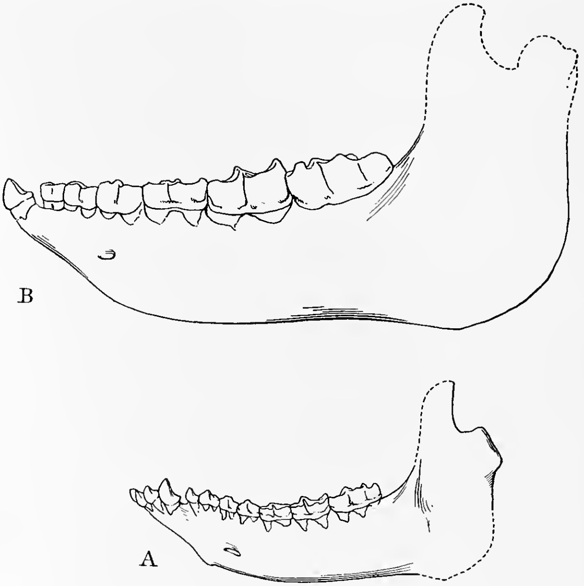


FIGURE 404.—Lower jaws of *Metarhinus fluviatilis* and *Brontotherium hatcheri*

A, *M. fluviatilis*, Am. Mus. 2059; White River, Uinta Basin, Utah; Uinta B 1; two-ninths natural size. B, *B. hatcheri*, Am. Mus. 1070; Hat Creek, Nebr.; Chadron formation; one-sixth natural size.

Diploclonus phylum.—The existence of a second phylum is indicated by specimens that are probably from the upper parts of the lower and from the middle *Titanotherium* zone. The stratigraphic records in regard to them are incomplete. This is the species *Diploclonus bicornutus* (Osborn), which is remotely related to *B. dispar* and is distinguished, as the name indicates, by a duplication of the horns on the inner sides but especially by its very narrow, elongate nasals and the straight outer contour of the horns, as seen from the front. Nasals of somewhat similar type are observed in the animal from Assiniboia, Canada, which was named *Menodus selwynianus* by Cope.

The most interesting biologic conclusion to be drawn from this assemblage of varied types is that in the lower and middle *Titanotherium* beds there were many kinds of small and middle-sized titanotheres more or less closely related to *Brontops*. The group is certainly diphyletic, possibly polyphyletic, and is therefore all the more difficult of analysis.

The type Brontops in the upper Titanotherium zone.—On the lower levels of Chadron C, the upper *Titanotherium* zone, are found the great animals to which Marsh gave the name *Brontops robustus*, as well as the surviving members of the *Brontops dispar* series. At first this animal appears to be widely separated from *Brontops brachycephalus* and *B. dispar*, but like *B. dispar*, which Marsh also placed in the genus *Brontops*, *B. robustus* is represented by a large number of skulls in different stages of growth, and there can be no question that certain characteristics of age, growth, and sex of *B. robustus* are close to some of the variations in *B. dispar*, but no direct ancestor to the type stages is known. The more important ascending mutations will be expounded in the more precise study of the phylum which follows.

Special distinctions from Menodus.—As already stated, these animals belong to the same group as the Menodontinae and are more closely related to *Menodus* than they are to either *Megacerops* or *Brontotherium*. It is therefore desirable to summarize their distinctive characters: (1) The males show brachycephaly, having a zygomatic index that ranges in general from 79 to 91 (mesaticephaly); the females have a zygomatic index that ranges from 64 to 69; (2) all retain one or two pairs of upper and lower incisors, which are full sized and round crowned; (3) the canines in males are progressively shortened in the ascending series, whereas in *Menodus* they are persistently long and pointed; (4) the tetartocones of the premolars are retarded in evolution, whereas in *Menodus* they evolve rapidly; (5) as the horns shift forward the nasals are progressively reduced in length—they are not quadrate but broadly expanded distally at their extremities; (6) the horns are typically suboval or cylindrical in basal section and have rounded rather than trihedral tops as in *Menodus;* (7) the face progressively shortens, whereas in *Menodus* it remains persistently long; (8) in correlation with the shortening of the face the tooth row becomes bent upward anteriorly; (9) the zygomata expand progressively.

A phylum somewhat intermediate between *Brontops* and *Menodus* is *Allops*, from which members of the *Brontops* phylum are distinguished by their retarded tetartocones and by the fact that the horns in the males are upright or slightly divergent, in contrast with the depressed and widely divergent horns of *Allops*.

Retarded evolution of the Brontops premolars.—The retarded molarization of the premolars is a conspicuous character of this phylum. The following facts should be noted:

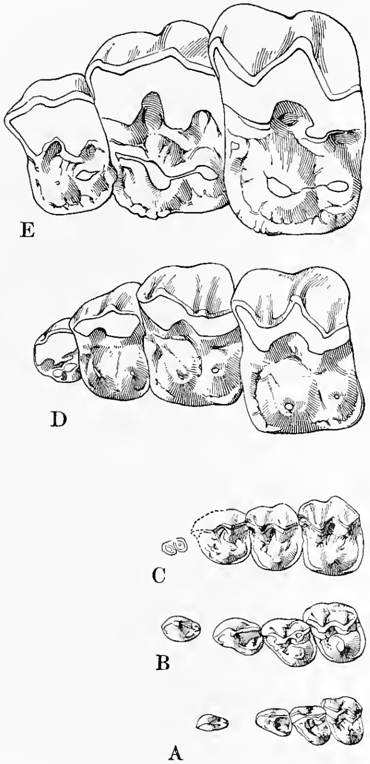


FIGURE 405.—Progressive evolution of the upper premolars in *Brontotherium* and its predecessors

A, *Eotitanops borealis*, Am. Mus. 14887, Wind River; B, *Palaeosyops paludosus*, Am. Mus. 13032, lower Bridger (although this genus is not in the *Brontotherium* series, it illustrates a stage of premolar evolution); C, *Rhadinorhinus diploconus*, Am. Mus. 1863, Uinta B; D, *Brontotherium leidyi*, Nat. Mus. 4249, Chadron A; E, *Brontotherium gigas*, Am. Mus. 492, Chadron C. All one-half natural size.

1. The exact stage of evolution of the tetartocones is partly obscured by the degree of wear, so that much worn teeth appear simpler in structure than unworn teeth, and the greatest degree of complication appears in the intermediate stages of wear.

2. All the specimens referred to the *Brontops* and *Diploclonus* phyla show essentially similar premolar characters; in the primitive forms the tetartocone of p^4 is a concave spur from the deuterocone, continuous postero-internally with the internal cingulum; the spur becomes more convex on the buccal side, less concave on the lingual side, and gradually loses its connection with the cingulum; the point of constriction between the deuterocone and tetartocone moves forward so that the tetartocone enlarges at the expense of the deuterocone. In all species of *Brontops* the tetartocone never appears entirely distinct from the deuterocone, as it does in *Brontotherium.*

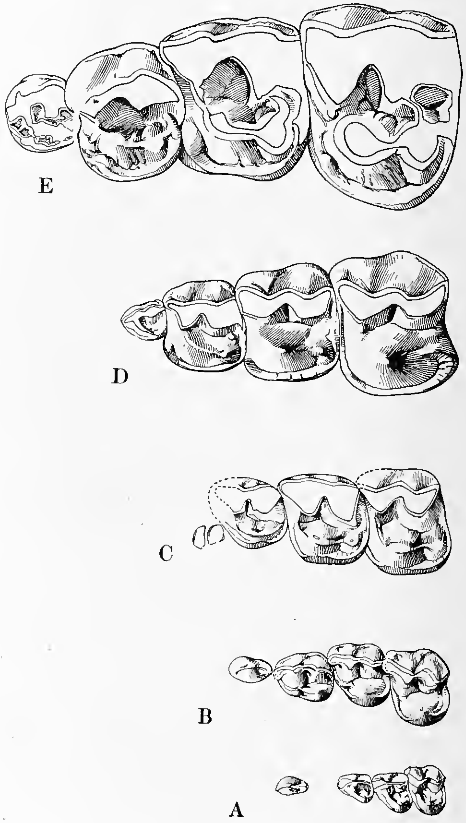


FIGURE 406.—Progressive evolution of the upper premolars in *Menodus* and *Brontops* and their predecessors

A, *Eotitanops borealis*, Am. Mus. 14887 (neotype), Wind River; B, *Manteoceras manteoceras*, Am. Mus. 12683, upper Bridger (*Telmatherium cultridens* illustrates this stage even better); C, *Diplacodon elatus*, Yale Mus. 11180, Uinta C; D, *Brontops brachycephalus*, Nat. Mus. 4258 (type), Chadron A; E, *Menodus giganteus*, Am. Mus. 505, Chadron C. All one-half natural size.

3. Within the species *B. dispar* there is considerable range of evolution in the progressive development of the tetartocone, possibly due to the crania having been found on different levels.

4. An interesting fact is that occasionally there are noticeable differences in the tetartocones on opposite sides of the same individual.

5. Comparison reveals the general kinship of *Brontops*, *Allops*, and *Menodus* in the evolution of the premolars.

The most important biologic fact disclosed is that the tetartocones show a somewhat different rate of evolution, or retardation and acceleration, in each of these subphyla. A second fact of importance is that *Brontops* in its later stages is convergent in many characters with *Brontotherium*.

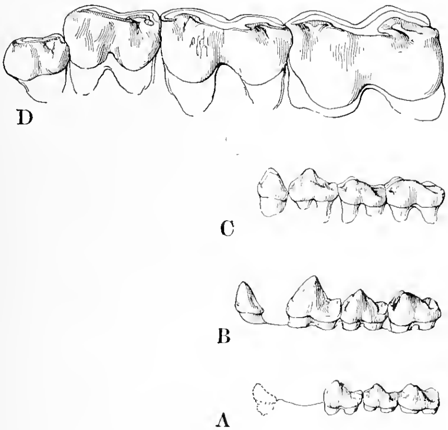


FIGURE 407.—Progressive evolution of the lower premolars in *Brontotherium* and its predecessors

A, *Eotitanops princeps*, Am. Mus. 296 (type), Wind River; B, *Palaeosyops paludosus*, Am. Mus. 11680, lower Bridger (although this genus is not in the direct line, its premolars well illustrate this stage of evolution); C, *Metarhinus earlei*, Am. Mus. 13179, Washakie B; D, *Brontotherium medium*, Am. Mus. 1051, Chadron C. All one-half natural size.

Ascending mutations between species.—That species referred to *Brontops* and *Diploclonus* are allied generically is shown by numerous skulls that combine features of two species, either in the same or in different phyla, such as *B. brachycephalus* and *B. dispar* (Nat. Mus. 4258, 1214) or *D. bicornutus*, *D. amplus*, and type of *D. tyleri*, Amherst Museum.

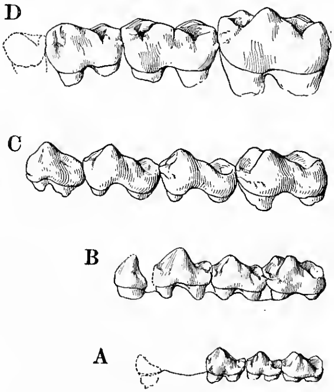


FIGURE 408.—Progressive evolution of the lower premolars in *Brontops* and its predecessors

A, *Eotitanops princeps*, Am. Mus. 296 (type), Wind River; B, *Manteoceras manteoceras*, Am. Mus. 1556, upper Bridger; C, *Protitanotherium emarginatum* Princeton Mus. 11242, Uinta C; D, *Brontops brachycephalus*, Am. Mus. 1495, Chadron A. All one-half natural size.

The Brontops-Diploclonus phylum as represented in the Hatcher collection of 60 skulls and jaws from the Chadron formation, in the United States National Museum

Catalog No.	Sex	Genus and species	Specimen	Notes
4710	Female	Diploclonus amplus Osborn	Skull	
8733	Male	Brontops robustus Marsh	Skull	Extremely large male, exceeding in size the type of B. robustus.
8732	Male	do	Skull, anterior half and jaws.	Very typical of the species.
8766	Male	do	Skull	
8767	(?)	do	Skull	
4943	Male	do	Skull (typical)	
8315	Male	do	Skull	Showing transition from B. dispar (type) to horns and canines.
8747	(?)	do	Skull	Inferior to type in measurements dental series.
4696	Male	do	Skull	Transitional B. dispar to B. robustus. Agrees in tooth measurements with type of B. robustus.
1242	Male	do	Right ramus	Jaw of old animal.
4941	Male	Brontops dispar Marsh	Skull and jaws	Type specimen.
1217	Male	Brontops (serotinus) dispar Marsh	Skull and jaws	Fine skull and jaws attached.
4245	Male	Brontops dispar Marsh	Skull	
4248	Male	do	Skull	
4253	(?)	do	Skull	Hyperbrachycephalic; old individual.
4703	Male	do	Skull	Fine skull.
4706	Male	do	Skull	Do.
4738	Female	do	Skull	

The Brontops-Diploclonus phylum as represented in the Hatcher collection of 60 skulls and jaws from the Chadron formation, in the United States National Museum—Continued

Catalog No.	Sex	Genus and species	Specimen	Notes
8316	Female	Brontops dispar Marsh	Skull	Large female (?) of progressive size.
7749	(?)	do	Skull	
7642	(?)	do	Broken skull	
4944	Female	do	Skull	Canines lacking; measurements agree well.
4942	(?)	do	Skull	Equals Allops marshi?
4939	Male	do	Skull	Medium size, adult.
8742	Female	do	Skull	Measurements typical of female (rare).
8746	Male	do	Skull	Vigorous male. Teeth poorly preserved.
8725	Female	do	Skull (part of skeleton).	Badly preserved and crushed.
8748	Male	do	Skull, anterior half, and jaws attached.	Vigorous male; young, m^3 just coming in; medium to small size.
4290	Male	do	Skull	
8792	(?)	Brontops? dispar Marsh	Pair of lower jaws	
8769	(?)	Brontops?	Posterior part of skull.	
8796	Female	Brontops (brachycephalus) dispar Marsh	Right ramus and symphysis.	
4948	Male	Brontops dispar Marsh	Lower jaws	
1241	Female	do	Skull E, right jaw in matrix.	
8319	Female	do	Lower jaws. Young	
8779	(?)	do	Pair of lower jaws	
8784	Female	do	Pair of lower jaws	
8785	(?)	do	Right ramus, ?Allops marshi.	
8788	Male	do	Pair of lower jaws	
8764	Female	do	Skull	Very fine female. Transitional in measurements from B. brachycephalus to B. dispar.
4258	Male	Brontops brachycephalus Osborn	Skull	Advanced stage, approaching B. dispar.
8776	(?)	Brontops (?dispar) brachycephalus Osborn.	Pair of lower jaws	
1233	Male	Brontops (brachycephalus) ?dispar Marsh.	Lower jaw	
1235	Female	Brontops (dispar) ?brachycephalus Osborn.	Pair of lower jaws	
4259	Male	Brontops brachycephalus Osborn	Skull	Advanced stage, approaching B. dispar.
4274	Male	do	Skull	Measurements agree precisely. Advanced stage, approaching B. dispar.
4261	Male	do	Skull	Type specimen.
8738	Male	do	Skull	Measurements typical.
8754	Male	do	Upper dentition	Superior dentition of both sides; advanced in size.
8739	Male	do	Skull, lower jaws, and femur.	Vigorous male skull; measurements typical.
4940	Female	do	Skull	Canine alveoli small; molars inferior to type of B. brachycephalus.
4947	Female	do	Skull	Paratype.
8750	(?)	do	Upper dentition	Dentition of smaller dimensions.
1214	Male	do	Skull	
1237	(?) Female	do	Lower jaw	Juvenile, imperfect.
4246	Male	do	Lower jaw	
8320	(?)	Brontops? brachycephalus Osborn	Lower jaws	
8782	(?)	do	Anterior half of lower jaw.	
1862	(?)	Brontops brachycephalus Osborn	Imperfect skull	Measurements agree closely with B. brachycephalus.

Out of a multiplicity of specimens we are able to select evidences of two or three directly successive phyla, as follows:

I. *Teleodus avus*, an ancestral form to *Brontops*, from the lowest geologic levels.

Teleodus primitivus, of doubtful relationship, preserving three lower incisors.

II. *Brontops* phylum, occiput progressively prolonged backward behind zygomata; rounded horns vertically placed:

- C. Upper beds: *B. dispar* Marsh.
- B. Middle beds: *B. dispar* Marsh.
- A. Lower beds: *B. brachycephalus* (Osborn).

IIa. *Brontops* phylum, less directly successive; occiput less extended backward, horns laterally overhanging maxillaries, obliquely to transversely oval in basal section:

- C. Upper beds: *B. robustus* Marsh.

III. Collateral phylum, less directly successive; occiput extended very far back, nasals narrow, progressively reduced, horns with internal hornlets. Levels largely undetermined:

- C. Upper beds: *Diploclonus amplus* Marsh.
- B. Middle beds: *D. tyleri* (Lull).
- B. Middle beds: *D. bicornutus* (Osborn).

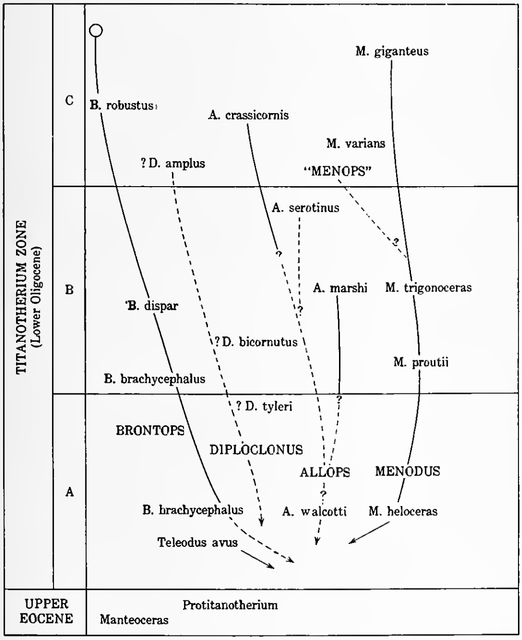


FIGURE 409.—Phyla of the Brontopinae and Menodontinae, titanotheres of the short-horned group

CONSPECTUS OF CHARACTERS OF THE SUBFAMILY BRONTOPINAE

Summary of general characters.—Titanotheres extending through lower Oligocene time; incisor teeth 2–1, the crowns rounded; canines of medium size, pointed; premolars and molars cingulate; premolar transformation retarded; skull progressively brachycephalic to hyperbrachycephalic, indices 71–91; nasals progressively broadening and abbreviating; horns moderately elongate, rounded, or transversely oval; facial region progressively abbreviated.

Teleodus, a primitive stage.
Brontops, extreme brachycephaly, single-horned.
Diploclonus, brachycephaly to extreme brachycephaly, duplicate-horned.

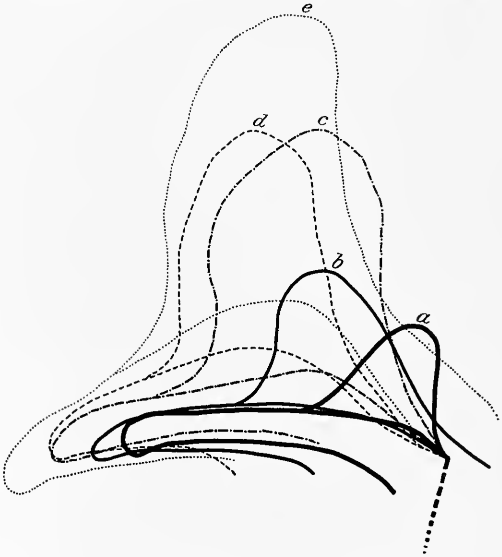


FIGURE 410.—Evolution of the horns in the *Brontops* phylum

a, *Brontops brachycephalus*, Nat. Mus. 4261 (type), Chadron A 1; *b*, *B. brachycephalus*, Nat. Mus. 1214, Chadron A 3; *c*, *B. dispar*, Nat. Mus. 4703, Chadron B 2; *d*, *B. dispar*, Nat. Mus. 4941 (type), Chadron B 2; *e*, *B. robustus*, Nat. Mus. 4696, Chadron C 2. All one-fourth natural size. These outlines show progressive increase in height and thickness of the horns; their gradual displacement forward, in front of the orbits; progressive thickening of the nasals and the confluence of their posterior upper border with the anterior border of the horns.

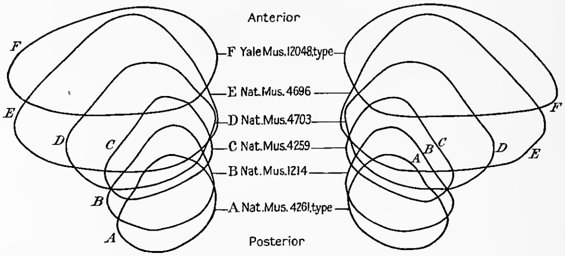


FIGURE 411.—Basal section of the horns in the *Brontops* phylum

A, *Brontops brachycephalus*, Nat. Mus. 4261 (type), Chadron A 1; *B*, *B. brachycephalus*, Nat. Mus. 1214, Chadron A 3; *C*, *B. brachycephalus*, Nat. Mus. 4259, Chadron B 1; *D*, *B. dispar*, Nat. Mus. 4703, Chadron B 1; *E*, *B. dispar*, Nat. Mus. 4696, Chadron C 2; *F*, *B. robustus*, Yale Mus. 12048 (type), Chadron C 3. All one-fourth natural size. These outlines show a progressive change in the basal section of the horns from the obliquely oval section in *B. brachycephalus* through the rounded trihedral section of *B. dispar* to the transversely oval section of *B. robustus*.

Summary of special characters.—$I\frac{2-3}{1-2}$. Third upper and second lower incisors the largest; second (or median) upper incisor frequently shed in adult; circular, smoothly rounded crowns; incisors smaller than in *Brontotherium.* Canines ♂ usually of medium size, anterior face 40, 42, 48 millimeters, recurved, pointed crowns, often compressed anteroposteriorly; canines ♀ more slender, shorter, and in section rounder. Opposite molar-premolar series rectilinear to arched. Upward flexure of premolars in side view progressive and especially pronounced in hyperbrachycephalic skulls; dental (premolar-molar, basilar) index ♂ 46–50. Premolars, tetartocone of p^4 typically retarded, often a concave spur; tetartocones of p^3, p^2 more progressive, but less so than in *Menodus*; external cingulum typically less prominent than in *Menodus.* Molars with internal cingula less prominent than in *Menodus*, crowns less hypsodont than in *Menodus.* Skull ♂ brachycephalic to hyperbrachycephalic, zygomatic index 73–91, skull ♀ with narrow buccal arches. Nasals primitively elongate, progressively shortened and swelling at the extremities; nasal index 61–140. Horns ♂ primitively low, elongate, ovoid, becoming cylindrical (*B. dispar*), club-shaped (*Brontops robustus*) or with a small secondary branch (*Diploclonus*), roundly trihedral (*B. dispar*) or broadly oval (*Brontops robustus*). Face progressively abbreviate.

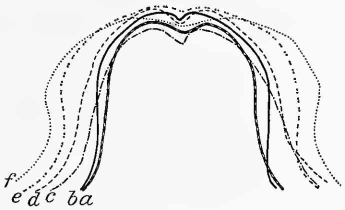


FIGURE 412.—Progressive broadening of the nasals in the *Brontops* phylum from *B. brachycephalus*, with narrow nasals, through *B. dispar* to *B. robustus*, with broad nasals

a, Brontops brachycephalus, Nat. Mus. 4947, Chadron A; *b, B. brachycephalus,* Nat. Mus. 1214, Chadron, A; *c, B. brachycephalus,* Nat. Mus. 1258, Chadron B; *d, B, dispar,* Nat. Mus. 4703, Chadron B; *e, B. dispar,* Nat. Mus. 4696, Chadron C; *f, B. robustus,* Am. Mus. 1083, Chadron C (?)

CONSPECTUS OF CHARACTERS OF SPECIES

The salient features of the several species are set forth in the following summary:

Teleodus avus Marsh. The most ancient form recorded from the base of the lower beds. Readily distinguished by the three incisor teeth with rounded crowns in the lower jaw, although the type is somewhat larger than *B. brachycephalus.* Phyletic position somewhat doubtful.

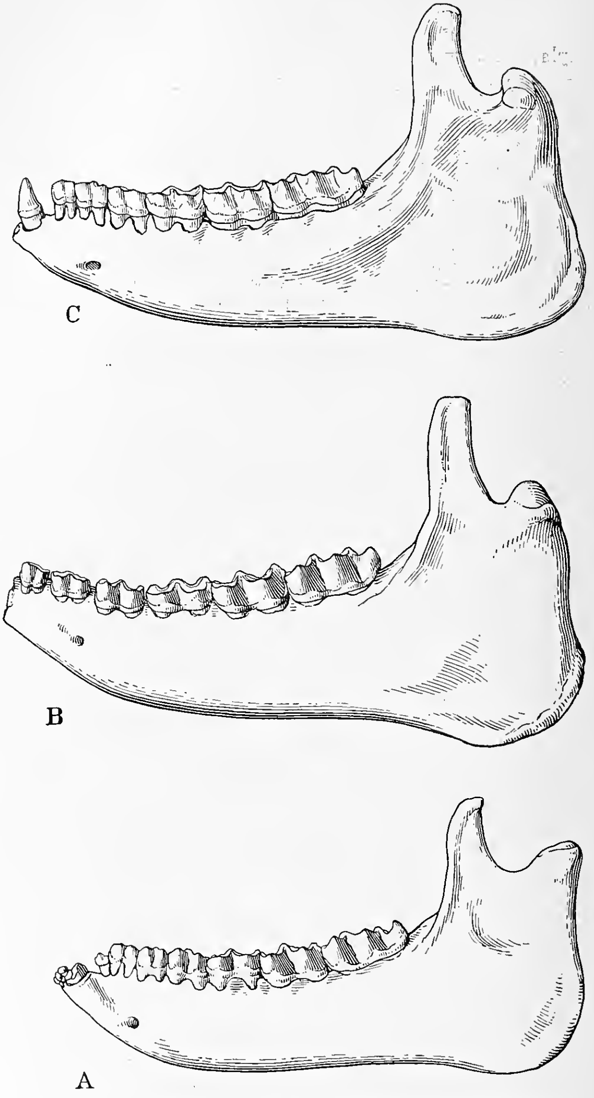


FIGURE 413.—Lower jaws of *Teleodus primitivus, Brontops brachycephalus,* and *Allops walcotti?*

A, *Teleodus primitivus,* Ottawa Mus. (type); Cypress Hills, Saskatchewan; perhaps the smallest and most primitive known jaw of an adult Oligocene titanothere, with horizontal ramus long and moderately deep, chin gently convex, angle not projecting sharply backward, ascending ramus relatively broad, coronoid of moderate height, three incisors, and a prominent postcanine diastema. The external cingula of the cheek teeth are partly confluent with the ectolophs, whereas in all other Menodontinae they are sharply defined.

B, *Brontops brachycephalus,* Am. Mus. 1495; compared with the preceding has a horizontal ramus very shallow anteriorly, angle projecting downward and backward, coronoid high, and molars relatively larger.

C, *Allops walcotti?,* Nat. Mus. 4247; differs from the typical *Brontops* in having sharply defined external cingula and no diastema in front of p_1 (p_1 has dropped out). It differs from the known *Menodus* in possessing incisors.

All one-fifth natural size.

Teleodus primitivus (Lambe). Known from a jaw found in the Cypress Hills, containing three lower incisor teeth, of which i_2 is the largest and i_1 the smallest.

Brontops brachycephalus (Osborn). Very abundant in the lower beds, extending from the lower into the middle levels and passing into transitional forms in the upper levels. Readily distinguished by the broad, rounded skull, and very simple premolar teeth.

Brontops dispar Marsh. Very abundant and characteristic of the middle levels. Transitional in structure between *B. brachycephalus* and *B. robustus.*

Brontops robustus Marsh. An enormous animal characteristic of the lower levels of the upper beds. It presents in an extreme degree the progressive characters of this genus—great width of the skull combined with decided abbreviation of the horns as well as of the nasals and surprisingly backward development of the premolar teeth.

Diploclonus bicornutus (Osborn). Closely related to *Brontops dispar,* from which it differs in its longer, narrower nasals and internal hornlets on the horns. Geologic level unknown, probably the lower part of the middle beds.

Diploclonus tyleri (Lull). Intermediate between *D. bicornutus* and *D. amplus.* Brachycephalic, with shortened nasals and well-developed internal hornlets. Geologic level propably middle beds.

Diploclonus amplus Marsh. Extremely brachycephalic, with short nasals; divergent horns with steep connecting crest. Probably from the upper beds.

Conspectus of characters of jaw in the menodontine group

Character	Teleodus	Brontops	Diploclonus	Allops	Menodus
Horizontal ramus	Deep.	Shallow.	Shallow.	Intermediate.	Deep.
Symphyseal region in side view below mental foramen.	Convex.	Very shallow.	Shallow.	Intermediate to convex.	Fuller.
Region of angle	Barely produced.	Usually produced downward.	?Produced, truncate.	Intermediate.	Produced backward and downward into a convex elbow. Posterior border oblique.
Incisors	$I_{\bar{3}}$	$I_{\overline{2-1}}$	$I_{\overline{2-1}}$	$I_{\overline{2-1}}$	$I_{\bar{0}}$ (typically).
P_1 in fully adult jaws	Present.	Usually present.	Present.	Present or absent.	Present or absent.
Diastema in front of p_1	Present.	Present, wide.	Present.	Absent.	Absent.
Canines	Slender.	Slender to short; stout.	Slender to short; stout.	Conic to compressed anteroposteriorly.	Conic.
External cingulum of canines, premolars, molars.	Not sharply defined.	Present in early types, lost in B. robustus.	Intermediate.	Present.	Strongly marked.
Upward flexure of premolar series.	Moderate.	Slight or moderate.	Slight or moderate.	Very slight.	Absent.

MEASUREMENTS OF THE BRONTOPS SERIES

The species of the genus *Brontops,* like the species of *Menodus,* constitute a closely graded ascending series beginning in the lowest and running up into the latest beds of the *Titanotherium* zone. The range in the chief measurements of the successive stages may be summarized as follows:

Measurements of Brontops, in millimeters

	B. robustus, ♂	B. dispar, ♂	B. brachycephalus, ♂
P^1–m^3	340–376	310–345	265–297
P^1–p^4	132–151	123–145	101–123
M^1–m^3	215–236	195–215	160–180
Pmx to condyles	743–843	660–687	580–610
Zygomatic index	77–87	78–87	72–?82
Nasal length	52–90	85–90	60–85
Horn length	130–210	155–198	59–135

Hence the series of measurements exhibits small gaps between *B. brachycephalus* and *B. dispar* in the measurements p^1–m^3, m^1–m^3, in the basilar length (pmx to condyles), and in the length of the horns; but the two species are continuous or overlap in respect to the length of the premolar series, in the zygomatic index, and in the nasal length. On the other hand *B. dispar* is continuous with or overlaps *B. robustus* in the measurements p^1–m^3, p^1–p^4, m^1–m^3, as well as in the zygomatic index, nasal length, and length of horns; but there is a sharp gap between the two species in the basilar length, *B. robustus* being a far larger type.

Standard measurements in the Brontops phylum, in millimeters

	Upper teeth					Skull							Jaw and teeth					
	P^1–m^3	P^1–p^4	M^1–m^3	Canines, anterior vertical	Canines, anteroposterior diameter	Pmx to condyles	Zygomatic breadth	Cephalic (zygomatic) index	Nasal tips to occiput vertex	Nasals, free length	Nasals, free breadth	Horns, external length	P_1–m_3	P_1–p_4	M_1–m_3	Canines, anterior vertical	Canines, anteroposterior diameter	Symphysis to condyles
B. robustus, Am. Mus. 1069, ♂	376	147	236			813	640	76	675	87	153	123						
B. robustus, Carnegie Mus. 313	355	144	220	47	37	743	620	83		52	126	130						
B. robustus, Am. Mus. 1083, ♂	363	145	225	47	34	755	600	79	[a] 640	90	133	180						
B. robustus?, Carnegie Mus. 314	376	149	232			[a] 843	508											
B. robustus, Yale Mus. 12048, ♂ (type)	350	137	220	42	36	765	667	87	635	76	149	207	385	136	250	40		683
B. robustus, Carnegie Mus. 315	363	151	223			795	628	79				140						
B. robustus, Princeton Mus. 11015, ♂	345	139	215	48		795	615	77				174	385	137	240	43		
B. robustus, Nat. Mus. 4696	340	132	220	41	26					[a] 85	125	210						
B. robustus?, Am. Mus. 518			237				[a] 540		730	77	124				250			[a] 598
B. dispar, Nat. Mus. 4706, ♂	345	145	215	47	27	665	515	79										
B. dispar, Nat. Mus. skull V	[a] 315		203			687	553	[a] 80										
B. dispar, Nat. Mus. 4248, ♂	[a] 340	140	207			685	535	78										
B. dispar, Nat. Mus. 4941, ♂ (type)	[a] 340	131	210	48						94	102	188	[a] 365			41	30	
B. dispar, Nat. Mus. 4245, ♂	330	130	207	45	27	685			655	92	110	155						
B. dispar, Nat. Mus. 4253	[a] 330	123	203															
B. dispar?, Nat. Mus. 4738, ♀	320	126	205	35	24	660			545	93	108							
B. dispar, Nat. Mus. 8742, ♀	315	128	195			650	435											
B. dispar, Nat. Mus. 4290, ♂ (type of "validus")	320	130	203	40	27	660	565	85	605	85	120	198						
B. dispar, Nat. Mus. 8764, ♀	308	128	185			640	428			93	100							
B. dispar, Nat. Mus. 4703, ♂	310	127	195	45	30	670	520	87	585	90	110	162						
B. dispar?, Carnegie Mus. 123, ♀	320	122	200			643	420	65										
B. brachycephalus, Nat. Mus. 1214, ♂	295	121	179	39		600												
B. brachycephalus, Nat. Mus. 4274, ♂	297	123	180			596	456											
B. brachycephalus, Am. Mus. 1495	288	118	171		23	[a] 560				85	92	59	310	104	195			[a] 505
B. brachycephalus, Nat. Mus. 8738, ♂	278	118	171			605	441											
B. brachycephalus, Nat. Mus. 4259, ♂	280	110	175				[a] 470		[a] 500	60	93	135						
B. brachycephalus, Nat. Mus. 8739, ♂	275		170			648												
B. brachycephalus, Nat. Mus. 4258, ♂	280	114	175	43	28	610	440	72	[a] 520	65	113							
B. brachycephalus, Nat. Mus. 1862	273	113	163															
B. brachycephalus, Nat. Mus. 4261, ♂ (type)	280	[a] 104	178	40		[a] 580	[a] 480	82?				85						
B. brachycephalus?, Nat. Mus. 4940, ♀	265	101	160							[a] 109	82	102						
B. brachycephalus, Nat. Mus. 4947, ♀	253	105	150	34		590	380	64		98		81						
Percentage of change from B. brachycephalus (type) to B. robustus (type)	+25	+32	+24			+31	+39			—?	?	143						

[a] Estimated.

Measurements of skulls and jaws associated with or referred to the Brontops phylum, in millimeters

	Brontops robustus			Brontops dispar		Brontops brachycephalus, Am. Mus. 1495	Teleodus avus, Yale Mus. 10321 (type)	Teleodus primitivus, Ottawa Mus. (type)
	Am. Mus. 10690, ♂	Yale Mus. 12048, ♂ (type)	Princeton Mus. 11015, ♂	Nat. Mus. 1217, ♂	Nat. Mus. 4941, ♂ (type)			
Skulls and upper teeth:								
Anterior canine to hypoconulid fossa of third molar	--------	307	--------	--------	--------	[a] 310	--------	--------
P^1–m^3	376	345	345	--------	[a] 330	288	--------	--------
M^1–m^3	236	215	215	196	210	171	--------	--------
Symphysis to glenoid	597	529	--------	--------	--------	443	--------	--------
Lower jaws and teeth:								
Posterior canine to hypoconulid of third molar	--------	[a] 397	--------	--------	--------	313	--------	[a] 270
P_1–m_3	--------	385	385	--------	[a] 365	310	320	[a] 273
M_1–m_3	--------	255	240	230	233	195	--------	183
Symphysis to condyle	--------	665	--------	--------	[a] 610	[a] 505	--------	[a] 450
Depth below third molar	--------	193	--------	--------	--------	129	--------	99

[a] Estimated.

SYSTEMATIC DESCRIPTIONS OF GENERA AND SPECIES IN THE BRONTOPS-DIPLOCLONUS PHYLUM

Teleodus Marsh

Plate XIX, D^1, D^2; text figures 188, 204, 409, 413

[For original description and type references see p. 227]

Generic characters.—Related to or identical with the lower Oligocene *Brontops.* Three lower incisors in each jaw, instead of two as in other Oligocene titanotheres; i_2 the largest of the series; rounded or noncingulate incisor crowns.

Species.—*Teleodus avus* Marsh, *Teleodus primitivus* (Lambe). As the most primitive Oligocene genus known *Teleodus* should be distinguished from the most progressive upper Eocene species, *Protitanotherium superbum, P. emarginatum,* and other Eocene types. *Teleodus* is distinguished from *Protitanotherium* by three characters—(1) incisors smaller, round topped, not flat topped; (2) canines erect, more slender; (3) premolars more advanced in evolution.

Teleodus avus Marsh

("*Megacerops avus*" Osborn, 1902)

Plate XIX, D; text figures 188, 409

[For original description and type references see p. 228]

Type locality and geologic horizon.—Chadron formation, lower *Titanotherium* zone. Exact locality not published.

Specific characters.—Dental formula $I_{\overline{3}}$, $C_{\overline{1}}$, $P_{\overline{3}}$, $M_{\overline{3}}$. Of the three lower incisors in place on each side the middle one is the largest; there is a short diastema behind the lower canine, but no first premolar. P^2–p^4 106 millimeters; molars incomplete. Type, Yale Mus. 10321.

As already indicated, this species is known only from the type lower jaw in the Yale Museum collection and is of exceptional interest because it retains, either as a reversional or as a fixed generic or specific character, the full number (6) of lower incisor teeth, as in all the Eocene titanotheres, the formula thus being $I_{\overline{3}}$ as against $I_{\overline{2-0}}$.

Consistent with this primitive morphologic condition the type jaw was found by Hatcher near the base of the lower *Titanotherium* zone, and if the structural indications are supported by other specimens it may well remain as the type of a distinct genus, *Teleodus* Marsh; yet other structural characters relate it closely to *Brontops* and point rather to affinity to this genus.

Dentition.—The summits of the incisors are obtusely rounded and noncingulate, as in *Brontops;* the lateral pair (I_3) is so much reduced and crowded as to furnish conclusive evidence that it is the lateral incisors (I_3) which first disappear in all the brontopine titanotheres. The second incisors (I_2) are relatively large—larger, in fact, than the median pair, which in turn are a trifle larger than the external pair. The incisors of *Teleodus avus* thus differ widely from those of *Protitanotherium emarginatum*, since they are round topped and small instead of being flat topped and large. The canines are of medium size, rounded in basal section, with faint posterior cingula. The presence of only three premolars is also noteworthy. There is no alveolus for p_1. P_2 is separated by a narrow diastema from the canine. The combined measurement of the three premolars (106 mm.) is only 5 millimeters greater than that of the posterior molar, which shows in a marked way the inferiority of the premolar to the molar series.

The jaw represents an individual slightly smaller than the paratype of *Menodus proutii* Leidy and larger than the jaws attributed to *Brontops brachycephalus*. The canines show that this specimen was a male, and the advanced wear of the molar teeth indicates that the animal was fully adult. The external cingulum is deficient opposite the widest part of the molar crowns, whereas in *Menodus* and *Brontops* the cingulum tends to surround the molars completely; in fact, throughout the series the external cingulum is not very prominent. The internal crest of the hypoconulid of m_3 is moderately developed and crenulate.

Taken together the characters of the canines, of the incisors, and of the grinding teeth suggest affinity to *Brontops*, and for the present we may regard the genus *Teleodus* as of subgeneric rank.

Teleodus primitivus (Lambe)

Text figures 204, 413, A

[For original description and type references see p. 235]

Type locality and geologic horizon.—Cypress Hills, Saskatchewan; lower *Titanotherium* zone.

Specific characters.—$I_{\overline{3}}$, $P_{\overline{4}}$. Second lower incisor the largest, median lower incisor the smallest, crowns rounded. Premolars, 103 millimeters (estimated); molars 183 (estimated). Lambe writes:

> In the Cypress Hills specimen the crowns of the incisors are of a depressed spherical shape, with a tendency to come to a rounded central point above. The second incisor is the largest, and the first is slightly smaller than the third, which is the most upright. The first is more procumbent than the second. Between the inner pair is a very decided interval, leaving a space of 6.5 millimeters between the crowns of the two teeth. The crowns of the canines are broken off, * * * and the right first premolar is lost from its alveolus. [Lambe, 1908.1, pp. 49, 50.]

This apparently valid type represents the smallest and most primitive Oligocene titanothere known at the present time (1914). It is from the Cypress Hills of Saskatchewan. It differs from *T. avus* in its inferior size, in the presence of four lower premolars and in the proportions of the incisor teeth, in which i_3 is smaller than i_1. The rounded form of the crowns of these incisors relates them to those of *B. brachycephalus*. Another *Brontops* affinity is seen in the presence of an external cingulum on the grinding teeth. Lambe's detailed comparison with "*Menodus*" *angustigenis* Cope is as follows (op. cit., p. 50):

> Compared with *Megacerops angustigenis* (Cope) * * * *M. primitivus* differs in the following respects: There are six incisors instead of four, and the breadth of the jaw between the canines, which are of smaller diameter, is relatively greater; the diastema between the canine and the first premolar is twice as long; the symphysis is of greater length, reaching back to a point almost in line with the posterior edge of the fourth premolar (in *angustigenis* in line with the anterior root of the corresponding tooth); the exterior cingula are much less developed; the coronoid process is shorter. In both species the premolars have reached about the same stage of development toward the molar pattern, and the molars have very much the same proportions. In *angustigenis* the internal cingula are partially developed. In *primitivus* the mandible is shorter, proportionately deeper, and not so thick in the neighborhood of the alveolar border posteriorly.

Brontops Marsh

("*Megacerops* phylum," Osborn, 1902)

Plates XVIII, XX, XXI, XXIII, XXIV, XXXIII–XXXVI, XLIII, XLVII, LXXXII–CIII, CLIII, CLX, CXCV–CCXXIX; text figures 24, 28, 176, 179, 180, 195, 374, 375, 384–387, 389, 391, 393, 394, 396, 398–400, 406, 408–425, 482, 483, 510, 606–611, 616, 618, 622–624, 626, 628, 630, 635, 636, 639, 640, 650, 651, 653–655, 657–660, 665, 669, 673, 685, 686, 693, 699, 708, 712, 719, 727, 744, 746

[For original description and type references see p. 222. For skeletal characters see pp. 674–676]

Geologic horizon.—From lower to upper *Titanotherium* zones.

Generic characters.—Upper and lower incisors 2–1. Canines pointed, becoming obtuse. Premolars cingulate; tetartocones retarded. Horns of an elongate to transverse oval section, shifting forward. Skulls progressively brachycephalic.

Incisors.—The *Brontops* phylum exhibits an assemblage of characters that sharply mark it off from the main phyla of *Brontotherium* and *Megacerops*, as follows: In young animals there are two upper incisor teeth on each side (i^2, i^3), which in some specimens tend to be reduced in old age to one on each side (i^3) by the loss of the median incisor; thus the incisive formula, $\frac{2-1}{2-1}$, clearly distinguishes these animals from *Menodus* and *Megacerops*, in both of which the incisors are vestigial, the formula being $\frac{2-0}{2-0}$. In *Brontotherium* the formula is the same ($\frac{2-1}{2-1}$,) but both upper incisors, in the males at least, are strongly persistent.

Canines.—In the early stages of *Brontops* the canines are less elongate and less pointed than in *Menodus*, less robust and obtuse than in *Brontotherium*, but somewhat larger than in the feebly armed *Megacerops;* they are generally of a graceful, recurved form.

Premolars.—As noted above, the premolar grinding teeth are decidedly retarded in complication—that is, in the assumption of tetartocones and a molar pattern. Thus the premolars of these animals from levels B and A can readily be distinguished from those of *Menodus*, which are advanced or progressive in complication, as well as from those of *Brontotherium*, which are rapidly progressive. The presence of both internal and external cingula is a character which *Brontops* presents in common with *Menodus*.

Skull.—It is to be noted that the horns shift forward and evolve at the expense of the nasals, as in *Megacerops* and *Brontotherium*, whereas in *Menodus* the horns are stationary in their relative position. The progressive brachycephaly of *Brontops* affects chiefly not only the zygomatic arches, which spring strongly outward, especially in the old males, but also the entire vertex of the skull.

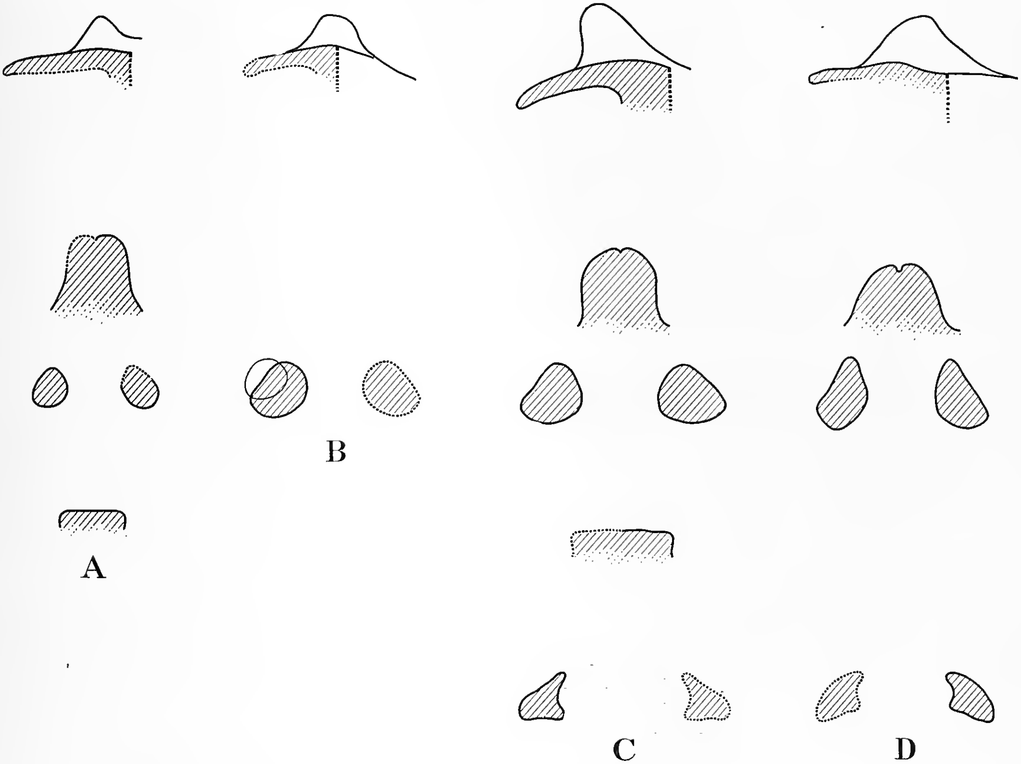


Figure 414.—Sections and contours of skulls of *Brontops brachycephalus*

A, Nat. Mus. 4947, ♀ (cotype) and B, Nat. Mus. 4261 (type); both from Chadron A. In these more primitive members the horns are small bosses, rounded to elongate oval in basal section, the nasals are long and tapering, the parietal crest is narrow. C, Nat. Mus. 1214; upper levels of Chadron A; horns distinctly larger, rounded trihedral in section with external, internal, and posterior faces; nasals thicker and relatively shorter. D, Nat. Mus. 4258; base of Chadron B; an immature animal of more progressive type with horns larger and oblique oval in section, nasals wider, zygomata stouter. All one-seventh natural size. (Cf. fig. 376.)

Brontops brachycephalus (Osborn)

(*Megacerops brachycephalus* Osborn, 1902)

Plates XXI, XLVII, LXXXIII–LXXXVIII; text figures 195, 374, 387, 389, 391, 393, 396, 399, 406, 408–419, 610, 611, 712 719, 744

[For original description and type references see p. 231. For skeletal characters see p. 675]

Geologic horizon.—Lower *Titanotherium* zone (Chadron A, A 1, A 2, A 3).

Specific characters.—Skull small, premaxillaries to condyles about 580 to 590 millimeters; males with strongly expanded zygomata, zygomatic index 82; transverse measurement about 480 millimeters. Females more mesaticephalic, zygomatic index 64. Horns very short; outside length in transitional skulls (male), 85 to 135 millimeters; horn section anteroposteriorly elongate to roundly trihedral. Nasals elongate, not spreading distally; free length (estimated), 85 to 109 millimeters. Nasal index, 90 to 140. Grinding series, p^1–m^3, in males 280 millimeters, in females 253; dental index in males 48, in females 43; true molars, in males 178 millimeters, in females 150. Canines not strongly compressed anteroposteriorly, length of crown in males 34 to 40 millimeters, in females 34. Tetartocone of p^4 rudimentary (a concave spur from the deuterocone continuous with the internal cingulum); tetartocones of p^2 and p^3 small, constriction separating tetartocone from deuterocone in the hinder third of the crown. Backward prolongation of occiput moderate.

Brontops brachycephalus is distinguished from its successor, *B. dispar*, by the much smaller size of all parts of the skull. From *Allops marshi* it is distinguished by its somewhat smaller dimensions. From *Menodus proutii* it is distinguished especially by its shorter molar series and relatively wider premolars, with less progressive tetartocones. These differences are shown below.

Measurements of skulls of Brontops, Allops, and Menodus, in millimeters

	B. brachycephalus		A. marshi	M. proutii
	♂	♀ (Nat. Mus. 4947)		
P^1–m^3	265–297	253	300–335	333
P^1–p^4	101–123	105	119–135	135
M^1–m^3	160–180	150	185–205	203
Pmx to condyles	590–610	590	630–675	628
Zygomatic index	72–82(?)	64	64–71	(?)

A female skull (Nat. Mus. 4947) that is referred to *B. brachycephalus* differs from the male skulls in its smaller size and lesser width throughout. From the type of *Allops walcotti* this female skull differs in its smaller size, especially of p^1–m^3 (253:285 mm.). In the males of *B. brachycephalus* the fourth premolar is narrower than in the species of *Allops*.

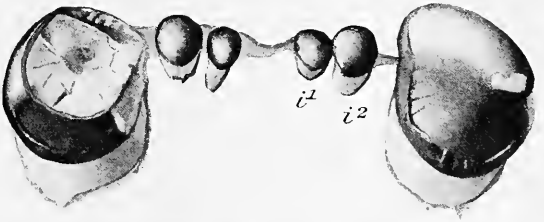


FIGURE 415.—Upper canines and incisors of *Brontops brachycephalus*
Nat. Mus. 4947, ♀; canines subconic with slender cingula; incisors (i^1, i^2) small, with circular and rounded crowns. Natural size.

Materials.—The specific characters of *B. brachycephalus* rest upon exceptionally complete material, most of which is in the National Museum. The type of this species is the adult male skull Nat. Mus. 4261 (Pl. LXXXVII), from the base of the lower *Titanotherium* zone. The paratype is the exceptionally aged female skull (Nat. Mus. 4947; Pls. LXXXIII, LXXXVII) found by Hatcher at the very base of the *Titanotherium* zone only 14.4 feet above the Cretaceous Pierre shale. A third specimen is skull Nat. Mus. 4940, also recorded from the lower beds but from the upper level (A 3). A jaw (Am. Mus. 4247) agrees closely in size with this skull but may belong with *Allops walcotti.* A fourth specimen (Nat. Mus 1214, fig. 418) also comes from the upper level of A, or the lower beds, and it shows features of approach to *B. dispar.* A fifth skull (Am. Mus. 1495) is distinguished by its very small horns.

General characters.—These small, broad-skulled titanotheres are distinguished by the lateral arching and relatively broad section of the zygomatic buccal processes. The nasals taper toward the extremities and are slightly decurved. The horns rise above the skull from 25 millimeters in the females to 60 in the male skull, the corresponding outside measurements being 85 and 102. The basal section of the horns (fig. 414) is highly characteristic, consisting of a broad outer maxillary face, lying in an oblique plane, and a broad, highly convex inner face. The horns are obtusely rounded at the top. The superior incisors (fig. 415) are two in number on each side in young animals, but the internal pair, I^3, are variable and likely to disappear in aged animals. The canines are elongate, pointed, with a posterior cingulum only and a strongly convex posterior face, varying in length from 33 millimeters in the females to 43 in the males. A very distinctive character is the structure of the premolars, the main internal portion of the crown being composed of the deuterocones, while the tetartocones are small and rudimentary, especially in p^3, p^4. In the type male skull the tetartocone of p^4 on the right is a prolongation of the deuterocone, concave and continuous with the cingulum on the lingual or internal border; on the left side the tetartocone is more circular. In Am. Mus. 1495 the tetartocone on p^4 is a concave spur from the cingulum; the tetartocone on p^3 is concave on the lingual side, convex on the buccal side, which is evidence that the buccal side develops faster. The premolar cingula are developed progressively in ascending levels but are never so broad as in *Menodus*. A primitive feature of m^3 is the aborted metaloph extending inward upon the crown. There are incipient protostyles on the superior molars.

Paratype female skull.—The very aged female skull (Nat. Mus. 4947) in the eleventh stage of growth, discovered by Hatcher in 1887 on the bottom level of the lower *Titanotherium* zone, is the paratype of this species. The palate is finely preserved (Pl. LXXXVII). It is by far the smallest and one of the most primitive skulls of the brachycephalic series; it measures only 590 millimeters from the occipital condyles to the premaxillae and 380 millimeters across the zygomata, while the total premolar-molar series is only 253 millimeters as compared with 320 millimeters in the lower jaw of the type of *Teleodus avus.* The nasals are rather elongate, contracting anteriorly. The horns are small, rounded knobs rising 25 millimeters above the top of the skull from a point slightly anterior to the orbits—in fact, immediately in front of the preorbital malar bar; they are directed outward and backward, rugose at the tips and set wide apart, overhanging the sides of the maxillae; the horn sections are obliquely placed ovals that converge anteriorly.

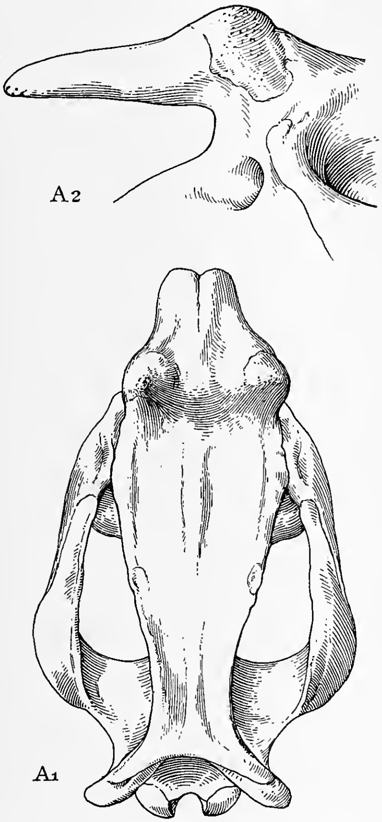


Figure 416.—Reconstruction of crushed skull of *Brontops brachycephalus*

Am. Mus. 1495; Chadron A; South Dakota. A_1, Skull fully adult, less brachycephalic than the type of *B. brachycephalus*, and one of the most primitive known of all Brontopinae. One-sixth natural size. Very small horns (fundamentally similar to those of the Eocene *Manteoceras*) consisting of swellings on the frontals which overlap the nasals. The surface of the horn swelling (A_2) is roughened and pitted as if for the attachment of a tough or even horny epidermal cap. A_2, Horn region. One-third natural size. The upper teeth of this skull are shown in Figure 417; the lower jaw in Figure 413, B.

The cranium proper is narrow, measuring 80 millimeters across the vertex; the occiput is broken away; the zygomata arch outward and give a brachycephalic character to the skull, although the measurements show that it is in reality mesaticephalic, the zygomatic index being only 64. This mesaticephaly is a female character. In section these arches are deep, thin bars. The posterior nares are placed very far back, opposite the posterior face of m^3. The vomer extends well back on the basisphenoid with a median keel in the portion lying between the pterygoids, extending back almost as far as the basisphenoid rugosity, as seen also in succeeding types. The alisphenoid canal, foramen ovale, f. lacerum medium, and f. condylare are clearly defined. The somewhat rugose junction of the basisphenoid and basioccipitals foreshadows the prominent projection for the rectus capitis muscle, which is so characteristic of succeeding species of *Brontops*.

Dentition.—Of the incisors two (i^1, i^2) persist on one side and only one on the other. The premolars are completely worn down, but so far as one can observe the deuterocone constitutes almost the entire inner face of the crown of p^4. The hypocone of m^3 is a cingule connected with a very interesting abortive metaloph, as seen in some other titanotheres. The inner contour of the crown is very rounded, the primitive triangle being scarcely altered by the addition of the slight protostyle and hypocone.

Type male skull.—The upper surface of this aged male skull (Nat. Mus. 4261, Pl. LXXXVII, figs. 399, 410, 411, 414) is especially well preserved. Although compared with the female it is a relatively large and adult animal, in the ninth stage of growth, the horns rise only 85 millimeters above the nasals (outside measurement). They exhibit the primitive or original position of these structures—namely, very far back and immediately above the orbits, directed outward. The very robust section of the horn base is a male character distinguishing this from the above-described female horn. This skull is very interesting, moreover, because it illustrates the great breadth (480 mm., estimated) attained by the zygomatic arches in this low geologic level. This brachycephaly is a male character. The dental formula is I^{2-}, P^{4-3}. The premolars are distinguished by narrow internal cingula and rudimentary tetartocones; the teeth exhibit faint external and decided internal cingula, but the most decided feature is the sessile character of the tetartocones, which occupy barely one-third of the inner face of the premolar crowns. The incisors are absolutely transverse in position with perfectly smooth, rounded crowns; the canines are quite large.

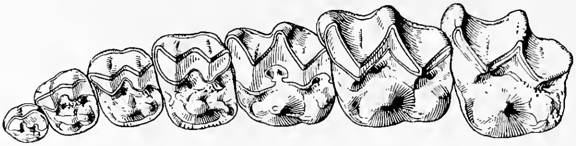


Figure 417.—Left upper grinding teeth of *Brontops brachycephalus*

Am. Mus. 1495. One-third natural size. These teeth agree well in form and measurements with those typical of *B. brachycephalus*. They differ from those of *Allops walcotti* (type) in minor points, and from those of *Menodus proutii* in being less elongate anteroposteriorly, especially the molars, which also have the internal cingulum less pronounced. The premolar pattern resembles that of all the more primitive members of the menodontine group. (See figs. 413, 416.)

The American Museum specimen (No. 1495), the skull of a young animal, also exhibits the characteristic features of this species; the horns are somewhat smaller than in *Protitanotherium emarginatum* of the upper Eocene. They present an elongate oval section, with sloping anterior face. The zygomata are fairly developed and typical in section. The anteroposterior and transverse diameters of the molars are subequal. The tetartocone of p^4 is a concave spur from the cingulum. P^1 is set on a line with p^2 (outer wall) and is separated by a diastema from the canine. The canines are procumbent, as in Nat. Mus. 4261, with faint external cingula. M^3 has crenulate metalophs, m_3 a hypoconulid not greatly different from that of *Menodus*. The jaw of this specimen is shown in Figure 396, A. As compared with *Teleodus avus* this jaw has the horizontal ramus very shallow anteriorly; the angle projects downward and backward; the coronoid is high; the molars are relatively larger.

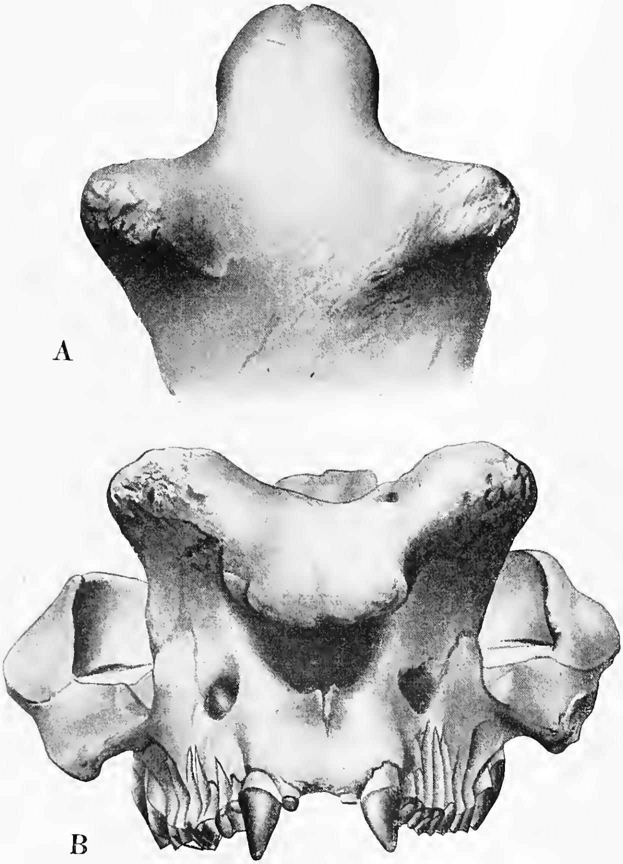


FIGURE 418.—Skull (B) and horn region (A) of *Brontops brachycephalus?*

Nat. Mus. 1214; Chadron A 3. The horns are more progressive than in the type of this species and in their trihedral section suggest *Allops marshi*. The dental measurements agree better with those of *B. brachycephalus*, although the premolar series is unusually long. The large canines probably indicate male sex. One-third natural size.

As arranged in the order of sequence from the base to the summit of the lower zone the remarkable series of skulls in the National Museum (see table on p. 480) gives us a complete series of ascending mutations toward the higher stages of *B. dispar* in the middle beds.

Proportions of teeth of Brontops brachycephalus, in millimeters

	Antero-posterior	Transverse
C	23	20
P^1	23	20
P^2	28	32
P^3	32	43
P^4	38	54
M^1	49	49
M^2	59	59
M^3	61	63

Transitional stages from Brontops brachycephalus to B. dispar.—A transitional stage is represented by a rather primitive skull (Nat. Mus. 4940), from the top level (A 3) of the lower beds, which is intermediate in the length of its horns between the type of *B. brachycephalus* and some of the more primitive varieties of *B. dispar*. This skull taken as a whole is also somewhat more progressive in character than the male type and female paratype above described. The nasals are thin, elongate, and contract anteriorly. The horns present a decidedly oblique oval form at the base but round up toward the summit into a more cylindrical section; they rise 60 millimeters above the midline of the skull, and since this animal is well advanced toward the eighth stage of growth, this is probably the maximum development of the horns in the males at this stage. The posterior nares open somewhat more anteriorly than in the type of *B. brachycephalus*.

There is but one incisor above on each side and the first superior premolar is represented by its alveolus only on the right side, the alveolus being closed on the left. It is important to note this reduction of the median incisor, or i_1, and the shedding of the first superior premolar. The remaining premolars, p^2–p^4, show a slightly stronger development of the tetartocones than in the *B. brachycephalus* type and paratype, although in p^4 the deuterocone still constitutes the main internal portion of the crown, as in the type of *B. brachycephalus*; in m^3 the abortive metaloph extends outward from the cingule without a distinct hypocone.

A second transitional skull from upper A (A 3) (Nat. Mus. 1214; fig. 418) may also be considered transitional between *B. brachycephalus* and *B. dispar*. It is in the seventh growth stage. The median pair of incisors ($i\frac{1}{1}$) has also dropped out entirely; the first superior premolar persists on one side and has disappeared on the other, so that the formula in both specimens is I^1, P^{4-3}, demonstrating absolutely the variability of p^1. The marked primitive feature of the premolars is that while in p^2, p^3 the tetartocones are becoming more distinct and rounded, in p^4 the deuterocone still forms almost the entire inner surface of the crown. In this, as in the preceding types, the metaloph extends from the hypocone cingule of m^3 outward toward the metacone. The rugosity on the basisphenoid is very prominent; the nasals are of medium length in this specimen, expanding slightly at the sides, which is an age character, and their form is somewhat similar to that in Leidy's type of *Megacerops*; the horns show a more trihedral section at the base than in the preceding specimens owing to the incipient development of the connecting ridge (cr).

A transitional stage from lower B is represented by the young male skull (Nat. Mus. 4258) found in B, or the middle levels—namely, 71.45 feet above the Cretaceous Pierre shale. It gives us valuable details of the architecture of the anterior portion of the face. Seen from above (Pls. LXXXIV, LXXXV) the frontals cap the nasals and constitute the entire tips of the horns. In side view, however (Pl. LXXXIV), the nasals are seen to support the main anterior portion of the base of the horn, resting postero-inferiorly on the lacrimals, elements which are not quite so extensive as represented in Plate LXXXIV, A². Subsequently the lacrimal coalesces with the malar, and we speak of the ridge extending down from the side of the horns as the malar or external ridge. In palatal view the posterior nares open between m^2 and m^3. The vomer (Pl. LXXXVI) extends well backward.

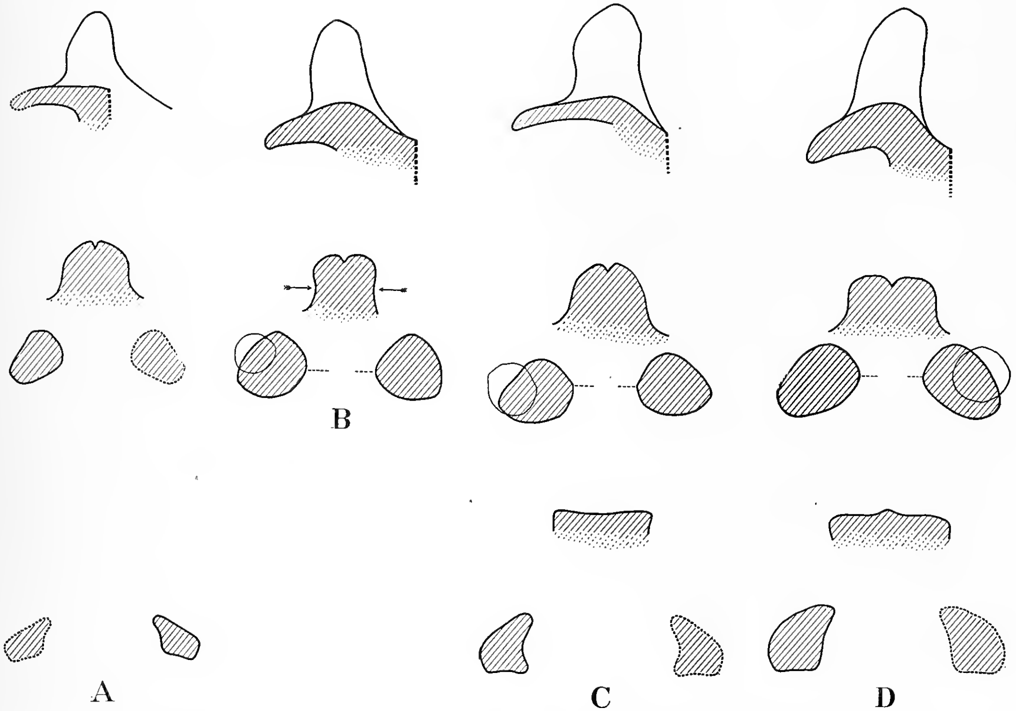


FIGURE 419.—Sections and contours of skulls of *Brontops brachycephalus* (A) and *B. dispar* (B, C, D)

A, Nat. Mus. 4259; B, Nat. Mus. 4941; C, Nat. Mus. 4703; D, Nat. Mus. 4290 (type of *B. validus*). All one-eighth natural size. The more progressive members of *B. brachycephalus* (A) approach *B. dispar* but are distinguished by their smaller size, small horns, low connecting crest, and relatively slender zygomata. In *B. dispar* (B, C, D), which is characteristic of Chadron B, the horns are much stouter with rounded basal section, the nasals thicker and shorter, and the zygomata more massive. The more progressive members (D) approach *B. robustus*. Note the similarity of the buccal section in D to that of Am. Mus. 518, ♀ (fig. 424; see also fig. 376, showing position of sections and contours).

The transitional skull just described (Nat. Mus. 4258) and another skull (Nat. Mus. 4259) belong to *B. brachycephalus* rather than to *B. dispar*, because, as shown in the table of measurements above, they agree far better with *B. brachycephalus* in tooth measurements, the horn sections (figs. 414, 419) agree more closely with those of *B. brachycephalus*, and in their tetartocone development the premolars are more advanced than the type of *B. brachycephalus* but less advanced than in the type and referred specimens of *B. dispar*.

Review of primitive and progressive characters of Brontops brachycephalus.—Nasals: All the skulls exhibit nasals having a median terminal notch. The nasals are narrowest distally in the fourth stage of growth and expand toward the extremities in the seventh stage; the progressive shortening and distal widening of the nasals are distinctive features of the *Brontops* phylum. In general, abbreviation of the nasals is correlated with brachycephaly.

Horn growth: The sexual distinctions of size and form in the horns are well marked. The horns not only increase steadily in size in succeeding geologic levels but in course of individual growth they recapitulate clearly the ancestral Eocene history of this species. In young bulls the horns present an elongate oval, as in the upper Eocene *Protitanotherium emarginatum;* as the males become older the anteroposterior diameter relatively decreases, the transverse diameter increases, and the horn gains in height, rising only 37 millimeters above the skull in the fourth stage.

Skull growth: In the meantime the summit of the skull, or parietal vertex, does not perceptibly increase in width; the top of the occiput extends considerably back of the zygomata. The zygomatic arch sections are as highly distinctive as the horn sections, since the transverse diameters nearly equal the vertical diameters; the zygomatic arch is relatively broad and shallow and contrasts with that of *Menodus heloceras*, which is distinctly dolichocephalic.

Teeth; variability of incisors: There are two well-developed incisors in the youngest skull transitional to *B. dispar* (Nat. Mus. 4258); the median pair has dropped out of another skull in the later part of the seventh stage (Nat. Mus. 1214); but both incisors persist in the still older type male (Nat. Mus. 4261). In all the male skulls the canines are prominent and pointed, measuring from 40 to 43 millimeters in length in the males and resembling in form those of *B. dispar*.

Premolars: The first superior premolar is small; it exhibits an imperfectly formed internal crest and no tetartocone. The constitution of the remaining premolars, p^2–p^4 (Nat. Mus. 4258, 1214), is interesting as exhibiting the relative rate of evolution of the internal cusps and bringing out the fact that the anterior premolars are more progressive than the posterior; this condition is adaptively correlated with the fact that the anterior premolars come into use earlier than the posterior premolars, as shown by Hatcher (1901.1, p. 261). Thus p^2, although the smallest tooth, exhibits the largest tetartocone, forming a direct continuation of the crest of the deuterocone; p^3 has its tetartocone distinctly budded off, with conical sides; while in p^4 the tetartocone is a mere cingule (figs. 406, 417). Whereas in the typical *B. brachycephalus* of the lower A levels the deuterocone constitutes almost the entire inner surface of the crown, especially in p^{3-4}, and the tetartocones are rudimentary, in the later geologic stages (Nat. Mus. 4258, 4259) the tetartocones evolve into small, low, irregular-shaped cusps, leading into the condition found in the type of *B. validus* (Nat. Mus. 4290). The variability of the first superior premolar is shown, as mentioned above, in one of the older *B. brachycephalus* skulls (Nat. Mus. 1214), in which it persists on one side but has disappeared on the other; this reduction and variability is seen also in *B. dispar* and in *Menodus.* A very important character consists in the fact that whereas the external cingulum on the premolars is variable and feebly developed in some skulls and more strongly marked in others (Am. Mus. 1495, Nat. Mus. 4258), the internal cingulum is constant but never very broad, as it is in *Menodus trigonoceras.*

Molars: The ratio of molar length to premolar length in this evolution stage is as 175 to 114. In the molar series m^3 also offers a very distinctive character: the hypocone is a cingule, and as in *B. brachycephalus* an abortive crenulate crest (metaloph) extends from this toward the metacone; the strong cingule in front of the protocone known as the "protostyle" is here a feeble, inward-directed ridge.

Brontops dispar Marsh

(*Brontops validus* Marsh; "*Megacerops dispar*" Osborn, 1902)

Plates XXIV, XXXIII, LXXXVIII, XCIV; text figures 24, 180, 375, 384–386, 389, 391, 394, 396, 399, 409–412, 419, 421, 423, 609, 616, 719, 744

For original description and type references see p. 223. For skeletal characters see p. 664]

Geologic horizon.—Middle beds (Chadron B) to lower portion of upper beds (C).

Specific characters.—Skull of intermediate size in males; incisive border to condyles 660 to 685 millimeters, in female 610. Males brachycephalic, zygomatic index 73 to 87, average 80; zygomatic width 555 millimeters (average). Females more mesaticephalic, zygomatic index 60–71, zygomatic width 390 millimeters. Horns progressively shifting anteriorly, more elongate, 162 to 200 millimeters. Basal section rounded, summits cylindrical. Nasals progressively abbreviated (105 to 85 mm.), with forward-shifting horns, spreading distally. Grinding series 310 to 340 millimeters, average 329. Dental index 46 to 49, average 47. Canines pointed and more or less compressed anteroposteriorly. Premolars more progressive; tetartocones p^{3-2}, more advanced than in *B. brachycephalus.* Tetartocone of p^4 progressively developed from a concave spur from the deuterocone, continuous with the cingulum, to a rudimentary cusp. Backward prolongation of the occiput behind the zygomata very pronounced.

This significant species connects closely with the most progressive stages of *Brontops brachycephalus* and with certain skulls which may be referred to *Brontops robustus,* although the typical *B. dispar* does not appear to be directly ancestral to the typical *B. robustus.*

The range in size in skulls referred to *Brontops dispar* is given above.

From *Allops marshi,* as well as from *Brontops brachycephalus,* the skull of this species is distinguished especially by its greater robustness (zygomatic index 78–87, as compared with 64–71), larger horns, and shorter, thicker nasals, as indicated in the following measurements:

Measurements of Brontops dispar and Allops marshi, in millimeters

	B. dispar, Nat. Mus. 4290 (type of B. validus)	A. marshi, Am. Mus. 501 (type)
P^1–m^3	320	310
P^1–p^4	130	122
M^1–m^3	203	191
Canine:		
Vertical	40	34
Anteroposterior	27	25
Pmx to condyles	660	673
Zygomatic width	565	450
Cephalic index	85	67
Nasal length	85	100
Nasal breadth	120	105
Horns, external length	198	105

From *Menodus proutii* we observe that *B. dispar* is distinguished by its brachycephaly, by the greater relative width of its premolars and molars, and by the more retarded development of the premolar tetartocones, especially in p^4.

From *Allops serotinus* and *A. crassicornis* we observe that *B. dispar* is usually distinguished by its higher zygomatic index and by the lesser width of the premolars.

The type of *B. dispar,* unfortunately a badly crushed skull, has less robust horns and nasals than the type of *B. validus,* but the general agreement in measurements as well as in dental characters appears to indicate that these two types belong either to the same or to very nearly related species.

Geographic and geologic distribution.—According to Hatcher's record, the typical *B. dispar* skulls were found mainly in B or the middle *Titanotherium* zone, but they extend also into the lower levels of the upper beds, namely, lower C (Chadron C 1). The four ascending skulls in the National Museum most accurately recorded by Hatcher and Stanton in 1901 are from 55 to 71 feet above the Cretaceous Pierre shale, as follows:

Skull 4258, *Brontops brachycephalus* (transitional), 71.45 feet above the Pierre.

Skull 4259, *B. brachycephalus* (transitional), 55.6 feet above the Pierre.

Skull 4290, *B. dispar* (type of *B. validus*), 62 feet above the Pierre.

Skull 4703, *B. dispar,* 62 feet above the Pierre.

Geologic variation.—Inconsistent with the general observation that the more progressive forms are found on higher levels is the fact that the specimen first named (Nat. Mus. 4258) is a very primitive form which is distinctly related to *B. brachycephalus,* as noted above. The type of *Diploclonus tyleri,* although very advanced, was also found at a very low level—namely, 35 feet above the Pierre shale, in 200 feet of beds belonging to the *Titanotherium* zone (Lull). These inequalities are certainly due to the uneven surfaces of the Pierre shale on which the White River was deposited.

Materials of B. dispar.—This species is represented in Hatcher's collection for the Geological Survey by twenty-one or more skulls and several jaws now in the National Museum, including especially the following: The juvenile transitional skull (No. 4259) from lower B, or the middle beds, referred to *B. brachycephalus;* the male type of *B. dispar* (Nat. Mus. 4941) from middle B; four finely preserved male skulls—namely, No. 4703 from middle B, No. 4290 from middle B (this specimen is the type of *Brontops validus*), and Nos. 4245, 4248 from B. The two skulls last named are in the seventh and ninth stages of growth. The female sex is represented by No. 4738 from lower B. There is also a complete skull and ower jaw (Nat. Mus. 1217) from the upper zone (level C).

This magnificent collection of well-recorded material in the National Museum enables us to determine positively the range of *Brontops dispar* from lower Chadron B to the base of Chadron C. In this long geologic range there are marked progressive advances in evolution.

B. validus a synonym of B. dispar.—Careful comparison of the measurements and characters of the type of *B. dispar* (Nat. Mus. 4941), from middle B, with the type of *B. validus* (Nat. Mus. 4290), also from middle B, together with the supplementary evidence furnished by the collection of skulls in the National Museum, shows that these nominal species are identical. They both represent the brachycephalic, short-horned titanotheres of the middle levels. Although the type of *B. validus* has on each side two upper incisors and four premolars, a study of other materia proves that both the median incisors and the anterior premolars may be shed at an early age. In other words, it is demonstrable in *B. dispar*, as in *B. brachycephalus*, that the median incisors (i^1) are variable, that they are found in all young animals, that they may or may not drop out in later life. The lateral incisors (i^2) are constant. The stage of evolution of the premolars in the type of *B. validus* is identical with that in the type of *B. dispar* and the sagittal sections of the skull in the two type specimens are closely similar. The horn and nasal sections in the two type specimens are essentially similar; the differences (fig. 419) are due to the lateral crushing and less advanced age of the skull of *B. dispar*.

Chief distinctions from other species.—*B. dispar* is thus readily distinguished from *B. brachycephalus* by its greater measurements and more progressive characters throughout; from *Allops marshi* by the cylindrical section of its horns and by the great backward extension of its occiput; and from the geologically succeeding *B. robustus* by the smaller size and cylindrical section of the horns and the backward extension of the occiput.

Detailed characters of the type of Brontops dispar.—The type of *Brontus dispar* consists of a male jaw and skull (Nat. Mus. 4941) with the occipital region entirely wanting (Pl. XCIII). The extreme lateral crushing of the skull obscures its real characters and actual resemblance to the type, which Marsh subsequently named *Brontops validus*. As association of the skull and jaw is rare and as this specimen represents one of the predominant species of the middle zone, the type deserves full description and measurements in addition to those given in the comparative columns above.

Measurements of type of Brontops dispar, in millimeters

Inferior canine (partly worn), anterior	41
Inferior canine, anteroposterior	30
Length of symphysis	159
Width of condyle	137

Premolars and molars:

	p^2	p^3	p^4	m^1	m^2	m^3
Superior series:						
Anteroposterior	30	40	43	62	78	80
Transverse	39	50	60	72	80	90
	p_2	p_3	p_4	m_1	m_2	m_3
Inferior series:						
Anteroposterior	31	39	45	63	77	108
Transverse	22	29	33	40	44	44

Teeth: Formula, $I\frac{1}{1}$, $P\frac{4-3}{4-3}$. A stout lateral pair of incisors persists in both upper and lower jaws, though the animal is in the beginning of the eighth stage. The median incisors are wanting in both jaws. The canines are prominent and recurved, the superior canine is embraced by a posterior cingulum, while the inferior canine has a faint external cingulum surrounding all except the inner side. The anterior premolars ($p\frac{1}{1}$) have dropped out in both upper and lower jaws, being represented only by large alveoli; p^2, p^3, p^4 have moderately developed internal and vestigial external cingula and tetartocones in the middle stage of development. The hypocone is a prominent cingule on m^3. The second lower premolar, p_2, is an elongate simple tooth, the metalophid not being defined at all, and the hypolophid forming an incipient crescent; p_3, p_4 present double crescents and a rudimentary metastylid. The lower molars exhibit partly developed external cingula, reduced opposite the protoconid and hypoconid; they also exhibit rudiments of the metastylid. The last inferior molar is highly characteristic of the *Brontops-Menodus* group, a broad internal shelf extending inward from the hypoconulid, with a trace of a posterior cingulum beneath it. The much crushed jaw exhibits a shallow symphysis, a large mental foramen beneath p_3. Plate XCIV gives its partly restored outlines.

Skull: The skull exhibits the short, truncate, and cleft nasals, short horns with a subtrihedral section at the base, rounded malar, nasal and connecting ridges, and rounded faces. The posterior face is broad and uniformly convex, as in the other advanced members of this phylum. The horns have a characteristic angle of the outer border, leading into a rounded summit, as shown in the section. The zygomatic arches are robust and convex, but they are too much crushed for an accurate section.

Type of Brontops validus.—The type of the synonymic species *Brontops validus* (Nat. Mus. 4290) is a male in the seventh growth stage. It is well figured in Plates LXXXVIII, LXXXIX of the present monograph. The principal measurements are as follows:

Measurements of type of Brontops validus

	Millimeters
Molar-premolar series	320
Condyles to premaxillary tips	660
Free portion of nasals, length	85
Free portion of nasals, breadth	120
Length of horn to nares	199

There are two incisors above and below; the canines are large and pointed, indicating that this specimen was a male; the fourth premolar has a rather feeble tetartocone without a distinct valley separating it from the protocone; the hypocone of the third superior molar is a shallow ridge arising from the cingulum. The species is clearly characterized by the short, square nasals and horns borne well forward; but it can not be separated specifically from the previously described *Brontops dispar*.

General characters of B. dispar.—The measurements of the skulls referred to *B. dispar* are singularly uniform and constant, as shown in the table above. In the males the superior premolar-molar series measures 310 to 345 millimeters in length. The basilar length, premaxillaries to occipital condyles, ranges from 660 to 685 millimeters, the male zygomatic arches from 515 to 565, the horns from 155 to 200. In the females the dental and cranial measurements exhibit the usual sexual contrasts of inferiority.

Main features of skull: The nasals are short but broad and thick in section in the type of *B. validus*, 85 to 103 millimeters in length and 100 to 143 millimeters in breadth; in other males (Nat. Mus. 4245, 4703, 4706) they are somewhat long and narrow, resembling those in *B. brachycephalus* and thus affording a complete transition, as may be readily seen in Figure 419. The adult or growth changes are prophetic of the higher specific stages of this phylum. Thus in early stages of growth the nasals are somewhat thinner and more narrow distally; in later stages of growth they thicken and broaden near the ends, while the median cleft deepens. The form of the horns is highly distinctive of this species; seen from in front (Pl. XCIV) the lateral contours of the horns exhibit a strong convexity above the middle portion; from this point upward they suddenly contract into rounded, rugose tips; this rounding and pointing of the tips of the horns is a very distinctive feature as compared with the broad oval tips in members of the *Brontotherium* phylum. The basal section of the horn in the type skull of *B. dispar* (figs. 399, 419) approaches that of *B. robustus* (fig. 421) in the rounding out of the "anterior" or "nasal" angle or ridge and in the anteroposterior flattening; the posterior faces of the horns of *B. dispar*, however, unlike those in the type of *B. robustus*, are directed obliquely inward toward each other and present a long, uniform convexity. Some horn sections are more trihedral because of the prominence of the nasal ridge. In lateral view the horns are seen to be slightly recurved and to be united, especially in the old males, by a deep and broad connecting crest. The zygomata present prominent convex buccal processes, which have a deep, thick section, similar to that of *B. robustus* but somewhat less heavy.

Details of male skull: The type skull of *Brontops validus*, "skull K," Nat. Mus. 4290 (Pls. LXXXVIII, LXXXIX, XCI, XCII; fig. 419), found at the 62-foot level above the base of the *Titanotherium* zone, in middle B, admirably exemplifies the distinctive features of the skull. It is in the seventh stage of growth. Seen from in front (Pl. XCIV), the nasals are supported by a vertical bony septum, which in life may have been united by cartilage with a similar bony septum that extends up from the premaxillae (cf. *Tapirella bairdi*). The top of the skull is seen to be a larger development of the *B. brachycephalus* type (compare Pls. LXXXV and XCI), broad above the orbits, narrowing at the vertex, with a rugose supratemporal crest. In the middle of the parietal vertex of certain specimens (Nat. Mus. 4703) a very large central pit (Pl. XCII) is observed. This is a vestige of the space between the convergent supratemporal ridges and is similar to the median pit in some of the Eocene forerunners of *Brontops*—namely, *Manteoceras*. The occipital pillars are strong, but the rugosities at the summits are somewhat narrower than in *B. robustus*. The palatal view (Pls. LXXXVIII, LXXXIX) also illustrates the brachycephalic character. The vomer extends back as a prominent keel upon the basisphenoid, which exhibits a robust, paired rugosity for the rectus capitis muscle at its junction with the basioccipital.

The progressive size evolution of the skull is distinguished first by the slight increase in length and great increase in width over that of *B. brachycephalus*, owing partly to the rapid expansion of the buccal processes but also to the broadening of the skull itself; second, by the elongation and strengthening of the horns as described above. Additional observations on this specimen are given above.

Dentition: The teeth show many characters inherited from *B. brachycephalus*. The formula ($I\frac{2-1}{2-1}$, $P\frac{4-3}{4-3}$) exhibits hereditary variability, manifested in the occasional loss of one incisor and one premolar. The median incisor sometimes disappears before the seventh stage (Nat. Mus. 4941, 4703), or it may persist late in life (Nat. Mus. 4290, 4245). The canines are relatively long and rounded in section at the base, more or less compressed anteroposteriorly, foreshadowing the *Allops* sublanceolate canine, less elongate than in members of the *Menodus* phylum, and much less obtuse and recurved than in members of the *Brontotherium* series. The first superior premolar is a fairly large and persistent tooth, but it also sometimes aborts and disappears early (Nat. Mus. 4703). The ectoloph of p^1 is well in line with the ectoloph of p^2, p^3 (contrast *Brontotherium*). In the advanced stages of *B. dispar* the transformation of the premolars has proceeded much further than in any specimen of *B. brachycephalus;* the tetartocones of p^2 and p^3 are relatively distinct, but in p^4 the tetartocone is still a backward spur from the deuterocone, more rounded than in *B. robustus*, but never sharply rounded off or prominent and always a much less distinct and separate cusp than in p^3. In the type of *B. dispar*, in fact, the tetartocone of p^4 is only a little more advanced than in the typical *B. brachycephalus*. The external cingulum of the superior premolars is fairly well marked; the internal cingulum is progressive or stronger than in *B. brachycephalus*. On m^3 the hypocone is a prominent cingule.

Lower jaw (fig. 423): In the type jaw (Nat. Mus. 4941) vertical crushing has greatly diminished the depth of the horizontal ramus, but the symphyseal region was probably shallow. There was a diastema between p_1 (which has dropped out) and the canine.

The canine is stout and conical; the incisors are subspherical; the external cingula are not as sharply defined as in *Menodus*.

Female skulls: The females of this species (Nat. Mus. 4738) are, according to the principle expressed above, distinguished by smaller and much less robust canines; the greatly reduced canines, the more slender zygomatic arches, and the inferior dimensions of this skull and teeth as a whole constitute the distinctive sexual characters. The internal and external premolar cingula are quite as strong as in the male representatives of this species.

The skull forming Nat. Mus. 4738 (fig. 391, A) presents rather slender zygomatic arches; the nasals, although imperfectly preserved, indicate a slender, unexpanded contour. This skull is in the eighth stage of growth, yet it retains two superior incisors on each side. The canines measure only 35 millimeters anteriorly as compared with 47 in the largest males. The protocones of m^2, m^3 are rather low, are set well in from the inner margin of the tooth, and have a slight concavity on the lingual side near the top—an individual variation. A peculiar feature of this specimen is the reduplication of the tetartocone of p^4, an anomalous character (see explanation above) also observed in *B. brachycephalus* (Nat. Mus. 4259) and in the type of *Allops crassicornis* as well as in the type of *Menodus* (*Menops*) *varians*. A character reversional to *B. brachycephalus* is the abortive crenulate metaloph of m^3, extending forward and inward from the hypocone. In palatal view the less robust character of the basisphenoid and the narrowness of the zygomata are well illustrated. Another character, which may be an individual variation, is the nonclosure of several of the sutures, the median suture between the nasals and frontals being still widely opened. Similarly the external portion of the mastoid is still well defined between the post-tympanic and the exoccipital processes. The post-tympanic and postglenoid processes of the squamosal are not conjoined below.

FIGURE 420.—Restoration of *Brontops robustus*
By Charles R. Knight. About one-ninth natural size.

Extension of B. dispar into upper beds, or C.—Although *B. dispar* is especially characteristic of the middle *Titanotherium* zone, evidence of its occurrence in the upper beds even to a point a little below middle C is apparently indicated by skull No. 1217 in the National Museum. This fine specimen with the lower jaw attached (Pl. XCIII) appears to represent a very large male of *B. dispar*, the length from condyles to premaxillaries being estimated at 702+ millimeters, m^1–m^3 196, m_1–m_3 230. The detailed measurements of the grinding teeth, however, as in the large upper zone brontotheres, are smaller throughout than those of the large *B. dispar*, Nat. Mus. 4696, from the middle beds.

Brontops robustus Marsh

("*Megacerops robustus*" Osborn, 1902)

Plates XVIII, XX, XXXIII–XXXVI, XLIII, XLVII, XCV–CIII, CXCV–CCXXIX; text figures 24, 179, 387, 389, 393, 394, 396, 399, 400, 409–412, 420–423, 482, 483, 510, 608, 618, 622, 624, 626, 628, 630, 635, 636, 639, 640, 650, 651, 653–655, 657–660, 669, 685, 686, 693, 699, 712, 719, 727, 744

[For original description and type references see p. 222. For skeletal characters see p. 666]

Geologic horizon.—Lower level of the upper *Titanotherium* zone (C).

Specific characters.—Length of skull 765 to 813 millimeters, strongly brachycephalic, zygomatic index, 77 to 87, average 79; backward prolongation of occiput slight or absent; horns shifted forward and inclined forward, basal section broadly transverse oval, summit obtuse, outside length 207 millimeters (type); nasals abbreviate, free length 76 millimeters, breadth 149, nasal index 51; dental index 46, same as in *B. brachycephalus* and *B. dispar*, total grinding series 345 to 376 millimeters; molars 215 to 236, average 223; canines rounded in section, obtuse, stout, length of crown 42 to 48 millimeters; tetartocones of p^{3-2} somewhat less developed than in typical *B. dispar*.

This species marks the end of the *Brontops* phylum, toward the end of lower Oligocene time. It is related to *B. brachycephalus* but does not directly succeed any of the known mutations of *B. dispar*.

General characters.—This is the most fully known species of titanothere. The fine type skull and skeleton in the Yale Museum (Yale Mus. 12048) represent a middle-aged animal. Both were found in "Corral

Draw," near the base of Chadron C (upper *Titanotherium* zone), 60 feet below the summit, as recorded by Hatcher. This skeleton is so complete that almost all its parts were figured for this monograph in plates and woodcuts under the direction of Professor Marsh. *Brontops robustus* appears to have been the predominant animal during the deposition of the beds of the lower C 1 levels of the upper *Titanotherium* zone in South Dakota. It is a comparatively short-horned type, contemporaneous with the early members of the long-horned series of brontotheres, such as *B. gigas.* The long axis of the basal horn section tends to become directly transverse, and the posterior face is somewhat flattened; the nasals are still broad, resembling closely those in some specimens of *B. dispar.* The presence of two large upper incisors in the type skull of this species was believed by Marsh to be its most distinctive character; two upper incisors are observed also in skulls of the same species in the Yale and American Museums. The male skull (Princeton Mus. 11015), however, carries but one lateral superior incisor, a fact that raises a doubt as to the invariable persistence of the median incisor. These and other characters relate this animal to *Brontops brachycephalus* and *B. dispar*, in which the median superior incisor is also variable.

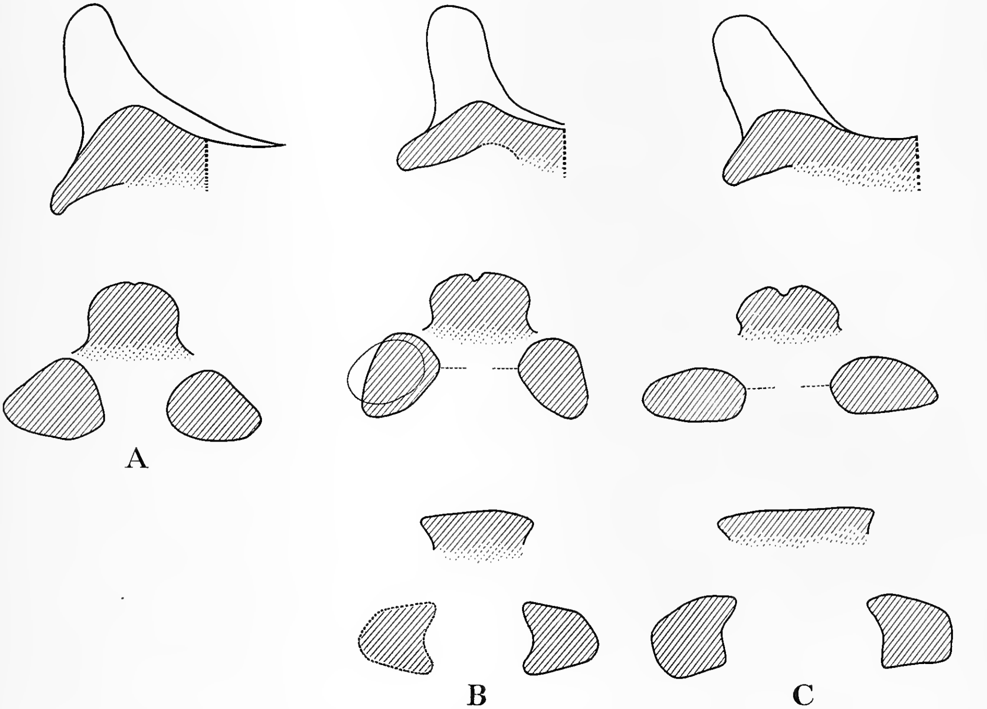


FIGURE 421.—Sections and contours of skull of *Brontops robustus*

A, Nat. Mus. 4696; middle levels of Chadron C; either a very large and progressive *B. dispar* or a primitive *B. robustus*, with stout cylindrical horns far in front of the orbits, broadly and roundly trihedral in section. Nasals short and wide. B, Am. Mus. 1083, referred to *B. robustus*, although the horns are roundly trihedral in section. C, Yale Mus. 12048 (type); lower levels of Chadron C; very thick horns inclined forward and far in front of the orbits, in basal section very widely oval; nasals very short and thick, zygomata massive, and parietal crest wide. All one-eighth natural size.

Convergence of Brontops robustus to Brontotherium.—The typical *B. robustus* is very easily distinguished, but there are at least six other skulls that simulate *Brontotherium* in the premolars, in the expansion of the zygomata, and in the flattening of the horns. In some of these also the skull vertex appears long, but it never has the midparietal protuberance, and the nasals and horns are nearer to *B. robustus* than to *Brontotherium;* also the internal cingula of the premolars are well rounded, and the canines are pointed at the tips.

Observations on the measurements of Brontops robustus.—The males of this species exhibit a convergent resemblance to *Brontotherium* in the buccal expansion of the zygomata, in the reduction of the external cingula of the premolars, in the progressive well-rounded premolar tetartocones of certain specimens, and in the massive form of the canine. The internal cingula of the premolars, however, are pronounced and well rounded as in *Brontops*. The reference of these specimens to *Brontops robustus* rather than to *Brontotherium* is confirmed by the following contrasting measurements:

Measurements of Brontops, Brontotherium gigas, and Brontotherium platyceras, in millimeters

	Brontops robustus		Brontotherium gigas		Brontotherium platyceras, Field Mus. 12161
	Carnegie Mus. 313	Yale Mus. 12048 (type)	Am. Mus. 492	Carnegie Mus. 341	
P^1–m^3	355	350	353	355	340
P^1–p^4	144	137	126	132	120
M^1–m^3	220	220	241	218	223
Pmx to condyles	743	765	830	773	880
Nasals to midvertex occiput	------	635	793	------	895
Canines:					
Vertical	47	42	35	35	36
Anteroposterior	37	36	32	23	29

In general *Brontops robustus* is distinguished from *Brontotherium* by the greater length of the premolar series, by the shorter skull base and skull top, and by the larger canines, which are also more pointed at the tip. The horns are much shorter than in the flat-horned species of *Brontotherium*, and the connecting crest is lower.

The range of size in skulls referred to this species is indicated as follows:

	Millimeters
Skull, basilar length	743–813
P^1–m^3	340–376
P^1–p^4	132–151
M^1–m^3	230–237
Zygomatic index	77– 87
Outside length of horns	130–210

The premolars and molars are wide compared with those of *Menodus:*

	P^4, ap.×tr.	M^3, ap.×tr.
Brontops robustus	40×65 to 46×69	73×84 to 90×89
Menodus trigonoceras	43×51 to 41×55	72×70 to 82×79

Geologic and geographic distribution.—So far as recorded, all the known specimens of this species were obtained from the *Titanotherium* zone (Chadron formation) of South Dakota. It appears probable that the geologic level recorded for the type specimens by Hatcher, namely, lower C of the upper *Titanotherium* zone, is characteristic.

Materials.—The type skull and skeleton in the Yale Museum (No. 12048) afford the best knowledge of the extreme characteristics of this type. In the American Museum there are two fine skulls (Nos. 1083, 1069) which confirm or supplement the characters observed in the type. In the Princeton Museum there are two male skulls, also found in "Corral Draw," South Dakota (Nos. 11439, 11015), associated with many parts of the skeleton; also a valuable skull (No. 10061) which is transitional between *B. robustus* and *Allops marshi* in the disposition of the horns. In the National Museum there is an extremely brachycephalic, robust skull (Nat. Mus. 4253) of smaller size than the typical *B. robustus*, which may represent a primitive or transitional variety of this species. It agrees in all its principal characters with the type skull, although smaller and in many features more primitive.

Skull.—The most prominent cranial characters of this well-defined species are extreme brachycephaly, extreme abbreviation of the occiput, marked depression of the midregion of the cranial vertex, rapid elevation of the summit of the occiput, downward and forward inclination of the zygomata. In female specimens of *B. dispar* the length exceeds the breadth by 200 millimeters; in the type of *B. validus* the length exceeds the breadth by 100 millimeters. In this skull also the length exceeds the breadth by only 100 millimeters. This feature stands in widest contrast with the dolichocephaly of the contemporary *Menodus giganteus*, in which the length exceeds the breadth by over 230 millimeters. The type skull, with its abbreviate occipital region, also contrasts with that of the contemporary *Brontotherium gigas*, which shows a decided backward extension of the occiput, especially in the males. The age or growth characters of this skull are similar to those in some of the collateral ancestors of this phylum—namely, expansion and not very marked elongation of the horns, which shift progressively forward and reach an extreme overhanging position in the type. Old skulls exhibit a thickening of the connecting crests between the horns, also the distal growth, widening and rugosity of the nasals, and thickening of the buccal swellings of the zygomata. These buccal swellings are somewhat crushed laterally in the Yale type specimen; but in all the skulls examined the buccal section appears to be smaller and more concave above, and on the outer border a less strong flaring out at the sides is observed than in the skulls of *Brontotherium medium* or *B. curtum.*

In general, the skull apart from its much greater brachycephaly resembles on a grander scale that of *Allops marshi*, both in its superior and inferior aspects and in the form of the nasals, yet the retarded condition of the premolar tetartocones, the extremely wide transverse sections of the horns, and the relative obtuseness of the canines do not point to direct relationship to *A. marshi.*

Horns.—Horns are found, however (as in Am. Mus. 1083, 1069, Princeton Mus. 10061), which are transitional in position and basal section between those of *Allops marshi* and of this species; progressive varieties of *B. dispar* also show more or less transition to this transversely flattened type of horn.

Correlated with the general brachycephaly, the palate is broader and the grinding series more widely arched. Similarly we observe great breadth in the postglenoid and paroccipital processes. It is to be noted that the postglenoid and post-tympanic processes unite late in life (Am. Mus. 1069), whereas in the contemporaneous species of *Brontotherium* (*B. gigas* and *B. curtum*) these processes unite early in life. The vomerine ridge is prominent, and there is a downward continuation, or septum, of the vomer tending to unite with the palatine and thus divide the posterior nares. This feature is observed also occasionally in *B. dispar*. Rugosities for the attachment of the recti capitis antici majores muscles are located at the junction of the basioccipital and basisphenoid (type skull and Am. Mus. 1069), another *Brontops* character. The external bridge over the infraorbital foramen is relatively narrow in contrast with its more primitive width, correlated with the longer face in *A. marshi*. The antorbital malar ridge is less rounded than in *B. gigas* and its congeners. There is a pair of small protuberances (k, k) on either side of the median line of the upper portion of the occiput, which very probably were situated between the insertion areas of the median ligamentum nuchae and of the paired semispinalis capitis muscles. These protuberances are also observed in *A. marshi*, *B. gigas*, and *B. curtum*. The great strength of the occipital pillars and the broadly rugose flare of their summits contrast with the narrow ridges observed in *B. dispar*.

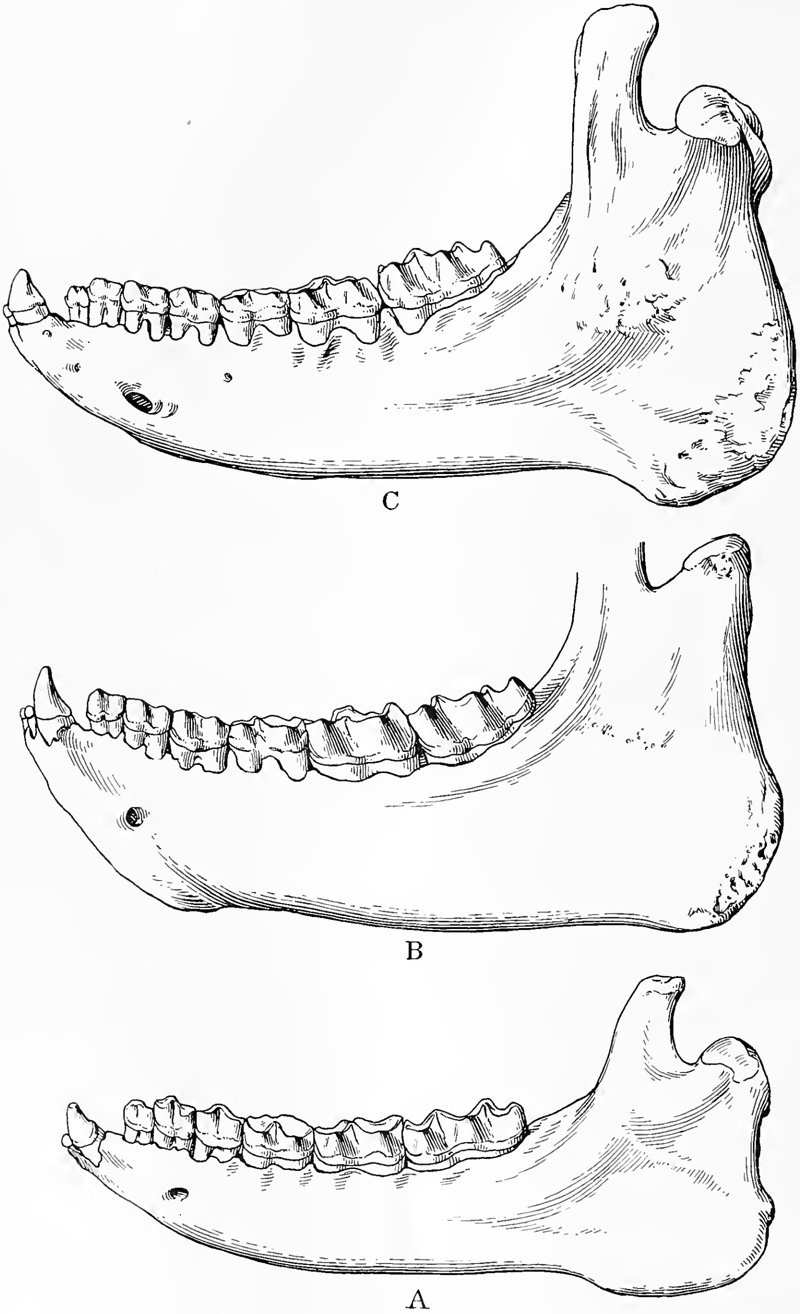
The hyoid elements, represented in Figure 425, include the stylohyals, 265 millimeters in length, which are expanded superiorly and exhibit a long, flattened shaft and a slight distal expansion terminating in cartilage; the ceratohyals, 80 millimeters in length, expanded at both extremities. The epihyals were probably almost vestigial, as in other perissodactyls. In the horse they consist of a small nodule of bone embedded in the cartilage that connects the ceratohyal with the stylohyal.

Dentition.—The variability in the upper incisors has already been mentioned. The formula is probably $I\frac{2-1}{2-1}$. The incisors exhibit the strongly convex, smoothly rounded crowns so characteristic of *Teleodus avus*, *B. brachycephalus*, *A. marshi*, and *B. dispar*. The canines are quite distinctive of this species. In the males they are large and robust, recurved, pointed, and some specimens (Am. Mus. 1069) possess a strong posterior cingulum, thus being readily distinguishable from the canines of the contemporary *Menodus* and *Brontotherium*. The diastema behind the canine of the Yale type skull is unusual, although it is seen occasionally in the earlier *Brontops brachycephalus* and appears to be a somewhat distinctive specific character, since it is also observed in the two male skulls (Am. Mus. 1083, 1069). The premolars are highly distinctive in their retarded stage of evolution; p^1 exhibits a rudimentary postero-internal cusp; the tetartocones of the succeeding p^{2-3} are rather feebly developed; in p^4 the tetartocone is a mere spur; the external cingula are barely indicated, and the internal cingula of the premolars are rounded and crenulate. In the molars also the cingula are irregularly developed. The hypocone of m^3 is variable in form, either cingulate (Am. Mus. 1083) or a small, acute cusp (Am. Mus. 1069). A reversional feature of interest is a crenulate crest or abortive metaloph connected with the hypocone, recalling the similar structure in *B. brachycephalus*. Skull Am. Mus. 1069 exhibits on m^2 a well-defined "crochet" and "antecrochet," and also a minute "crista." As observed above, the grinding series tend to rise anteriorly.

FIGURE 422.—Skull of *Brontops robustus*

Top view. One-ninth natural size. Am. Mus. 1069; resembles the type of *B. robustus* in its extreme brachycephaly. The horns are shorter and thicker at the tips. The midparietal opening is seen also in certain skulls of *B. dispar*.

Additional details of the type skull.—In reference to the characters noted above, it is important to observe that the top of the type skull is somewhat crushed from front to back, increasing the concavity along the top line and the spread of the vertex. The grinding series are in the ninth stage of wear. It is in this skull that we observe extraordinary breadth and relative shortness, extremely robust zygomata, horns extremely far forward and oval in transverse section, well overhanging the abbreviated nasals, and the arching character of the opposite grinding series. The chief measurements are as follows: Top of occiput to tip of nasals 635 millimeters, transverse



A, *Brontops dispar,* Nat. Mus. 4941 (type); depth of horizontal ramus greatly diminished by vertical crushing, but the symphyseal region was probably shallow. A short diastema between p_1 (which has dropped out) and the canine, which is stout and conical. Incisors subspherical, external cingula not so sharply defined as in *Menodus.*

B, *B. robustus,* Princeton Mus. 10061; symphyseal region crushed laterally, ramus with long, straight lower border, angle produced. Two well-developed incisors, canine stout, diastema in front of p_1 (which has dropped out), external cingula not sharply defined.

C, *B. robustus,* Yale Mus. 12048 (type); ramus long and shallow, symphyseal region very shallow, angle very large and produced downward, coronoid high, vertical truncate. Incisors stout, canines very stout and short, diastema in front of p_1, external cingula reduced, crowns of premolars and molars less hypsodont than in *Menodus.*

All one-fifth natural size.

FIGURE 423.—Lower jaws of *Brontops dispar* and *B. robustus*

width of zygomata 667, transverse width of occipital condyles 225, condyles to tip of incisors 765, molar-premolar series 350, true molars 220, p^{1-4} 137; anterior enamel of canines, worn, 42; anterior diameter of canines, 36.

Teeth (Pls. XX, C, CI).—The canines are relatively robust, obtuse, and recurved, with narrow posterior cingula. The incisors have smooth, rounded crowns of equal size, two on each side. The diastema behind the canine is 20 millimeters and forms a very characteristic feature of the type. The premolar cingula are nearly obsolete except on the inner sides of p^{2-4}; a cingulum is faintly shown on the outer side of p^2. The tetartocones are feebly developed throughout, especially on p^4, in which the deuterocone constitutes the chief inner portion of the crown with a ridge-like tetartocone extending posteriorly.

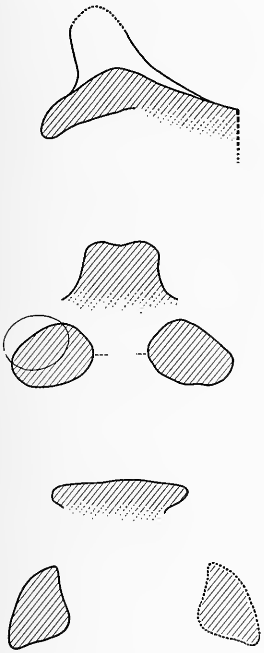


FIGURE 424.—Sections and contours of skull of *Brontops* sp.

Am. Mus. 518 (for mounted skeleton, see Pl. XXXV). The horn sections and zygomata suggest those of *Brontops robustus*. One-eighth natural size.

Lower jaw (Pl. CII and fig. 423).—The jaw is very deep from the condyles to the bottom of the angle; there is a robust, depressed angle, prominent, tall, rectangular coronoid process; the mental foramen is very large; the symphysis is long (20 mm.). There is a single lower incisor on either side of the lower jaw, with the vestigial median alveolus of a second incisor on the right side. There is a deep median cleft in the incisive border. The inferior canines are heavy and laterally compressed (transverse diameter 25 mm., anteroposterior diameter 32). The anterior premolars, p_1, are small but bifanged on either side and are ready to drop out; there is a single alveolus on the left side. The external cingulum is reduced, being marked only upon the valleys and anterior face of the premolar-molar series, with the exception of m_{2-3}, in which the external cingulum is somewhat more developed. In all titanotheres the inner side of the molar crowns is entirely devoid of a cingulum. The hypoconulid of m_3 is not very broad but has a crenulate internal crest, which is entirely absent in *Menodus*.

Transitional skull to B. robustus.—In the Princeton Museum is a fine skull (No. 10061, Pl. XCV) which in many respects is transitional to *B. robustus*. It belongs to a large male and was used in the first published restoration of "*Menodus*" *coloradensis* by Scott and Osborn (1887.1). Although of smaller size it agrees with *B. robustus* in the presence of a pair of smooth, rounded upper incisors, decided diastemata behind the canines, and in the general conformation of the zygomata, retarded development of the tetartocones on the premolars, absence of external cingula, and large upper and lower canines. It is more primitive than *B. robustus* in the presence of two rounded lower incisors, in the more rounded summits of the horns, and in the somewhat less expanded zygomatic and nasal sections. The angle of the jaw is produced backward rather than downward.

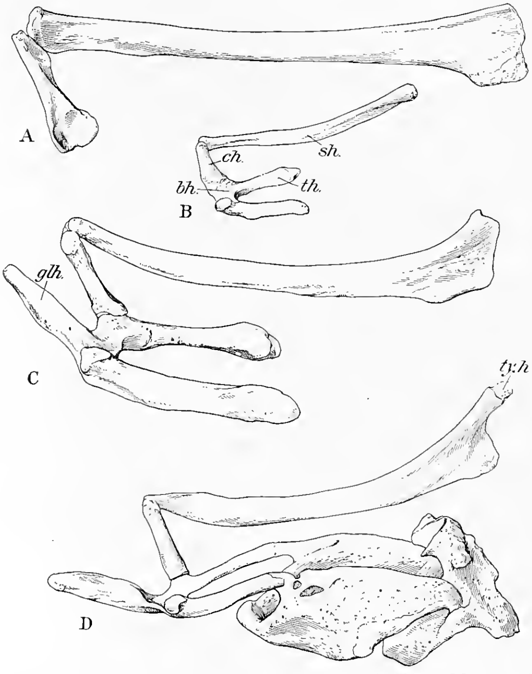


FIGURE 425.—Hyoid bones of *Brontops* sp. (A) (Am. Mus. 518) compared with those of the tapir (B), black rhinoceros (C), and horse (D)

Oblique medial aspect of right side. *sh*, Stylohyal; *ch*, ceratohyal; *bh*, basihyal; *th*, thyrohyal; *glh*, glossohyal. Compare hyoid bones of *Dolichorhinus longiceps* (fig. 345). The glossohyal is lacking in *Dolichorhinus* and possibly in all other titanotheres.

Observations on the skull of the mounted skeleton referred to Brontops robustus (Am. Mus. 518).—The generic and specific determination of this skeleton is difficult owing to the imperfection of the skull.

It was originally referred by Osborn to *Titanotherium robustum*, but later he referred it to *Brontotherium* *gigas*, ♀, chiefly because the carpus of this specimen is slightly different from that of Marsh's type of *Brontops robustus*. Unfortunately the specimen lacks all the front teeth, as far back as p^3 and p_2. The upper premolars have the tetartocones well constricted, as in *Brontops*, and very different from the circular tetartocones of male brontotheres. A supposed female of *Brontotherium gigas* (Am. Mus. 1006) also has the tetartocones much restricted, but the reference of this specimen to *Brontotherium* is very doubtful.

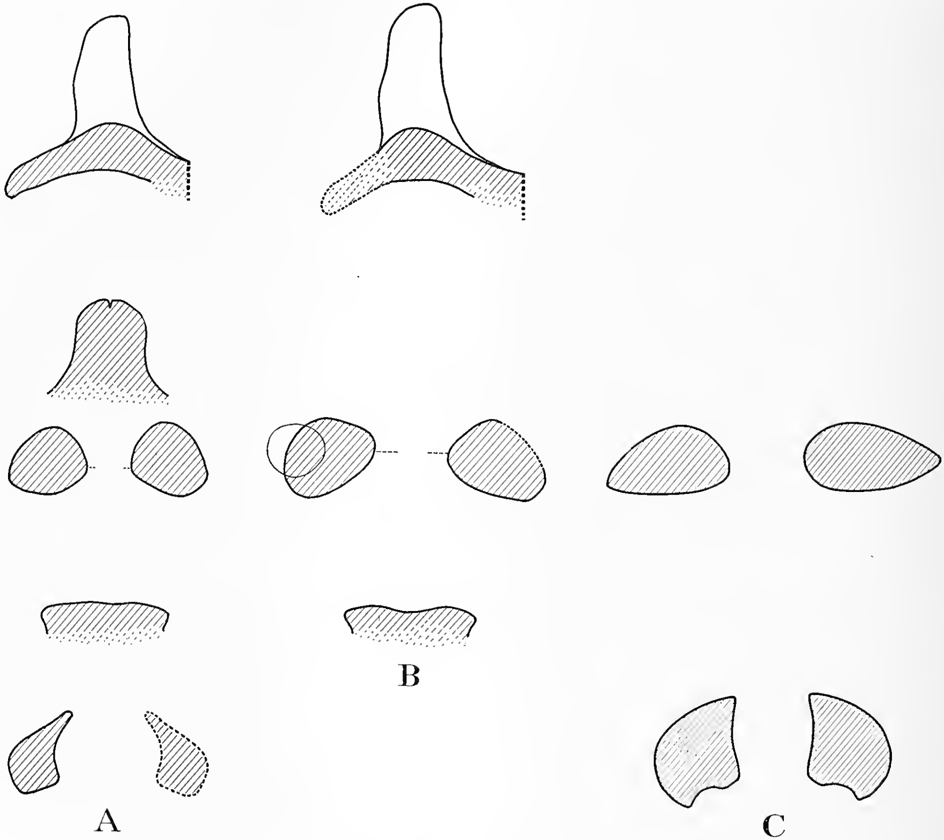


FIGURE 426.—Sections and contours of skulls of *Diploclonus bicornutus* and *D. tyleri*

A, *Diploclonus bicornutus*, Am. Mus. 1476 (type); horns much as in *Brontops dispar* but with an accessory hornlet, basal section roundly trihedral, nasals long, zygomata little expanded. B, Am. Mus. 1081, referred to *D. tyleri;* stout horns roundly trihedral in section, connecting crest high, zygomata stout. C, *D. tyleri*, Amherst Mus. 327 (type); horns widely oval in section, accessory hornlets more pronounced than in *bicornutus*, zygomata expanded. One-seventh natural size. Sections and contours of *D. bicornutus* and *D. selwynianus* (see fig. 185) indicate that these forms, with their peculiar narrow nasals, are not ancestral in type to *D. amplus*, with its broad and abbreviate nasals.

In Am. Mus. 518 the external cingulum of the upper premolars and molars is absent, as in both *Brontops robustus* and *Brontotherium*, so this character is not decisive. The external cingulum of the lower premolars is reduced, but on the whole the dentition appears closer to that of *B. robustus* than to that of *Brontotherium*. The lower jaw presents no close resemblance to the jaws of brontotheres; from *Brontops robustus* type it differs to some extent; perhaps its nearest resemblance is to the type of *Diploclonus tyleri*. The available measurements of the skull and dentition, though few, are nearer to those of *Brontops robustus* (especially Am. Mus. 1069) than to those of large male brontotheres. The specimen is much larger than the supposed female brontotheres of *B. curtum* and *B. gigas*. The sections and contours of the horns and nasals are certainly different from those of the supposed female brontotheres and still more so from those of male brontotheres. The sections are, in fact, closer to those of *Diploclonus tyleri* and *Brontops robustus* (especially Am. Mus. 1083). The manus has the magnum broader, more angulate than that of *B. robustus* as figured by Marsh, but as a whole the manus is similar in proportions to that of *Brontops* *robustus.* The hind limbs mounted with this skeleton belong to other individuals.

On the whole the evidence indicates that the mounted skeleton is not a female brontothere but is a member of the Brontopinae and probably *Brontops robustus.*

Diploclonus Marsh

("*Allops*" Marsh, Osborn, 1902)

Plates XXXVII, CIV–CX; text figures 185, 187, 196, 200, 201, 375, 389, 391, 394, 397, 409, 426–428, 630, 639

[For original description and type references see p. 227. For skeletal characters see p. 675]

Generic characters.—A phylum collateral to other *Brontops* phyla, apparently distinguished by the budding off of a second hornlet on the inner side of the horns and hence known as *Diploclonus;* also by the narrow and elongate nasals in the middle members of the series; hornlets rising from the inner faces of the horns.

Incisors 2–1. Premolars about as in *B. dispar,* but with external cingula becoming obsolete. Nasals progressively abbreviating. Bridge over infraorbital foramen rather sharp and narrow. Progressive brachycephaly; also backward prolongation of the temporal fossae. Other characters as in *Brontops.*

A tendency to give off an internal branch, knob, or "hornlet" (fig. 427) on the inner and anterior faces of the main horns is observed in a number of titanothere skulls which otherwise show strong affinities to the *Brontops* phylum and especially to the species *B. dispar.* Marsh regarded this internal hornlet as of so much importance that he assigned it generic rank in proposing the genus *Diploclonus,* the genotype of which is the species *Diploclonus amplus.* The presence of a small accessory horn swelling has also been observed in certain skulls of *Menodus* and of *Brontotherium.* It is doubtful, therefore, whether this hornlet is of generic value. *D. amplus* and *D. tyleri* resemble *B. robustus* in many features but may represent a distinct subphylum. Subsequently the same character was observed by Osborn in two skulls in the American Museum (Nos. 1476, 1081) which were made the type and paratype respectively of the species *Diploclonus* ("*Megacerops*") *bicornutus* (fig. 426), the latter now referred to *D. tyleri;* and finally a fine skeleton with skull was obtained by the Amherst Museum and described by Lull as a third species *Diploclonus* ("*Megacerops*") *tyleri* (Amherst Mus. 327).

The sum of progressive characters is as follows: (1) Hornlets on the inner sides of the horns; (2) increasing brachycephaly; (3) gradual or retarded evolution of premolars, p^4 being the most retarded tooth. The sum of retrogressive characters is as follows: (1) Relative abbreviation of the premolar-molar series, the index in *D. bicornutus* being 45, which is less than that in *D. amplus;* (2) apparent reduction or loss of median incisors.

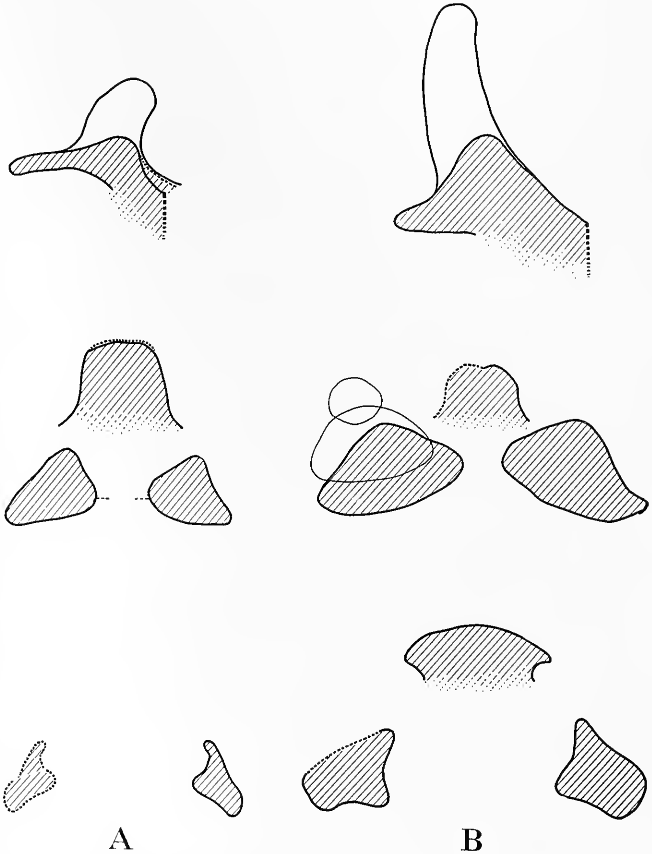


FIGURE 427.—Sections and contours of skull of *Diploclonus amplus*

A, Nat. Mus. 4710. In this supposed female the horns are relatively short, the connecting crest well developed, horn section trihedral, nasals broad, zygomata slender. B, Yale Mus. 12015a (type); a male, with horns relatively long, directed forward and placed far in front of the orbits, basal horn sections trihedral, connecting crest high, zygomata well expanded, nasals small and narrow. One seventh natural size.

A doubtful genus and phylum.—There is no question whatever of the affinities of these animals to *Brontops* and of their substantial proximity to this genus.

From the materials at hand, which are limited to four or five skulls at present, it is doubtful whether they should be separated as a distinct phylum of generic value. The question turns on whether the hornlet is a sport character or a permanently progressive character, which can be settled only by more extensive material than is now available. On the whole, it seems to be wisest at present to regard these species as a subphylum collateral with the main phyla of *B. dispar* and *B. robustus.*

Affinities with Brontops dispar and Allops marshi.—Among the chief resemblances to *Brontops dispar* are (1) the marked brachycephaly, especially in the widely expanding buccal processes of the zygomata, emphasized most distinctly in *D. tyleri* and *D. amplus;* (2) the marked backward prolongation of the occiput behind the widest portion of the zygomatic arches, which distinguishes these skulls at once from those of *Allops marshi* and *B. robustus* and relates them to *B. dispar;* (3) the short horns with rounded summits which partake of the general characters of those of *B. dispar,* although a tendency to broaden and flatten becomes marked in *D. tyleri* and extreme in *D. amplus.* The nasals show progressive abbreviation: they are elongate in *D. bicornutus,* more abbreviate in *D. tyleri,* and extremely abbreviate in *D. amplus.* Features of difference from *B. dispar* are not only the internal hornlets upon the horns but the somewhat more marked development of the connecting crest between the horns.

Unfortunately the records as to geologic distribution are very incomplete. The geologic level of the least progressive stage, *D. bicornutus,* is not recorded. The level of the intermediate stage, *D. tyleri,* is recorded as 35 feet above the Pierre shale, 200 feet below the summit of the *Titanotherium* zone; this would place this animal in lower B or even in A. The level of the most progressive species, *D. amplus,* is not recorded.

Distinctive characters of the species of Diploclonus.—This is not a monophyletic series, like *Menodus* or *Brontotherium;* it is diphyletic. The skulls at once seem to be distinguished from those of *Allops marshi* and *Brontops robustus* by the great backward extension of the occipital region behind the zygomata. The pit in the center of the vertex relates them to other species of *Brontops.* The progressive broadening of the zygomata closely parallels that of the other collateral phyla.

D. bicornutus (Osborn) is the most primitive form, with relatively long and narrow nasals, rounded and more erect horns, least expansion of the zygomatic arches, and least depression of the angular border of the jaw.

D. selwynianus (Cope) is a little-known animal from the Cypress Hills, Saskatchewan, represented only by the nasal bones, which are intermediate in size between those of *D. bicornutus* and *D. tyleri;* they resemble the nasals of *D. bicornutus* more closely in their narrow, elongate, and laterally decurved form.

D. tyleri (Lull) is an intermediate stage of evolution, characterized by relative abbreviation of the nasals, more anterior position of the horns, greater prominence of the hornlets, more widely arched zygomata, depression of the lower angular region of the jaw. This animal is a more pronounced development of the *D. bicornutus* type, the internal hornlets being larger, the horns much broader and more decidedly projecting forward. The geologic level of this animal is said to be 50 feet above the Pierre shale. It is probably from the middle levels, B.

D. amplus Marsh is distinguished by very short and obtuse nasals and a prominent internal hornlet on the horns, horns broadly divergent and compressed anteroposteriorly, excessively wide zygomatic arches, stout, recurved canines. The features of this progression as seen in the superior view of the skulls are displayed in Plate CVIII, A, and in Figure 391. This robust animal shows an extreme development of the characteristics of this subphylum. Massive skull, very broad zygomatic arches, very short horns, with a decided development of the internal hornlets. Probably belongs on the levels of Chadron of C.

Standard measurements in the Diploclonus phylum, in millimeters

	Upper teeth					Skull							Jaw					
	P^1–m^3	P^1–p^4	M^1–m^3	Canines, anterior vertical	Canines, anteroposterior diameter	Pmx to condyles	Zygomatic breadth	Cephalic (zygomatic) index	Nasals, tips to occiput vertex	Nasals, free length	Nasals, free breadth	Horns, external length	P_1–m_3	P_1–p_4	M_1–m_3	Canines, anterior vertical	Canines, anteroposterior diameter	Symphysis to condyles
D. amplus, Yale Mus. 12015a, ♂ (type)	?302	133	207	40	24	675	615	91	665	----	----	----	----	----	----	----	----	----
D. amplus, Nat. Mus. 4710, ♀	307	119	205	[a] 40	22	683	468	68	----	[a] 119	98	----	----	----	----	----	----	----
D. tyleri, Amherst Mus. 327, ♂ (type)	363	136	227	45	35	----	[a] 580	----	----	?140	?84	170	375	140	235	42	31	685
D. selwynianus, Ottawa Mus	----	----	----	----	----	----	----	----	----	115	93	----	----	----	----	----	----	----
D. tyleri, Am. Mus. 1081, ♂	355	127	222	----	----	710	608	85	[a] 690	130	----	192	----	----	----	----	----	----
D. bicornutus, Am. Mus. 1476, ♂ (type)	340	138	206	----	----	680	----	----	635	104	----	[a] 183	----	----	232	[a] 35	22	500
Percentage of change from Diploclonus bicornutus to D. amplus	−11	−6	0	----	----	0	----	----	----	----	----	----	----	----	----	----	----	----

[a] Approximate.

Measurements of skulls and jaws associated with or referred to the Diploclonus phylum, in millimeters

	Skull and upper teeth			Lower jaw and teeth				
	P^1–m^3	M^1–m^3	Symphysis to glenoid	Posterior canine to hyloid of m_3	P_1–m_3	M_1–m_3	Symphysis to condyle	Depth below m_3
D. tyleri, Amherst Mus. 327 (type)	363	227			375	235	685	
D. bicornutus, Am. Mus. 1476, ♂ (type)	340	206	500	[a] 325	[a] 343	232	500	154

[a] Estimated.

Diploclonus bicornutus (Osborn)

("*Megacerops*" *bicornutus* Osborn, 1902)

Plates CIV, CVII; text figures 196, 389, 397, 409, 426, 428

[For original description and type references see p. 231]

Geologic horizon.—Undetermined, probably middle beds (Chadron B).

Specific characters.—Skull index indeterminable from type; total length, 680 millimeters; length of grinding series, 340; index, 50. Nasals long and narrow (104 by 86 mm.). Horns subcircular (type) to transverse-oval (Am. Mus. 1081, ♂) in basal section; with anterior and internal hornlets; connecting crest moderately developed; horns placed anteriorly to orbits. Preorbital bridge of malar with a sharp edge. Occiput greatly produced backward.

This is the least specialized stage, one which is closest to *Brontops dispar* except in the narrow form of the nasals.

Observations on the measurements of Diploclonus bicornutus.—*Diploclonus* is a less conservative and less clearly distinguished phylum than *Brontops*, *Menodus*, or *Brontotherium*. Aside from the presence of a small secondary horn swelling, a character seen also in certain other skulls which are not referred to *Diploclonus*, the type of *D. bicornutus* presents a mingling of the characters of *Allops marshi*, *Brontops dispar*, and even in some features of *Menodus*. In comparison with these species the measurements of the type skull are given below:

Measurements of Diploclonus bicornutus, Brontops dispar, Allops marshi, and Menodus proutii, in millimeters

	D. bicornutus, Am. Mus. 1476, ♂ (type)	B. dispar		A. marshi, Am. Mus. 1445 (paratype)	M. proutii		
		Nat. Mus. 4248, ♂	Carnegie Mus. 92		Carnegie Mus. 3063, ♀	Nat. Mus. 4701	Nat. Mus. 4257
P^1–m^3	340	340		335	335		
P^1–p^4	138	140		135	135		
M^1–m^3	206	207		203	203		
Pmx to condyles	680	685		675	628		
Zygomatic index		78		69			
Nasal length	104		94	105		120	
Nasal breadth			102	100		125	
Horn length	183		188	113			150

The table shows that these specimens, which are referred to four genera, agree closely in dental measurements but differ in the proportions of their nasals and horns.

Characters of the type.—The type of *D. bicornutus* was long supposed to be female, but the canines and zygomata are stouter than in females of other species. The specific characters above set forth are based upon the type skull (Am. Mus. 1476). Associated with this type in the original description by Osborn as a paratype was the skull Am. Mus. 1081 (Pl. CV), which is now regarded as more nearly related to another species, *D. tyleri*.

The following description is thus based solely upon the type of *D. bicornutus*. The sex of this specimen is somewhat uncertain, but the anteroposterior diameter of the canine (506 mm.) indicates that it was a male.

The lateral compression of the type skull and jaws (Am. Mus. 1476) prevents the determination of the proportions of the skull or of the zygomatic index. The wearing of the grinders indicates that the specimen represents the eighth stage of growth. Thus we conclude that all the progressive characters are very distinctly developed and indicated.

Skull.—The relatively long, narrow proportions of the skull as seen from above (Pl. CIV) are due partly to lateral crushing. Even with allowance for some deformation the skull is not very broad. As seen in side view (Pl. CIV) it combines the long nasals of *A. marshi* with the vertically elongate horns and backward expanded occiput of *D. dispar*. An anterior hornlet is plainly visible. The tuberosities on the inner sides of the horns are only faintly developed, and were it not for comparison with the specimens of *D. tyleri* they would hardly be noticed.

Similar anterior tuberosities, or hornlets, are observed in certain male skulls of *M. giganteus* (Am. Mus. 505). As seen from above (fig. 444) the parietal vertex is moderately broad. A very distinctive feature is a sharp preorbital malar bridge. There is considerable expansion behind the orbits, as in *B. dispar;* as in all aged individuals, the supratemporal crests are sharp and overhanging. The summits of the occipital pillars are rugose and greatly expanded. In lateral view (Pl. CIV) the postglenoid process is seen to be relatively narrow and exhibits a short surface of contact with the post-tympanic. On the palatal surface of the skull the vomer apparently does not extend back to overlap the parasphenoid. There is only a slight basisphenoid rugosity.

This skull shows group resemblances to *Menodus trigonoceras* as follows: (1) Nasals long, set very high; (2) orbit very large; (3) tooth row very long (dental index 50, 46–51 in *M. giganteus*); (4) zygomata not expanded and in side view pitching sharply downward and forward; (5) lower jaw resembling that of *Menodus* in the well-developed chin and depressed angle.

Dentition.—The incisor alveoli are not well defined. The canines are much worn; they exhibit crowns of rounded form. The absence of external cingula on the premolars may be due in part to the extreme wear. The internal cingula are well developed. The tetartocone developments on the premolars are approximately of the same stage as in *B. dispar.* In m^3 the hypocone is an elevated part of the cingulum.

Summary.—This skull may be that of an old male, affording an example of a progressive offshoot of one of the *Brontops* lower beds phyla.

Diploclonus selwynianus (Cope)

(*Menodus selwynianus* Cope, 1889; *"Megacerops?" selwynianus* Osborn, 1902)

Text figure 185

[For original description and type references see p. 225]

Type locality and geologic horizon.—Swift Current Creek, Saskatchewan; *Titanotherium* zone.

Specific characters.—Nasals long (free length about 115 mm.), narrow (free width 75 mm.), abruptly rounded in front and sharply decurved at the sides, with a deep longitudinal inferior cavity.

The chief ground for referring the uniquely narrow nasals of the type of this species to *Diploclonus* is the resemblance they bear to those of *Diploclonus bicornutus,* which is closer than to that of any other form. The resemblances in the nasal bones consist in (1) the narrowness, (2) the deep longitudinal inferior cavity, (3) the decurved sides, and (4) the massive and decurved tips.

Cope's description of this specimen from the Swift Current Creek region is cited in full elsewhere (p. 226). To this description may be added the following observations. The inferior view (fig. 185) exhibits the paired cavities, or frontal antrum, at the junction of the nasals, frontals, and maxillaries; the suture between the nasal bones has entirely disappeared. These nasals are very characteristic and quite different from those of *Menodus* or *Megacerops coloradensis.* Lambe describes the type as follows (1908.1, p. 47):

> The coossified nasal bones of one individual constitute the type of this species. They are long and narrow, abruptly rounded in front, and bent downward at the sides. The lower surface is deeply excavated in a longitudinal direction.

Diploclonus tyleri (Lull)

(*Megacerops tyleri* Lull, 1905)

Plates XXXVII, CV–CVIII; text figures 200, 201, 397, 409, 426, 428, 630, 639

[For original description and type references see p. 234. For skeletal characters see p. 675]

Geologic horizon.—Recorded as 35 feet above the Pierre Cretaceous, or 165 feet below the summit of the *Titanotherium* zone. Regarded by Lull as in the upper part of the lower *Titanotherium* zone, but more probably belonging in the level of the middle beds.

Specific characters.—Brachycephalic. Zygomata widely arching. Nasals abbreviated or broad; free length, 140 millimeters. Grinding series, 363. Horns shifted forward; distinct hornlets on the inner surfaces; horn section at the base trihedral to transversely oval, with sharp outer angle. Canines stout, recurved. Superior incisors 2–1.

General characters.—This animal is certainly a member of a collateral branch of the *B. dispar* series, agreeing with the aged specimens of the typical *B. dispar* even more closely than the type of *D. bicornutus.* The species appears to represent a stage of phyletic evolution intermediate between that of the more primitive *D. bicornutus* and the more progressive *D. amplus.* This conclusion, however, awaits confirmation by additional evidence.

Materials.—The type of this specific stage or ascending mutation is the fine skeleton and anterior portion of the skull in the Amherst collection (No. 327). Apparently belonging to the same stage is the finely preserved skull and jaws (Am. Mus. 1081) originally described by Osborn as a paratype of *D. bicornutus* but presumably representing a more recent or progressive stage of evolution.

Observations on the measurements of Diploclonus tyleri.—The two skulls referred to *Diploclonus tyleri* differ from the type of *D. bicornutus* in having larger molars and more massive horns. They differ from the type of *D. amplus* in having larger molars. The type skull and jaw in side and top views approaches that of *Brontops robustus,* except that it has a well-developed pair of accessory horn swellings. The characters of the incisors, canines, postcanine diastemata, and premolars further suggest affinity with *B. robustus;* but the anteroposterior measurements of the dentition differ from those of *Brontops* and agree with those of *Menodus trigonoceras,* as shown below:

Measurements of Diploclonus tyleri and Menodus trigonoceras, in millimeters

	D. tyleri		M. trigonoceras, Nat. Mus. 4291, ♂
	Amherst Mus. 327, ♂ (type)	Am. Mus. 1081, ♂	
P^1–m^3	363	355	360
P^1–p^4	136	127	136
M^1–m^3	227	222	224
Pmx to condyles		680	770

This agreement with *Menodus trigonoceras*, taken in connection with the relatively slender manus and pes of the type of *D. tyleri* as compared with *B. robustus*, constitutes one of the many facts which suggest the possibility of occasional hybridization among the genera *Brontops*, *Menodus*, and *Allops* (W. K. Gregory).

Description of the type.—Lull's specific definition may be cited in full (Lull, 1905.1, p. 445):

> Horns well in front of orbits, directed somewhat forward and outward, an elongate oval in basal section with the long axes in line, rounded oval at the summit. Hornlets quite conspicuous, on the inner face of the horns midway between the base and summit. Connecting crest low and inconspicuous. Nasals broad, well rounded in front, and but slightly arched beneath. Zygomata expanded and deep, with a well-rounded outer face. Dentition: Superior incisors represented by the deep and well-defined median alveoli and by the lateral teeth, which remain in place and which have hemispherical crowns which show little sign of wear. The canines are lanceolate, with a well-developed postero-internal cingulum. There is a short diastema in front of, and a longer one behind, the canine. Premolars with a smooth internal cingulum, less pronounced in the middle of the tooth and with no external cingulum. The deuterocone is well developed, while the tetartocone, especially of premolar 4, is inconspicuous.
>
> The jaw is deep and robust, with the alveoli of two incisors, probably of the second and third, deep and distinct. There is no space between the lateral incisors and the canine, though between the two median alveoli a considerable gap occurs. There seems to have been a small diastema behind the lower canines, which are lanceolate, though with a less prominent cingulum and not so strongly recurved as the upper ones.

The same author observes that the creature most nearly resembles *D. bicornutus* (Osborn) and *D. amplus* Marsh, having certain characters suggestive of each; but there are enough important differences to render it distinct and to warrant the erection of a new species for its reception. The dental formula is I$\frac{2}{2}$, C$\frac{1}{1}$, P$\frac{4}{4}$, M$\frac{3}{3}$; the two median superior and all of the lower incisors are represented by deep inclosed alveoli, as if the teeth had dropped out after death. Toward the base the horns are oval to triquetrous in section; toward the summit they become rounder and roughened at the extremities. "It would seem," observes Lull, "from the similarity of the roughened patches to those on the rhinoceros nasals, as though the entire prominence had been clothed with skin, with two rhinoceros-like horns, a larger one at the apex and a smaller one on the summit of the hornlet."

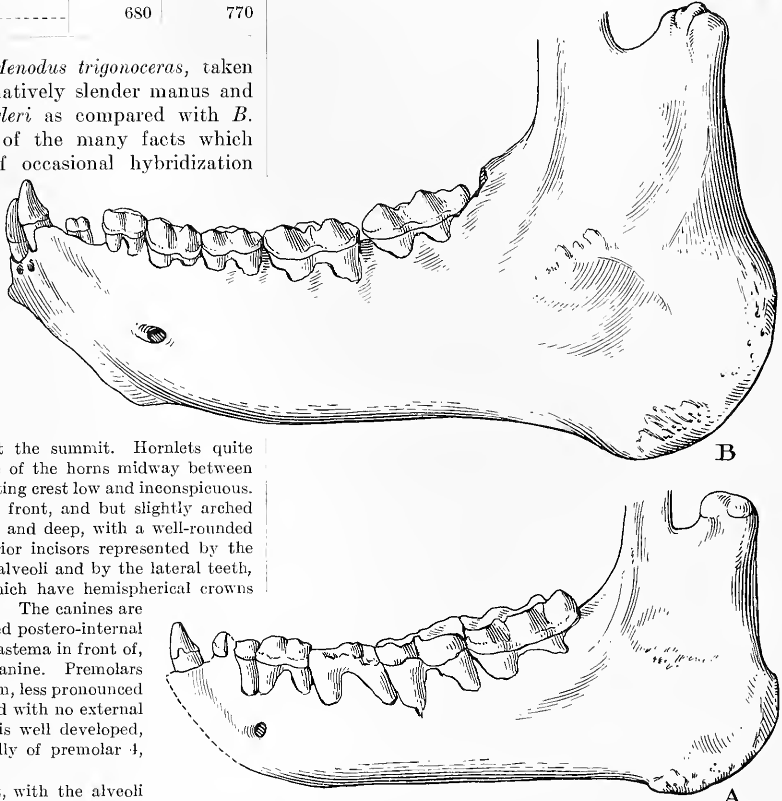


FIGURE 428.—Lower jaws of *Diploclonus bicornutus* and *D. tyleri*

A, *Diploclonus bicornutus*, Am. Mus. 1476 (type); animal very old and hence the angle is broad and prominent (compare the aged type of *M. torvus*, fig. 437, *A*). Canines stout and conical, external cingula not sharply separated from the ectoloph. B, *D. tyleri*, Amherst Mus. 327 (type); broadly resembles *B. robustus*. A diastema in front of p_1. One-fifth natural size.

Characters of referred specimen (Am. Mus. 1081).—This specimen was employed by Osborn as a paratype of *D. bicornutus*. Skull broad, index 85; tooth row elongate (367 mm.); index 50. Condyles to incisive border 710 millimeters. Horns anteriorly placed and directed obliquely forward. It is important to note that the plaster restoration of the nasals (Pls. CV, CVII) and of the anterior part of the zygomata prevents a true determination of the characters of these parts of the skull. This specimen is also of advanced age and shows many senescent characters. The teeth are extremely worn and reveal nothing decisive; the cingula of the premolars are smooth and worn down. The horn tips are extremely rugose, and the internal hornlets are well marked (fig. 426, B). The occipital vertex is rugose, with deep paired indentations and knobs. The zygomata are greatly swollen transversely. As in many aged specimens of *Brontops*, a single large incisor is preserved in either premaxilla; the superior incisive formula was thus 2–1.

Diploclonus amplus Marsh, 1890

("*Allops*" *amplus*, Osborn, 1902)

Plates CVIII–CX; text figures 187, 375, 389, 391, 394, 409, 427

[For original description and type references see p. 227]

Geologic horizon.—*Titanotherium* zone, level not recorded.

Specific characters.—Skull extremely brachycephalic, zygomatic-basilar index 91. Nasals greatly abbreviated and narrow, horns broadly oval in basal section, directed upward and outward, with conspicuous internal hornlets. Grinding series relatively reduced, length 302 millimeters, index 45. Upward flexure of premolar series anteriorly pronounced. Zygomata extremely broad with convex buccal expansions.

General characters.—The nasofrontal section of the type skull first suggested comparison with a form transitional between *Brontotherium gigas* and *B. curtum*, but numerous other characters forbid such a phyletic reference, especially the long-pointed canines, 40 millimeters (the type was a male), the presence of only one superior incisor on each side, the retarded development of the tetartocones of the premolars, the rounded tips of the horns. All these characters remove the animal from relationship with *Brontotherium, Menodus*, or *Megacerops* and indicate its affinity to *Brontops;* this is confirmed by more searching study of the character of this type, but especially by the existence of the more primitive and transitional forms *D. bicornutus* and *D. tyleri* above described.

Diploclonus amplus is by far the most progressive species in this phylum, as demonstrated by (1) the extreme abbreviation of its nasals, (2) the strong development of the connecting crests between the horns, (3) the greater prominence of the internal hornlets, and (4) the transverse-oval expansion of the basal horn section, which has now reached an extreme stage, parallel to that observed in *Brontops robustus.* This species, however, is readily distinguished from *Brontops robustus,* in common with other members of the phylum to which it belongs, by the marked backward elongation of the occipital region behind the zygomatic arches.

This specimen tends to confirm the hypothesis that the species grouped under *Diploclonus* formed one or more subphyla parallel with *Brontops.*

Materials.—The type skull of *D. amplus* in the Yale Museum (No. 12015a) is undoubtedly a male. A supposed female skull is found in Nat. Mus. 4710. The type is the only specimen which we have yet seen that certainly belongs to this species.

Observations on the measurements of Diploclonus amplus.—The type and only known male skull of this species is very brachycephalic, although crushing may have contributed to the extremely high zygomatic index (91).

The male skull approaches the paratype of *Allops marshi* in the anteroposterior measurements of the dentition, but in its general conformation it rather suggests *B. robustus.* The nasals are reduced in size.

Measurements of Diploclonus amplus and Allops marshi, in millimeters

	D. amplus, Yale Mus. 12015a (type)	A. marshi, Am. Mus. 1445 (paratype)
P^1–m^3	(?)302	335
P^1–p^4	133	135
M^1–m^3	207	203
Pmx to condyles	675	675
Zygomatic index	(?)91	69

Detailed description of the type.—As seen from above the skull is broad and short in proportion, the index, 91, expressing its marked brachycephaly. We are struck by the strong divergence of the horns, a feature which is probably intensified by vertical crushing. They are slightly convex on the anterior surface, with very prominent external ridges. They are united by a very deep connecting crest, as exhibited in the section. The prominent tuberosity or hornlet employed by Marsh as a generic character is 14 centimeters below the tip of the horns; it is especially well developed on the left side, measuring 37 millimeters anteroposteriorly and 35 transversely. A very distinctive feature of the horn is the sharpness of the preorbital crest. As seen from above (Pl. CVIII, A) the zygomata project widely outward. A slightly distorted section of the buccal processes is shown in the diagram. The upper surfaces are somewhat flattened. In the middle of the vertex is a slight tuberosity which probably indicates the vestige of the pit so characteristic of members of the *Brontops* phylum. The occiput is deeply excavated with stout lateral pillars and rugose summits. It is considerably produced backward behind the zygomata. In inferior aspect the posterior nares are seen to open just opposite the third molar. The pterygoid wings of the alisphenoid are short, rugose, flaring strongly outward; the presphenoid is keeled by the vomer, and there is a very prominent rugosity at the junction of the basisphenoid and basioccipital, as seen in *Brontops* and *Menodus.*

Dentition.—Since the animal is of advanced age, we find just within the canine a large alveolus which certainly contained a large incisor tooth. In early life there were probably two incisors, separated in the median line by a diastema. The canines are long (40 mm.) and pointed, with a postero-internal cingulum. The first premolar is a relatively stout, persistent, bifanged tooth, thrust closely against the canine, partly by crushing; the tetartocone of p^4 occupies a very small part of the inner face of the crown, as in *B. dispar.* Illustrating the mechanical ineffectiveness of the internal cones of the molar teeth is the fact that while the ectolophs are worn out of proportion in m^{1-3}, the internal cones of m^2, m^3 are still unaffected by wear. The hypocone of m^3 is quite prominent and still connected with the cingulum.

The abbreviation of the premolar-molar series is a retrogressive character which this phylum apparently shares with the *Brontotherium* phylum. The molar series, measuring 302 millimeters, is actually shorter (index 45) than that in the much less specialized form *D. bicornutus,* in which the teeth measure 340 millimeters with an index of 50. Similarly, in the great skulls of *Brontotherium* the tooth row is actually shorter in the highly specialized *B. platyceras* than in the ancestral species *B. gigas.*

Supposed female skull (Nat. Mus. 4710).—The result of searching comparison and measurements is the reference of this skull as a female of *Diploclonus amplus.* The morphologic difference is about as great as between the type of *D. bicornutus* and that of *D. tyleri.*

The affinities to *Brontops* in this female skull are shown in the following points: (1) Small lateral incisors persistent; (2) canines of rounded form; (3) premolars with retarded tetartocones, rounded internal and fainter external cingula; (4) horns of small size, with long, flat external face and rounded top section; (5) orbits with broad postorbital processes; (6) a broad zygomatic shelf, and downward extension of the occiput as in *B. dispar;* (7) rugosity on the basisphenoid, with the vomerine bridge carried well back.

The special resemblances of this supposed female to *D. amplus* are (1) the general similarity of the horns in respect to their position, basal sections, and connecting crests; (2) the smaller zygomatic section; (3) the sharp preorbital malar bridge.

The chief points of difference between this specimen (Nat. Mus. 4710) and the Yale type of *D. amplus,* which is a male, are (1) absence of hornlets, perhaps a sexual distinction; (2) greater width, flatness, and slenderness of the nasals, which may be attributed in part to the nondevelopment and lack of forward advancement of the horns; (3) smaller buccal processes of the zygomata, which, however, in section suggest those of *D. amplus* on the inner and inferior faces especially. (See fig. 427.)

The reference of this skull to *D. amplus* is therefore still provisional.

Subfamily **MENODONTINAE**

Titanotheres chiefly of lower Oligocene age, reaching their climax in the upper levels of the *Titanotherium* zone (Chadron formation). Distinguished by narrow heads (mesaticephalic) diverging into phyla with long heads (dolichocephalic) and broad heads (brachycephalic). Horns short, slightly shifting forward, broadly trihedral in basal section and widely divergent at the summits. Nasals typically elongate, broad and square distally, secondarily abbreviate. Incisor teeth reduced or vestigial. Grinding teeth with prominent cingula. Premolars with accelerated tetartocones.

This is the second branch of the short-horned titanotheres, which in many respects is closely related to the first branch, the Brontopinae; in others it appears to present original characteristics of its own. It is typified by the genus *Menodus,* also known as *Titanotherium,* and includes the related genus *Allops.* Between the two are transitional forms of subgeneric rank described as *Menops* and *Anisacodon* by Marsh. The resemblances of the original species of these two main phyla of *Menodus* and *Allops,* namely, *Menodus heloceras* and *Allops walcotti,* both occurring in the very base of the *Titanotherium* zone, are relatively close to *Brontops brachycephalus.* Yet it would appear that the Menodontinae diverged from the Brontopinae before the end of Eocene time. While the *Menodus* phylum maintains its mesaticephalic and dolichocephalic form throughout, members of the *Allops* phylum become brachycephalic and converge toward members of the *Brontops* phylum. Thus *Allops crassicornis* resembles *Brontops robustus* in its proportions.

The ancestors of *Menodus* and of *Allops,* although not readily distinguishable in the base of the *Titanotherium* zone (Chadron A), indicate that the divergence took place in late Eocene time, when the following main distinctions were established:

Menodus phylum

Primitively mesaticephalic, progressively dolichocephalic.
Incisors $\frac{0-0}{0-0}$, extremely vestigial, buried beneath the gums.
Canines very prominent, rounded, or compressed transversely.
Nasals typically broad and elongate.
Skeleton tall.
Feet stilted, of mediportal type.

Allops phylum

Primitively mesaticephalic, progressively brachycephalic.
Incisors reduced, $\frac{2-1}{2-1}$, with rounded summits.
Canines prominent, compressed anteroposteriorly, expanded transversely.
Nasals progressively abbreviating.
Skeleton little known.
Feet broader.

SYSTEMATIC DESCRIPTIONS OF GENERA AND SPECIES IN THE ALLOPS PHYLUM

Allops Marsh

Plates XX, XXI, XXXVIII, XC, CXI–CXXII, CXXXII; text figures 184, 189, 197, 207, 375, 378, 381, 387, 389, 391, 393, 394, 397, 399, 409, 413, 429-434, 608, 612, 615, 712

[For original description and type references see p. 224. For skeletal characters see p. 678]

Generic characters.—Mesaticephalic, progressively brachycephalic. Lateral pair of superior incisors persistent; canines compressed anteroposteriorly, flattened on posterior face; grinding teeth with moderately distinct cingula; premolars simpler than in *Menodus* but with progressive tetartocones; molars with elevated and pointed cusps, the transverse slightly exceeding the anteroposterior diameters. Nasals broad and intermediate in length, abbreviating in progressively brachycephalic types; horns short, broadly trihedral in section, directed obliquely outward.

This genus was established in 1887 by Marsh, who selected the species *A. serotinus* as the genotype. In 1891 this author strengthened the genus by adding the species *Allops crassicornis*, a more advanced form. In 1902 Osborn described the species *Megacerops marshi*, named in honor of Professor Marsh, which was later referred to the *Allops* phylum. Finally, in 1917, Osborn added the most primitive species *Allops walcotti*, named in honor of the former Director of the United States Geological Survey. Although these species are grouped within a single genus, they apparently do not constitute a direct phyletic succession. There are also puzzling affinities to *Menops varians*, the type of the genus *Menops*.

Progressive brachycephaly is characteristic of these scattered and loosely related species, as shown in the following ascending series in the *Titanotherium* zone:

	Zygomatic index
Upper beds: *Allops crassicornis* (type), brachycephalic	76
Upper beds: *Menops varians*, subbrachycephalic	73
Summit of middle beds: *Allops serotinus* (type), subbrachycephalic	72
Middle beds, lower levels: *Allops marshi*, mesaticephalic	64–69
Base of lower beds: *Allops walcotti* (type), mesaticephalic	(?)

Geologic distribution of Allops.—*Allops walcotti* Osborn: *A. walcotti*, from the lower levels of the lower *Titanotherium* zone, is a small, very primitive form, distinguished by a narrow head, long, broad nasals, and relatively long face, horns with elongate oval section, and two superior incisors.

Allops marshi (Osborn): *A. marshi*, from the upper levels of the lower beds, is distinctly mesaticephalic. Nasals long and broad, horns subtrihedral in section, premolars more progressive than in *A. walcotti*. This animal is finely represented by eleven skulls in several museums, which present a series of ascending mutations.

Allops serotinus Marsh: In *A. serotinus* the nasals are still elongate and the horns are slender, elongate, subtrihedral, preserving the section characteristic of *A. marshi*. The premolars are still in a retarded stage of evolution. This species is represented by five specimens, two of which appear to present transitional stages toward *A. crassicornis*, as follows: Skull Am. Mus. 520 appears to be in a transitional stage between *A. serotinus* and the more brachycephalic species *A. crassicornis*, for the horns are in an intermediate stage of development and the dental measurements have the degree of development of the premolar tetartocones coincident with those in *A. serotinus*. Transitional skull Nat. Mus. 4938 nearly equals in some of its measurements the *A. crassicornis* type, but the premolar tetartocones are still decidedly retarded.

Allops crassicornis: The type specimen of the species *A. crassicornis* is distinguished both by the more massive proportions of the skull, the obtuse, short and massive horns, the abbreviation of the nasals, and especially by the more advanced development of the tetartocones upon the premolars. It is by no means certain that this massive, broad-headed animal is a descendant of the types named above.

Stratigraphic position of species of Allops

Stage	Level	Species
	Upper.	?A. montanus.
C	Middle.	?[Menops varians].
	Lower.	?A. crassicornis.
	Upper.	A. serotinus.
B	Middle.	
	Lower.	A. marshi.
	Upper.	A. marshi.
A	Middle.	
	Lower.	A. walcotti.

Progressive phyletic characters.—Members of the *Allops* phylum are known from the whole *Titanotherium* zone. In general, the skull and teeth are intermediate in character between the typical *Brontops* and typical *Menodus.* The skull in males, originally mesaticephalic, shows a marked progression toward brachycephaly, the zygomatic indices rising from 64 to 76. The nasal bones in the males progressively shorten as in members of the *Brontops* phylum. The broadly trihedral basal section of the horns connects these elements with *Menodus* rather than with *Brontops.* The face is relatively longer than in *Brontops* and more abbreviate than in *Menodus.* As in *Brontops* the incisors are round topped with a formula of 2–1. One of the most distinctive features of *Allops* is the transversely lanceolate form of the canine teeth which enables us to connect *A. walcotti* with this series rather than with the *Menodus* series. The opposite grinding series are rectilinear, or nearly parallel, as in *Menodus.* While the grinders approach those of *Menodus* in having elongate or subhypsodont crowns they are less dolichocephalic in proportion—that is, the transverse diameters of the molar teeth slightly exceed the anteroposterior diameters, whereas in *Menodus* the reverse is the case. The dental index is high—in males 46–47, in females 45–50. The premolars exhibit pronounced external cingula as in *Menodus.*

Briefly, these animals resemble *Menodus* in the trihedral shape of the horns and in numerous other characters. They differ from the true *Menodus* in the progressive abbreviation of the nasals, in the brachycephaly of the zygomatic arches, in the retention of at least one pair of upper incisor teeth. Thus they are provisionally assigned an intermediate phyletic position.

Several of the more advanced or upper-level specimens of *A. serotinus* were discovered in the overflow deposits of the upper *Titanotherium* beds rather than in the main sandstone or channel deposits. This may afford some clue to the rarity of these crania.

Characters of the genotype.—In describing the genotype, *Allops crassicornis,* in 1887 Marsh characterized it as a skull resembling in general that of *Menodus giganteus* but as differing in the possession of a single superior incisor tooth. The type possesses a pair of well-developed second incisor teeth which are always vestigial in *Menodus* but present in the subgenus *Menops.* There are other still more important differences, which will be enumerated in the description of this species.

Affinities of Allops.—*Allops marshi* has a very low zygomatic index (64–69) in comparison with *Allops serotinus* (72) and *A. crassicornis* (76), a fact which suggested the theory that *A. marshi* may represent the females of some other species such as *B. dispar.* Some of the smaller skulls referred to *Allops marshi* are with difficulty distinguishable from females of *Brontops brachycephalus;* others approach *B. dispar,* with which they agree in dental measurements (see above); many are also strongly suggestive of *Menodus trigonoceras* in the characters of the premolars and molars and in the horns. All known skulls of *A. marshi* are distinctly inferior in size to those of *A. serotinus.* As shown by the detailed characters of the skull and dentition and by the tables of measurement, *A. serotinus* and *A. crassicornis* combine the characteristics of *Brontops* and of *Menodus* in a remarkable manner. They exhibit the characteristic horn sections and distally squared nasals of *Menodus,* the sharp premolar and molar cingula of *Menodus,* combined with the broader skull and broader grinding teeth, expanded zygomata, shortened free nasals, and retained incisors of *Brontops.* The form of the canine also is more or less intermediate between the conical canine of *Brontops* and the sharp-edged canine of *Menodus.* The type and only known specimen of *Menops varians* resembles *Allops crassicornis* in the thick outwardly divergent horns, in the wide skull (index 73), in the wide premolars and molars, in the reduplicate tetartocone of p^4. On the other hand it approaches *Menodus giganteus* in the anteroposterior dimensions of the dentition and skull and in the nasal and horn sections, so that it is placed in the genus *Menodus.*

These facts suggest the possibility that some of the forms called *Allops* may represent a hybridization between species of *Brontops* and of *Menodus.*

Measurements, in millimeters, of lower jaws and teeth correlated with and referred to Allops

	A. marshi, Nat. Mus., Gidley's skull G	?A. walcotti, Nat. Mus., 4247
Posterior canine to hypoconulid of m_3	320	303
P_1–m_3	335	298+
M_1–m_3	225	200
Symphysis to condyle	375	510
Depth below m_3	94	108

Standard measurements in the Allops phylum,[a] *in millimeters*

	Upper teeth					Skull							Jaw and teeth					
	P^1–m^3	P^1–p^4	M^1–m^3	Canines, anterior vertical	Canines, anteroposterior diameter	Pmx to condyles	Zygomatic breadth, transverse	Cephalic (zygomatic) index	Nasal tips to occiput vertex	Nasals, free length	Nasals, free breadth	Horns, external length	P_1–m_3	P_1–p_4	M_1–m_3	Canines, anterior vertical	Canines, anteroposterior diameter	Symphysis to condyles
A. crassicornis, Nat. Mus. 4289, ♂ (type)	370	150	220	45	20	750	[b]570	76			143							
A. crassicornis, Nat. Mus. 2117, ♂	350	148	217	44	30					72	146	210						
A. crassicornis, Nat. Mus. 4709, ♂	350	142	213															
A. serotinus, Nat. Mus. 4938, ♀	335	131	210	38	23	739	[b]500	72	695	96	137							
A. serotinus, Am. Mus. 520	330	133	206	36		720	565	78	710	68	106							
A. serotinus, Nat. Mus. 2151, ♀	330	[b]140	196	26	20	665	430	64	648	115	118							
A. serotinus, Nat. Mus. 4251, ♂ (type)	330	140	195	40		705	525	74	690	81	133	240						
?A. (dispar) serotinus?, Nat. Mus. 1217			196			+702									230			
A. marshi, Am. Mus. 1445, ♂ (paratype)	335	135	203	37	[b]22	675	465	69	615	105	100	113						
A. marshi?, Nat. Mus. 4254, ♂	323	133	203															
A. marshi, British Mus. 4446–4447	323	129	198		23	663	427	64	620	99	105	140						
A. marshi?, Nat. Mus. 4738	320	126	205	35	24	660			545	93	108							
A. marshi, Carnegie Mus. 289	320	130	200			665	430	64	625	112			365	127	240	31	28	
A. marshi?, Nat. Mus. 4942	318	133	193															
A. marshi?, Nat. Mus. 8314	313	132	179	34	22	662	448	67					335	113	225	35	20	375
A. marshi?, Nat. Mus. 1213, ♀	317	129	194			655	420	64		98								
A. marshi, Harvard Mus., ♂	315	131	183			675	465	69										
A. marshi, British Mus. 5743M	[b]310	126	192	33	23	[b]640							310	115	207	33	20	520
A. marshi, Am. Mus. 501, ♀ (type)	310	122	191	34	25	673	450	67	625	100	105	105						
A. marshi, Field Mus. 6900	310	?80	185			655	[b]440	66	620	103		125	330					
A. marshi?, Carnegie Mus. (?) 341, ♀	308	124	186	27	19	643	?476	?74	596		103	97						
A. marshi?, Nat. Mus. 1215, ♀	300	119	185	34	20	630	450	71										
A. walcotti, Nat. Mus. 4260, ♂ (type)	285	112	169			640	[b]340		585	105	98	100						
A. walcotti, Nat. Mus. 8753		119		34														
Percentage of change from Allops walcotti to A. crassicornis	+30	+34	+30			+17	+67			−11	+40	+240						

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[a] *Allops*, like *Diploclonus*, is a less clearly consecutive and distinguished phylum than *Brontops*, *Menodus*, or *Brontotherium*. For observations on the measurements see p. 507.

[b] Estimated.

The Allops phylum as represented in the Hatcher collection of 26 skulls and lower jaws from the Chadron formation in the United States National Museum

Genus and species	Catalog No.	Material
A. crassicornis Marsh	4289, ♂	Skull. Type.
Do	4709, ♂	Skull. Measurements agree with type. Canine not typical.
Do	8740, ♂	Skull, right half of jaw. Agrees in size with type. Nasals, upper canines, and incisors lacking. Specific reference doubtful.
Do	2117, ♂	Skull.
A. serotinus Marsh	4938, ♀	Skull. Horn like that of A. crassicornis.
Do	2151, ♀	Skull.
Do	4251, ♂	Skull. Type.
Do	1226, ♂	Anterior part of skull.
Do	8318, ♀	Skull. Measurements agree with A. serotinus, female. Canine not typical. Specific reference doubtful.
Do	4945, ♀	Skull. Same size as large Brontops dispar. Specific reference doubtful.
Do	8731, ♂	Anterior half of skull and jaws.
A.? serotinus Marsh	8777, ♀	Pair of jaws.
A. marshi (Osborn)	1215, ♀	Skull and teeth. Measurements agree with A. marshi. Larger than B. brachycephalus.
Do	8759, ♂	Skull. Larger than any specimen of A. marshi; approaches A. serotinus in molars.
Do	4252, ♂	Skull. Resembles paratype of A. marshi.
Do	8737, ♂	Skull and jaws, left humerus, and pelvis. Close to type. Molars same length as those of Brontops dispar.

The Allops phylum as represented in the Hatcher collection of 26 skulls and lower jaws from the Chadron formation in the United States National Museum—Continued

Genus and species	Catalog No.	Material
A. marshi (Osborn)	1213, ♀	Skull. Tooth measurements agree with A. marshi. Slender zygomatic arch.
Do	8798	Right lower jaw and symphysis.
Do	8317?	Skull. Generic reference doubtful in absence of canines and nasals.
A.? marshi? (Osborn)	4738	Skull. Agrees in measurements with other skulls of A. marshi.
Do	4942	Upper teeth.
Do	4778	Skull. Very young individual. Generic and specific reference doubtful.
Do	4254, ♂	Skull. Vestigial lateral superior incisors. Generic and specific reference doubtful.
A. walcotti Osborn	4260, ♂	Skull. Type advanced in age; see paratype (No. 8753).
Do	4247, ♀	Jaws.
Do	8753	Nearly complete upper dentition (i^2–m^2). Paratype. Palate slightly smaller than in type. Canine measurements very characteristic of the genus.

Allops walcotti Osborn

Plates XX, XXI, CXI, CXII: text figures 207, 389, 391, 394, 397, 409, 413, 429, 430

[For original description and type references see p. 241]

Geologic horizon.—Lower *Titanotherium* zone (Chadron A) of South Dakota.

Specific characters.—Premolars with small tetartocones; p^1–m^3 285 millimeters. Incisors $\frac{2}{0}$. Horns elongate oval, no connecting crest. Mesaticephalic. Nasals elongate, broad. Face relatively elongate.

The type skull of this species (Nat. Mus. 4260) from Chadron A is narrow and elongate, partly owing to lateral crushing. This feature conceals its resemblance to *Allops marshi*, which is apparent in other features—namely, (1) primitive, long nasals, (2) horns primitively short and obliquely oval, (3) large lateral incisor (i_2) and small first (i_1) or median incisor, (4) premolars accelerated, tetartocones more advanced than in *Brontops robustus* of level C.

Observations on the measurements of Allops walcotti.—The type of this species exhibits the following measurements in comparison with skulls of *B. brachycephalus* and *Menodus heloceras*, which shows that the type of *Allops walcotti* has relatively large premolars and small molars.

Measurements of Allops walcotti, Menodus heloceras, and Brontops brachycephalus, in millimeters

	A. walcotti, Nat. Mus. 4260 (type)	M. heloceras, Am. Mus. 14576	B. brachycephalus	
			Nat. Mus. 4940, ♀	Nat. Mus. 4261, ♂ (type)
P^1–m^3	285	265	265	280
P^1–p^4	112		101	[a] 104
M^1–m^3	169	170	160	178
Pmx to condyles	640	603		580
Nasal length	105	132		
Horn length	100	70	102	85
P^4, ap.×tr	35×51		32×51	33×53
M^3, ap.×tr	60×61		62×70	68×73

[a] Estimated.

The skull is crushed laterally, but probably had a low zygomatic index—that is, it was mesaticephalic. While its reference to *Allops* requires confirmation, its nearer affinities appear to be with this genus rather than with *Brontops* or *Menodus*. The external cingula of the premolars are not as sharply defined as in other primitive members of the menodontine group.

Geologic and geographic distribution.—This species is represented at present by a single skull, the type (Nat. Mus. 4260), which is recorded as probably from the lower levels (A) of the lower *Titanotherium* zone of South Dakota.

Comparison with other species.—This animal should naturally be compared with other titanotheres from the lower beds. It is readily distinguished from *B. brachycephalus* by a number of characters as follows: (1) The skull is much more dolichocephalic, a feature that is intensified by lateral crushing (see below); (2) the nasals are long and subquadrate in form; (3) the individual measurements of the grinding teeth show that the series throughout is somewhat narrower than the grinding series in *B. brachycephalus*.

These contrasts with the broad-skulled *B. brachycephalus* naturally suggest comparison of this animal with primitive members of the long-skulled *Menodus* phylum, such as *M. heloceras*, remains of which from the lower *Titanotherium* zone are sparsely known. Comparison with *M. heloceras* shows that *A. walcotti* possesses the following distinctions: (1) Horns more elongate-oval in section, less trihedral; (2) no connecting crest between the horns; (3) alveoli for two incisor teeth of considerable size (incisors are extremely vestigial in the *Menodus* phylum).

There remains the comparison with *Allops marshi*, the form to which, on the whole, this cranium seems to present the largest number of resemblances. The animal differs from *A. marshi* in the inferior dimensions of the dental series as well as in the detailed proportions of the teeth and the characters of the premolars, but it appears to be an older and more primitive form which belongs to the *A. marshi* phylum. In the horn section, in the proportions of the nasals, in the shape of the canine teeth it strongly resembles *A. marshi.*

At the same time *Allops walcotti* presents certain resemblances to *Menodus heloceras* and was long regarded by the author as ancestral to *Menodus,* which it foreshadows in its apparent dolichocephaly and in the strongly developed external cingula of the premolars as well as in the somewhat accelerated premolar tetartocones.

Description of the type skull.—The type skull, No. 4260, as figured on Plates CXI and CXII of this monograph, was referred mistakenly by Marsh to *Brontotherium gigas* notwithstanding its marked inferiority in size to the type of that species, which properly belongs to the *Brontotherium* phylum. In studying the plate and figures emphasis must be laid on the fact that the skull is extremely crushed laterally, and that its original mesaticephalic proportions are artificially increased into dolichocephaly. In other respects the plate as well as the accompanying figures and sections give an admirable idea of the formation and proportions of this primitive titanothere.

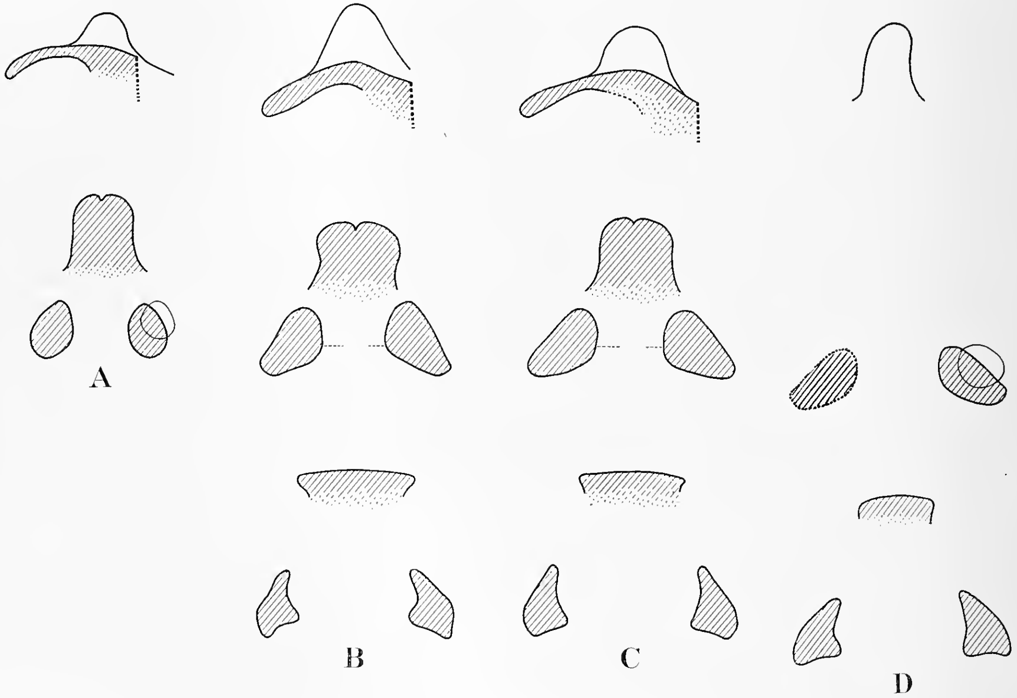

FIGURE 429.—Sections and contours of skulls of *Allops walcotti* and *A. marshi*

A, *Allops walcotti*, Nat. Mus. 4260 (type); lower levels of Chadron A; a very primitive stage, approaching both *Brontops brachycephalus* and *Menodus heloceras* in the character of its sections. Low horns elongate in basal section and placed not far in front of the orbits, nasals long and narrow, zygomata slender. No very definite marks of affinity with *Allops* are revealed by the sections. B, *A. marshi*, Am. Mus. 501 (type); horns elongate trihedral in basal section and placed considerably in front of the orbits, nasals broad distally, zygomata little expanded. C, *A. marshi*, Am. Mus. 1445 (paratype); the sections differ little from those of the type, although the skull as a whole is broader. D, *A. marshi*, Harvard Mus.; differs somewhat from the type in the steeper profile of the horns, basal section obliquely trihedral, zygomata little expanded, parietal vertex narrow. One-eighth natural size.

The skull is in the seventh stage of growth. It exhibits a slender but strongly indented occiput in the center of which is a median ridge which projects from the superior border. The cranial vertex is exceptionally long and narrow, with a decided lateral crest overhanging the supratemporal fossa; in the midregion of this supratemporal crest we note (Pl. CXI) two lateral projections which are also observed both in *Allops serotinus* (Nat. Mus. 4251) and in several skulls of the *Menodus* phylum. In front of these are the supraorbital projections. The horns are lateral in position, overhanging the sides of the face and of an elongate-oval basal section anteroposteriorly, distinct from that of the type of *Allops marshi.* The long axis of the section is anteroposterior, whereas in *A. marshi* it is oblique; the horn rises only 70 millimeters above the side of the narial aperture, 40 millimeters above the vertex of the skull. The nasals also resemble those in the type of *A. marshi;* they extend very far forward, contracting slightly, and cleft at the tips. The relative elongation of the face is a decided feature (Pl. CXI, A^3), the bridge over the infraorbital foramen being very broad, even broader than in *Menodus giganteus;* there is a preorbital knob on the lacrimal, which is seen also in *M. trigonoceras.* The zygomatic arches, as shown in all three views of the skull, are deep and narrow, not expanding widely, and resembling those of the *Menodus* type. There is a narrow contact between the posttympanic and postglenoid processes, and the paroccipital process is narrow in palatal view (Pl. CXII), wherein the dolichocephalic structure is again apparent but is somewhat exaggerated in this type by lateral crushing.

Dentition.—There are two incisor alveoli which show that these teeth had not undergone the degeneration observed in members of the *Menodus* phylum. The right canine so far as preserved shows somewhat less anteroposterior compression than in the type of *A. marshi.* The premolars of *A. walcotti* exhibit pronounced internal and faint external cingula and feebly developed tetartocones (fig. 430). The tetartocones, however, are better developed than in the contemporary *B. brachycephalus,* since the constriction separating the tetartocone from the deuterocone in p^{2-3} is a little more anterior in position. Furthermore, the tetartocone of p^4 is not a concave spur from the cingulum as in *B. brachycephalus* or *B. dispar.* Characteristic features are the crenulation of the internal face of the deuterocones and the broad internal cingula. In regard to the proportions of the grinding teeth, comparison with the average anteroposterior and transverse diameters of the grinding teeth of five skulls of *B. brachycephalus* shows that in this specimen the teeth are less markedly brachyodont, a fact in accordance with its supposed affiliations with the *Allops* phylum. The teeth are, in fact, as elongate as in members of the *Menodus* phylum, but this may be due partly to the lateral crushing. Detailed measurements of the tooth proportions indicate, however, that they are closer to *B. brachycephalus* than to those of *M. trigonoceras.*

Characters of lower jaw.—A lower jaw (Nat. Mus. 4247, fig. 413) agrees exactly in size and may be provisionally associated with this species. It presents the following characters: The coronoid is elevated; the angle projects downward and backward; the mental foramen is below p_3. $I_{\overline{1}}$, $P_{\overline{3}}$. The canines are pointed, erect, with an incomplete internal cingulum and somewhat flat inner face; p_1 is entirely wanting, a variable character; the cingulum on the remaining grinders is moderately developed; m_3 exhibits an incipient crenulate internal crest of hypoconulid.

Measurements of jaw of Allops walcotti, Nat. Mus. 4247

	Millimeters
Angle to symphysis	525
Condyle to angle	235
Canines, anterior enamel	34
Canines, anteroposterior	21
M_3, anteroposterior	88
M_3, transverse	38
P_2–m_3	290

This lower jaw has long, conical canines; it should be compared with the lower jaw of Am. Mus. 1495.

Allops marshi (Osborn)

(*Megacerops marshi* Osborn, 1902)

Plates XXXVIII, CXII–CXVI; text figures 197, 378, 381, 389, 391, 397, 399, 409, 429, 431, 432, 615, 712

[For original description and type references see p. 233. For skeletal characters see p. 678]

Geologic horizon.—The geologic levels of the type and paratype of *Allops marshi* in the American Museum are not recorded, but they are probably from upper A or lower B. A fine skull (Field Mus. P 6900) is recorded as from 50 feet above the Pierre shale and 50 feet below the level of a skull of *Brontotherium hatcheri*—that is, probably the upper levels of A or the lower levels of B. A female skull (Nat. Mus. 1215) slightly smaller than *A. marshi* is recorded from middle B.

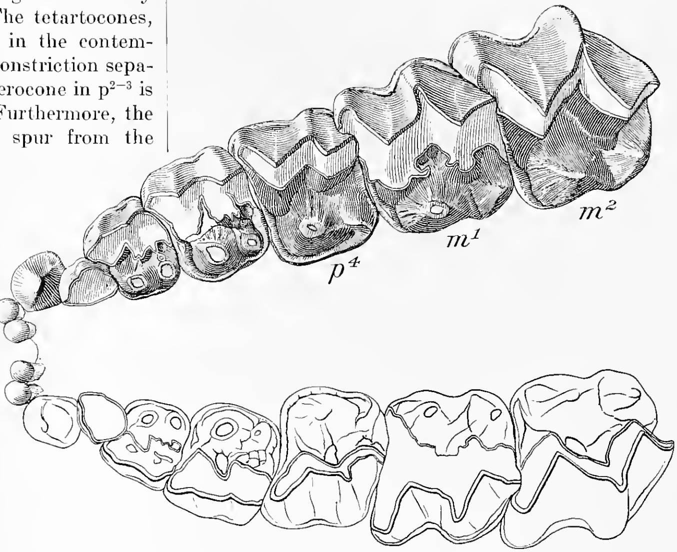

FIGURE 430.—Upper teeth of *Allops walcotti*

Nat. Mus. 8753 (paratype); m^3 is missing. One-half natural size.

Specific characters.—Skull longer than in *Brontops brachycephalus* (645 to 675 mm., average 665), but shorter than in *B. dispar,* of mesaticephalic proportions; zygomatic index, 64 to 69, average 66, and thus similar to females of *B. brachycephalus.* Horns (105 to 140 mm.) longer than in *B. brachycephalus;* basal section trihedral, more or less pointed or trihedral at the summits. Nasals elongate, free length 98 to 105 millimeters. Incisors 2–1, large i^2, small i^1. Grinding series, length 310 to 335 millimeters, average 319; molars average 192; dental index same as in *B. brachycephalus* and *B. dispar*, namely, 47. Canines strongly compressed anteroposteriorly, length of crown 34 to 37 millimeters. Premolars with tetartocones of p^4 better developed than in *B. brachycephalus*, tetartocones of p^2 and p^3 better developed than in *B. brachycephalus* and similar to progressive members of *B. dispar*. Occiput not greatly prolonged back of zygomatic arches.

Observations on the measurements of Allops marshi.—From *Brontops dispar* the skulls of *A. marshi* are distinguished above all by their very low zygomatic index, 64 to 69, as compared with 77 to 87 in *B. dispar*. This marked narrowness, together with the small size of the canines (vertical diameter 34 mm., as compared with 40 in *B.* (*validus*) *dispar*), has led to the suspicion that *Allops marshi* may be the female of *B. dispar*. A comparison of the paratype of *Allops marshi* with the type of *B. validus* is given below:

Measurements of Brontops (validus) dispar and Allops marshi, in millimeters

	B. (validus) dispar, Nat. Mus. 4290 (type)	A. marshi, Am. Mus. 1445 (paratype)
P^1–m^3	320	335
P^1–p^4	130	135
M^1–m^3	203	203
Canines:		
Vertical	40	37
Anteroposterior	27	22
Pmx to condyles	660	675
Zygomatic index	85	64

The relative widths of p^4 and m^3 also appear not to differ very clearly in the two forms:

Anteroposterior and transverse measurements of p^4 and m^3 in Brontops (validus) dispar and Allops marshi, in millimeters

	P^4		M^3	
	Ap.	Tr.	Ap.	Tr.
B. dispar (type of validus)	40	60	72	75
A. marshi (type)	39	61	70	73

A. marshi is decidedly smaller than *A. serotinus* and *A. crassicornis*, and apparently no known skulls bridge over this gap. It is larger in all measurements than *B. brachycephalus*.

Materials.—This species is represented by 15 or more skulls, including the type (Am. Mus. 501, Pls. CXIV, CXV), a well-preserved skull; the paratype (Am. Mus. 1445, Pls. CXIV, CXV); a well-preserved skull (Brit. Mus. 4446 M, Pl. CXIV) whose geologic level is not recorded; an exceptionally perfect skull (Field Mus. P 6900), associated with the lower jaw and parts of the skeleton, from the upper levels of A or the lower levels of B; a fine skull in the Museum of Comparative Zoology, level not recorded, originally described by Scott and Osborn (1887.1, p. 158) as "*Menodus coloradensis*"; a cast of an unknown skull (Carnegie Mus. 289); a skull, recorded from upper A, probably a female (Nat. Mus. 1213); a skull from B (Nat. Mus. 1215).

Comparison of Allops with members of the Brontops phylum.—Are these specimens females of *B. dispar?* There is some evidence that the specimens attributed to *A. marshi* are female forms of *B. dispar*, consisting chiefly of the following items: (1) The dental indices are the same; (2) the tetartocone development is practically identical; (3) the cephalic index is mesaticephalic, like that of the females of *B. dispar*; (4) the specimens of *A. marshi* are found on lower levels of the range of *B. dispar*. On the other hand, the evidence against regarding *A. marshi* as the female form of *B. dispar* is somewhat stronger, as follows: (1) The skulls of *A. marshi* are generally recorded from lower geologic levels; (2) the skulls in the Field and Harvard museums have larger canines, indicating that they are males; (3) the occiput of *A. marshi* is not greatly prolonged behind the greatest width of the zygomatic arches, in contrast with *B. dispar*, in which the occiput is greatly produced posteriorly (see diagram); (4) the horns of *A. marshi* are more triquetrous or transversely oval, while the horns of *B. dispar* are rounded; (5) the nasals of *A. marshi* are much more elongate.

Although the specific and phyletic distinction of *A. marshi* from *B. dispar* thus appears certain, the "group" affinity of the animals is very strong. We observe (1) the pit in the vertex of the cranium, as in *B. brachycephalus, B. dispar;* (2) the features in which *A. marshi* differs from *B. dispar* tend to relate *A. marshi* more closely to the succeeding form *B. robustus*.

Among the similarities between *A. marshi* and *B. robustus* are the following: (1) The form of the canine, which tends to obtuseness; (2) the abbreviation of the occiput behind the zygoma; (3) the broad, rugose summit of the occipital pillars; (4) the breadth and squareness of the nasals; (5) the presence of two knobs on either side of the median line of the occiput for the recti capiti muscles. The horns in their prophetic growth do not acquire the trihedral section seen in the *Menodus* phylum but tend to become more oval. Thus in the paratype of *A. marshi* (Am. Mus. 1445) we find an approach to the transversely expanded horns of *B. robustus*. Among the more primitive characters of the skull distinguishing *A. marshi* from *B. robustus* are the smaller size and less robust structure in general, the shortness and obliqueness of the nasal section of the horns, the greater length and slenderness of the nasals, the greater breadth of the malar bridge over the infraorbital foramen, the narrower contact between the postglenoid and post-tympanic processes.

Against the theory that *A. marshi* is directly related to *B. robustus* is, however, to be noted the important fact that in the premolar teeth the tetartocones are more advanced than in *B. robustus*, in which they are singularly retarded in development. The transversely expanded canines constitute another clear distinction.

Specimens referred to Allops marshi seu crassicornis.—A skull in the British Museum of Natural History collection, London (No. 5743 M), may be regarded provisionally as a very advanced or progressive stage in the evolution of this species, although it exhibits some characters which lead us to regard it as aberrant from the typical *A. marshi*, especially the somewhat flattened superior section of the horns, which suggests resemblance to *Brontotherium leidyi;* but the internally placed tetartocones of the premolars differentiate this type from any member of the genus *Brontotherium*, in which the tetartocones are invariably externally placed—that is, toward the buccal side of the crown of the teeth rather than toward the lingual side, as in this specimen. The female sex of this specimen is apparently indicated by the small size of the horns and the slenderness of the canines and zygomata. The nasals are somewhat long and delicate, cleft distally; the short horns point obliquely outward, giving evidence of having been subflat posteriorly. They are otherwise of the general type seen in *A. marshi*. The zygoma, although crushed, was apparently deep, with slight buccal expansion. The external auditory meatus was a large, round opening, as in *Menodus* and *Allops*—that is, of mesaticephalic type. The measurements (see table, p. 508) agree better throughout with *A. marshi* than with any other type, although even in the paratype of *A. marshi* the tetartocones of the premolars are not so strongly developed as in this specimen. Two well-developed upper incisors are retained on the right side, i^1 being much smaller than i^2.

The lower jaw, with its flat, deep ramus, pronounced chin, slim, pointed canine (slightly flattened on the internal face), weak, noncrenulate hypoconulid of m_3, resembles the primitive type of the Menodontinae in general and to a less degree that of the *A. marshi* type. Our conclusion is that this animal corresponds more nearly with a very progressive stage of *A. marshi* than with any other known species. The extremely advanced condition of the tetartocones of the premolars may, however, entitle it to distinct specific rank. The skeletal parts which are thought to be associated with this skull are described below.

Skull in the Harvard Museum of Comparative Zoology.—This skull (fig. 431) agrees with the type in the specific characters of the horns and nasals and in the possession of round-topped incisors.

Progressive characters and ascending mutations in specimens referred to Allops marshi.—The type of *Allops marshi* (Am. Mus. 501) exhibits a zygomatic index of 67. It differs from the paratype (fig. 429) in the shape of the nasals and in the more retarded premolar tetartocones. There is a trace of the circular pit in the occipital vertex. The tooth row is short (310 mm.).

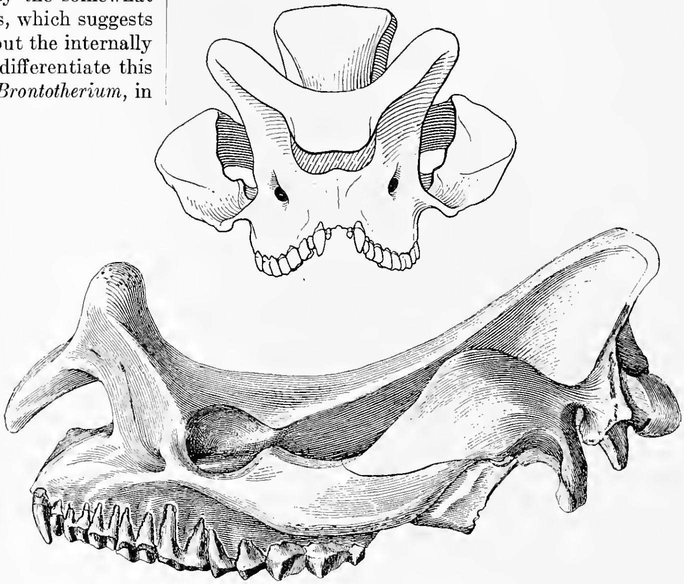

FIGURE 431.—Skull of *Allops marshi*

Harvard Mus. Front and side views. One-sixth natural size.

The paratype, probably a male (Am. Mus. 1445), represents a more progressive stage: (1) it is the broadest skull referred to this species (zygomatic index 69), the skull being broadly depressed with stout zygomata; (2) the tetartocones are very advanced; (3) the occiput is extremely short behind the zygomata; (4) the nasals are thin and do not spread distally; (5) there are traces of a circular pit in the occipital vertex; (6) the tooth rows are longer than in any other specimen in the series, namely, 335 millimeters; (7) the same may be said of the molars (average 205 mm.); the grinding teeth are also slightly more elongate; (8) the tetartocones are more advanced than in *B. robustus*—in fact, more advanced than in several specimens attributed to *B. dispar*.

The British Museum specimen (No. 5743 M) above described agrees well with the type and paratype in all measurements except in the zygomatic index, which is low and agrees with that of a supposed female (Nat. Mus. 1213) from the lower beds. The horns are more erect than in the paratype. The tetartocone development is about the same as in the type.

The Field Museum specimen (No. P 6900) agrees well with the type in measurements but differs in the somewhat more backwardly prolonged occiput; the canines, which are large, indicate that this specimen is probably a male. It is more fully described below.

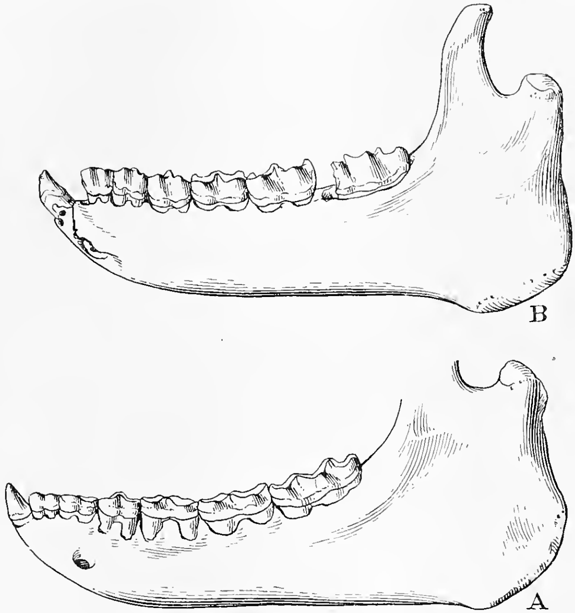

FIGURE 432.—Lower jaws of *Allops marshi* and *Allops?* sp.

A, *Allops marshi*, Field Mus. P 6900; ramus sweeping gently forward with lower border nearly horizontal and angle not produced downward, chin slightly convex, canine appressed to i_2, external cingula not sharply defined. B, *Allops?* sp., Ottawa Mus.; Cypress Hills, Saskatchewan. This specimen (one of Cope's cotypes of *M. angustigenis*) differs from the typical *Menodus* in the presence of incisors (as indicated by the alveoli) and in the somewhat less hypsodont form of the grinding teeth; the angle is not produced backward. The reference to *Allops* is provisional. About one-sixth natural size.

The skull in the National Museum (No. 1213) agrees closely with the type of *A. marshi* in measurements and is somewhat more progressive in premolar evolution than the type of *B. brachycephalus*.

Another skull (Nat. Mus. 1215) is recorded from the middle levels of B and may pertain to this species, although the occiput is more prolonged backward than in the type; the premolar tetartocones might represent either this species or *B. dispar*.

Equally interesting is the skull Nat. Mus. 1214, referred to *B. brachycephalus* but possibly an ancestor of *A. marshi*.

Detailed characters of Allops marshi.—The detailed characters of the type (Am. Mus. 501) are as follows: The skull, apparently belonging to a female, is in the seventh growth stage. The incisive border exhibits alveoli for a large lateral and small median incisor. The canines have short, obtuse, lanceolate crowns, a posterior and a slight lateral cingulum. The first superior premolar is bifanged, close behind the canine; it exhibits no tetartocone. The tetartocones are less advanced than in the contemporary *M. trigonoceras*, moderately developed on p^2 and p^3 and forming a depressed loop on p^4; the external and internal cingula are clearly defined. The molars exhibit partial cingula on the ectoloph and rudimentary cingula on the inner side. The hypocone of m^3 is connected with the cingulum (in the paratype, however, the hypocone is separated from the cingulum as a low cusp); there is a rudimentary metaloph, especially on m^3. The postorbital process of the frontal crest forms a rudimentary sharp angle; the orbit is large; the malar bridge is broad, with a low ridge; the buccal expansions of the zygomata are slight in top view; the edges of the frontal crest are seen to diverge widely, running to the malar ridges of the horns. The nasals are of medium length, deeply convex above and concave below, projecting beyond the premaxillaries anteriorly.

The paratype skull (Am. Mus. 1445), probably that of a male, is, as above noted, more progressive. In p^4 the tetartocone is more distinctly budded off. As in the type the canines have the short, sublanceolate section and posterior lateral cingulum quite distinct from the more pointed canines of *Brontops dispar*.

The Field Museum skull (No. P 6900) associated with a lower jaw and a manus of *Allops marshi*, from Phinney Springs, S. Dak., has been skillfully reconstructed by Mr. Riggs and is now one of the least distorted titanothere skulls of all that are known. It agrees closely in measurements with the other skulls referred to *A. marshi* and shows corresponding specific characters.

Detailed measurements of the upper grinding teeth prove that the transverse measurements exceed the anteroposterior measurements throughout. This proportionate excess of transverse diameter is progressive in this brachycephalic line.

Ascending mutations.—This species, therefore, includes specimens which represent several "ascending mutations" in increase of size, in the development of the premolar teeth, in separation of the tetartocones, and in expansion of the zygomatic arches. Of these the geologically oldest perhaps is the National Museum specimen No. 1214, which is distinctively a *B. brachycephalus* in its measurements. Next in order of evolution comes the female specimen (Nat. Mus. 1213), distinctly an *A. marshi* in its measurements.

On a higher plane but still in an intermediate stage of development is the female type skull of *A. marshi* (Am. Mus. 501). The Carnegie Museum skull No. 123, formerly referred to this species, is more probably a *Brontops dispar* (Am. Mus. 1445). The paratype is the largest and most progressive form known. This range of progressive evolution in the materials at hand affords strong additional proof of continuity.

Characters of the lower jaw.—The characters of the lower jaw of this species are illustrated in Figure 432, A. The chin is gently convex, not angulate; the angle is but little produced downward; the lower border of the ramus is nearly horizontal.

Allops serotinus Marsh

(*"Allops serotinus"* Osborn, 1902)

Plates XCIII, CXVII–CXX, CXXXII; text figures 184, 375, 387, 391, 393, 394, 399, 409, 433, 434

[For original description and type references see p. 225]

Geologic horizon.—*Titanotherium* zone of South Dakota; summit (?) of middle beds (Chadron B).

Specific characters.—Skull mesaticephalic. Length 705 millimeters (♂), breadth 525. Zygomatic index 74. P^1–m^3, 330 millimeters. In males nasals broad (133 mm.) and short (81 mm.). Horns subtriangular elongate, widely divergent. Incisors 2–1, external incisor large, median incisor reduced or wanting. Superior canines, males, 41 millimeters. Premolars with deuterocones forming main internal portion of crown. Tetartocones much smaller, especially on p^4. External cingula defined on premolars, more or less continuous on molars.

Measurements of Allops crassicornis and A. serotinus.—The skulls referred to *Allops serotinus* and *Allops crassicornis* form an ascending series, in which p^1–m^3 rises from 330 to 370 millimeters. The three skulls referred to *A. crassicornis* differ from those referred to *A. serotinus*, especially in the greater length of the premolar and of the molar series. The contrasts in measurements with *Brontops dispar* and with *Menodus trigonoceras* are shown in the accompanying table.

Measurements of Allops crassicornis, A. serotinus, Brontops dispar, and Menodus trigonoceros, in millimeters

[All specimens male]

	A. crassicornis	A. serotinus	B. dispar	M. trigonoceras
P^1–m^3	355–370	330	320–345	335–360
P^1–p^4	131–150	133–140	122–145	127–136
M^1–m^3	210–220	195–206	200–215	220–225
P^4, ap. by tr	46×68	43×59	40×60	43×51
M^3, ap. by tr	80×82	68×72	72×75	72×70 to 82×79
Pmx to condyles	750	705–739	643–665	670–770
Zygomatic index	76	72–78	78–87	66–79?
Nasal length	72	68–81	85–94	115–140
Nasal breadth	146	106–137	102–120	120–135

From this table it will be seen that *Allops crassicornis* and *A. serotinus* are distinguished by the great extent of p^1–p^4, by the relatively great width of p^4 and m^3, by their high zygomatic index as compared with that of *Menodus trigonoceras*, and by their relatively short, wide nasals. In general the skulls of *Allops serotinus* and *A. crassicornis* combine the characteristics of *Brontops* and of *Menodus*.

General characters.—This species includes crania that immediately suggest *Menodus giganteus*, but on close examination they are seen to be less powerful and less robust. It is noteworthy that the supraoccipital crest is less rugose and was probably provided with less powerful muscles.

Materials.—The type skull (Nat. Mus. 4251) was originally recorded by Hatcher from the top of the *Titanotherium* zone of South Dakota. This record, however, was subsequently revised by Hatcher as possibly due to secondary erosion and deposition of the overlying Brule formation (*Oreodon* zone) below the true upper level. Thus we may provisionally regard *Allops serotinus* as typically of the uppermost levels of the middle beds. It is noteworthy that the matrix is a fine clay, and the skull has a brilliant yellowish-white surface.

Another skull (Nat. Mus. 2151) is recorded as found by Hatcher is the same whitish clay matrix, about 15 feet away from the type, and entered as 80 feet above the Cretaceous Pierre shale. This further confirms the view that these animals belong in the upper portion of the middle beds, or B, and not in the upper *Titanotherium* zone (C).

Two other skulls are known, namely, Nat. Mus. 4938 and Am. Mus. 520.

Description of the type skull.—In addition to the general characters noted above in which this skull differs from that of the typical *Menodus* or the typical *Brontops*, it is important to record the following detailed characters:

The type skull (Pls. CXVII, CXIX) is vertically crushed, and owing to this the lateral spread of the horns is unnaturally increased. It is a male specimen. Although in the seventh stage of growth, the skull is decidedly delicate in its structure and proportions. It represents an animal about a fourth smaller than the majority of the specimens referred to the great animal *Menodus giganteus*. The inferior aspect of the skull is well represented in Plate CXVIII, Am. Mus. 520. The nasals of the type skull (Nat. Mus. 4251) are much shorter (81 mm.) than in *Menodus giganteus* and relatively as broad (133 mm.). The rugose expansion of the tips is an age character. The horns are long (240 mm.), expanding directly outward at the sides, with a low but broad connecting crest; the basal section (fig. 433) is peculiar in the incurvation of the outer border between the nasal and the malar ridges. The general form is similar to that in *M. giganteus*. Seen from in front the inferior contour of the horns is straight, as in *M. giganteus*; the angles of the basal portion are more sharply trihedral or defined than in the type of *A. crassicornis*. As seen from above we observe a decided midtemporal as well as supraciliary overhang of the supratemporal crest, as in the type of *A. walcotti* (Nat. Mus. 4260). The supratemporal crests exhibit, in fact, a prominent flare or projection a short distance behind the orbits. The occiput is deeply excavated, but the occipital pillars are relatively light and are surmounted by a simple rugose flare. As in *Brontops* and *Menodus* the occiput is decidedly produced behind the zygomata. As in *Menodus* the zygomatic arches are relatively deep and narrow, and the parietal vertex is also relatively more constricted than in *Brontotherium* and *Megacerops*.

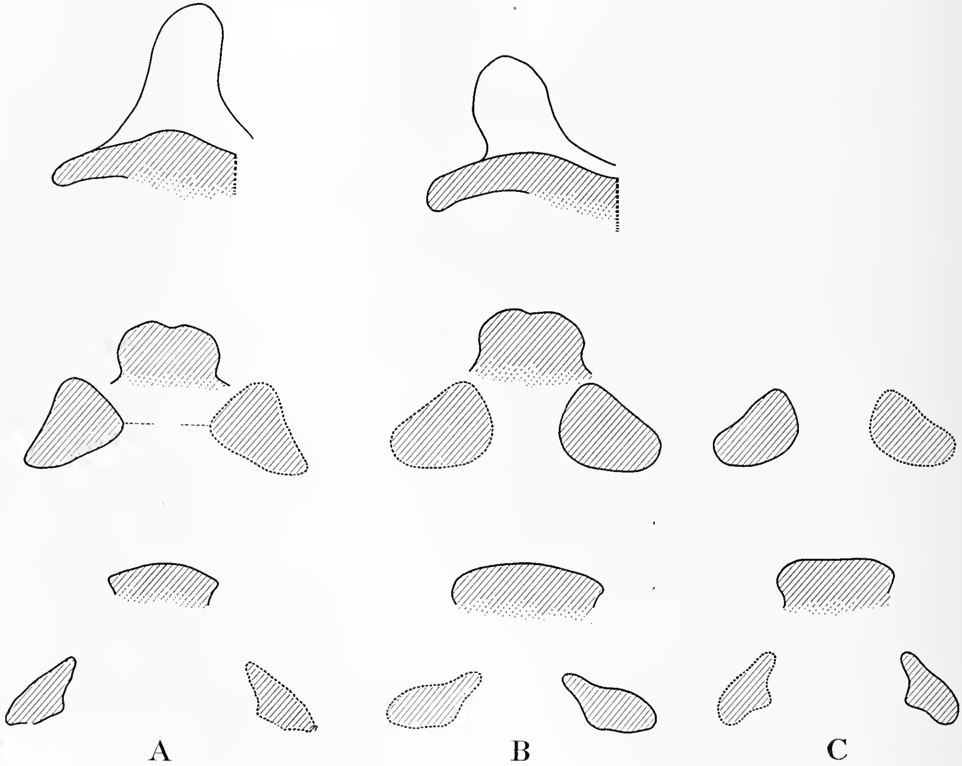

Figure 433.—Sections and contours of skulls of *Allops serotinus* and *A. crassicornis*

A, *Allops serotinus*, Nat. Mus. 4251 (type); upper levels of Chadron B; stout horns directed outward (although here represented as vertical) with a well-defined trihedral basal section (as in *Menodus*), nasals short and wide, zygomata relatively slender. B, *A. serotinus*, Nat. Mus. 4938; lower levels of Chadron C; horns directed outward and roundly trihedral in basal section, nasals short, thick, and very wide, zygomata expanded. C, *A. crassicornis*, Nat. Mus. 4289 (type); lower levels of Chadron C; horns stout and very thick, basal section roundly trihedral, zygomata not much expanded. All one-eighth natural size.

Dentition.—The dental characters of the type are highly distinctive. A large single incisor persists on each side, relatively more robust than that in *A. crassicornis*. The canine crowns measure 41 millimeters anteroposteriorly and are thus slightly smaller than in the large type *Menodus giganteus*. The distinctive anteroposteriorly compressed form of canine is well represented in Plate CXXXII, C. The postero-internal cusps of the premolars are much less developed than in *A. crassicornis* or in *M. giganteus*—in fact, in p^4 the tetartocone is a feebly developed ridge, and the deuterocone forms the most internal portion of the crown; in other words, this tooth is in a primitive stage of evolution. The tetartocone of p^3 is a mere spur. The hypocone of m^3 is an elevated cingule, contrasting with the cone which is so distinctive a feature of *Menodus*.

In its premolar evolution *A. serotinus* is more retarded than *A. crassicornis*.

Female skull Nat. Mus. 2151.—The skull (Pl. CXVII, D) found not far from the type of *A. serotinus* is believed to be a female of the same species. It differs from the type in several structural characters which may be attributed partly to the differences of sex, as follows: (1) It is of smaller size; (2) the horns are more sessile, resembling those of *A. marshi;* (3) the nasals are more elongate; (4) the zygomata are less widely expanded; (5) the canines are of feebler dimensions. In the grinding teeth the dental index, 50, is remarkably high, but the actual linear measurements of $p^1–m^3$, $p^1–p^4$, $m^1–m^3$ are the same as in the type male skull. This is in accordance with the general principle which we have found throughout titanotheres, that the females while inferior in other characters frequently present grinding teeth equal in size to those of the males.

Transitional skull or ascending mutations.—The American Museum skull No. 520, as seen from above (Pl. CXVII, B), resembles the type skull of *A. serotinus* in many respects. As seen from below (Pl. CXVIII) it has the true subgeneric characters of *Allops*, especially in the peculiar transverse, lanceolate form of the canine teeth and in the rounded form of the single incisor tooth. On the other hand, it differs from the type of *A. serotinus* and appears to be transitional toward a higher type in the decidedly greater abbreviation of the nasals. In top view the horns are seen to be intermediate between those of *A. serotinus* and *A. crassicornis*. Similarly, while the nasals are shorter than in *A. serotinus* they are narrower than in *A. crassicornis*. The linear measurements of the grinding teeth (330 mm.) agree precisely with those of the male and female specimens of *A. serotinus*, and a still more conclusive resemblance is seen in the decidedly retarded development of the tetartocones, so far as one can judge from their worn condition.

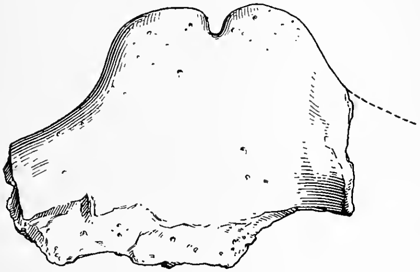

FIGURE 434.—Coossified nasals and proximal part of horns of *Allops? serotinus?*

Specimen from Cypress Hills, Saskatchewan, Canada, in the Ottawa Museum, referred by Lambe to *Megacerops assiniboiensis*. One-third natural size.

Skull Nat. Mus. 4938.—This is another skull which combines the primitive premolar structure of *A. serotinus* with the more abbreviated nasals and more massive form of *A. crassicornis*. The detailed measurements of the teeth in this skull agree more closely with those of *A. serotinus* than with those of *A. crassicornis*. On the other hand, in both size and shape of the sections of the horns the skull appears to agree more closely with *A. crassicornis*. Together with the skull above described (Am. Mus. 520) this skull might be cited to prove the existence of transitions between the two successive stages.

Summary.—The type (Nat. Mus. 4251) and the three other skulls provisionally referred to *A. serotinus*—namely, the female (Nat. Mus. 2151), the transitional form (Am. Mus. 520), and the second transitional form (Nat. Mus. 4938)—all agree in the retarded state of evolution of the tetartocones, which are little further advanced than in the species *Brontops dispar*. The characters in which they disagree with *B. dispar* are found in the horns and nasals, and these either represent ascending mutations of the *A. serotinus* type or more probably progressive stages toward the next higher species, *A. crassicornis*.

Allops crassicornis Marsh

("*Allops crassicornis*" Osborn, 1902)

Plates CXIX–CXXII; text figures 189, 387, 409, 433, 608, 612

[For original description and type references see p. 228. For skeletal characters see p. 679]

Geologic horizon.—*Titanotherium* zone of South Dakota, middle or upper level (B or C).

Specific characters.—Skull proportions of males more robust than in *A. serotinus*. Skull length 750 millimeters, width 570 (estimated). $P^1–m^3$ 370 millimeters. Nasals broad and abbreviate, horns massive and obtuse. A small pair of lateral incisors. Canines as in *A. serotinus*. Superior premolars with distinct tetartocones and well-defined external cingula. Tetartocone on p^3 distinct but somewhat smaller than the deuterocone. Hypocone wanting on m^3, replaced by rudimentary metaloph. Zygomata widely arched outward, with buccal expansions.

General characters.—The type (Nat. Mus. 4289) of this species resembles that of *A. serotinus* (1) in the peculiar lanceolate form of the canines, which are elongate, compressed anteroposteriorly, and flattened on the posterior face, perhaps a further development of a condition seen in *A. marshi;* (2) in the marked development of the cingulum on the premolars; (3) in the proportions of the premolars; (4) in the trihedral basal horn section. The type differs distinctly from *A. serotinus* (1) in the far greater development of the tetartocones; (2) in the larger and more robust proportions of the skull; (3) in the short obtuse horns. Its structural character, like that of *A. serotinus*, is intermediate between those of the *Brontops* and *Menodus* main phyla, and in its extreme size it perhaps presents an advanced stage of evolution of the subgenus *Allops*—that is, of the *Allops* collateral phylum—in the same manner that *Diploclonus amplus* presents an extreme evolution of its collateral phylum. It is noteworthy that this skull differs from all the preceding male and female skulls referred to the subgenus *Allops* in the following points:

1. Greater skull length, 750 millimeters; others 640 to 730.
2. Greater length of grinding series, 370; others 310 to 335.
3. Greater length of premolars, 155; others 131 to 140.
4. Greater length of molars, 220; others 192 to 215.
5. Greater length of canine; anterior face 45; others 33 to 40.

This uniform increase in size in all measurements implies that *A. crassicornis* comes from a higher geologic level than any of the other forms and is in thorough accord with the advanced condition of the tetartocones.

Geologic and geographic distribution.—The geologic level recorded for this specimen by its discoverer, Hatcher, is the upper part of the middle beds; in other words, it is the same as that assigned to the type and the female of *A. serotinus.* A marked progression in the evolution of the premolars is, however, positive proof that this animal belongs to a very much higher geologic level than *A. serotinus*, though there is little doubt as to its phyletic descent from that species.

Materials.—Four skulls in the National Museum (Nos. 4289 (type), 2117, 4709, 8740) are referred to this species.

Description of type.—The type skull (Nat. Mus. 4289) is undoubtedly that of an old male. The nasals are square and heavy, considerably longer than in *Brontops robustus* but much shorter than in *Menodus giganteus.* The horns are set very wide apart, and it is a noteworthy fact that they entirely lack the connecting crest which is so distinctly developed in specimens of *Menodus.* The basal section reveals the affinity to *A. serotinus;* it is distinctly trihedral, and the long axis is oblique rather than transverse as in *Brontops robustus.* In proportions this skull is dolichocephalic; ratio of length (750 mm.) and width (570 mm.) gives a zygomatic index of 75; the measurements are rendered less exact, however, by the artificial spreading of the left side of the type skull. The proportions are intermediate between the mesaticephalic and the dolichocephalic types.

Dentition.—We are first impressed by the reduced size of the superior lateral incisors (Pl. CXXI), which are more vestigial than in any member of the true *Brontops* series. The canines are a very distinctive progressive development of the *A. serotinus* form, attaining a length of 45 millimeters. The fourth superior premolar has a low but sharp and distinct tetartocone. The second and third premolars also have well-defined tetartocones. The third superior molar has a peculiar sharp elevation of the cingulum but no hypocone. The premolars and molars either parallel or indicate their affinity to those of *Menodus* in the decided development of the external cingula; p^2, p^3, p^4 also exhibit strong external cingula.

THE MENODUS MONOPHYLUM

("*Titanotherium* phylum," Osborn, 1902; "*Symborodon*" *torvus* (jaw), *Menodus, Menops, Diconodon*)

Like *Brontotherium*, the genus *Menodus* includes a nearly continuous series of ascending mutations from the base to the summit of the *Titanotherium* zone, which may be considered nearly if not quite monophyletic. The lines of separation between so-called "species" are wholly arbitrary.

Briefly stated, the distinctions of the *Menodus* phylum as a whole are as follows: (1) Skulls dolichocephalic, indices 62–70; (2) premolars rapidly progressive in molarization; (3) superior incisors aborted; (4) horns abbreviated, triangular, not shifted forward; (5) high dental index; (6) canines large, piercing.

Phyletic characters.—Large, long-limbed or cursorial titanotheres, long skulled and short horned. Ranging from the lower to the upper *Titanotherium* zone. Vestigial incisor teeth and long, pointed canines. Grinding series elongate, with a high dental index. Crowns of grinders subhypsodont and with prominent cingula.

These menodonts constitute one of the most sharply defined of all the titanothere phyla. The elongation of the feet and of the limbs indicates that of all the titanotheres known they were the most rapid travelers. While sparsely known in the lower *Titanotherium* zone and somewhat more abundant in the middle *Titanotherium* zone, they were relatively numerous in the upper zone, an indication of the more favorable conditions which this region presented toward the end of the *Titanotherium* period for animals of this type. They appear to have divided the honors with the great long-horned brontotheres, although their remains are much more rare.

The short, stout, pointed horns stood in wide contrast, however, with the great recurved horns of the brontotheres. While the canine tusks may have served as minor weapons of defense, it appears probable that the menodonts, as the swiftest members of this great group, had recourse to flight when attacked by herds of carnivores.

To the anatomist the menodonts are extraordinarily interesting in presenting extremes both of dolichocephaly and of dolichopody—that is, of long-headed, long-limbed, and long-footed development, in contrast with the broad headed. The group affinities of these animals with members of the *Brontops* phylum are indicated by the less intermediate characters of the *Allops* phylum. Whereas all other titanotheres exhibit progressive abbreviation of the nasal bones, in these animals the nasals retain the broad, elongate form first seen in the upper Eocene *Protitanotherium emarginatum.*

As compared with the more or less intermediate genus *Allops* these true titanotheres are more dolichocephalic, the zygomatic index being 62 to 70. They are distinguished also by the extreme reduction within the incisive alveoli of vestiges of the upper incisor teeth, a fact which is confirmed in every specimen, whereas in *Allops* we find two small but persistent upper incisors which pierce the gum. In the lower jaws the incisors appear to be wanting entirely, although the evidence is less conclusive. As distinguished from *Brontops* the premolar teeth are very rapidly progressive in the evolution of the postero-internal cusps or tetartocones. This character is also shared by *Allops.*

Characters of proportion.—The six great distinctive characters of *Menodus* are correlated with its length of limb, height of body, and relatively cursorial habit, as follows: (1) Dolichocephaly or length of skull controlling all the parts both of the bones and of the teeth; (2) short, triangular, and pointed horns, outward directed, and adapted to lateral motions of the head in defense or attack; (3) persistently elongate nasals, the only phylum in which this character occurs; (4) vigorous development of the grinding teeth, including a high dental index, a strong development of the cingula, and a marked vertical elongation or subhypsodonty of the crowns; (5) the elongate and piercing character of the canine tusks, which project so far above and below the line of the grinders that it is reasonable to regard them as weapons of defense and offense; (6) the entire absence of incisor teeth, a feature in which *Menodus* parallels *Megacerops* and *Brontotherium.* Of these six characters the elongation of the skull (mesaticephaly or dolichocephaly) is the most dominant in correlation with all parts of the skull and teeth.

The dolichocephaly of *Menodus* is demonstrated in every measurement in the table below. In length

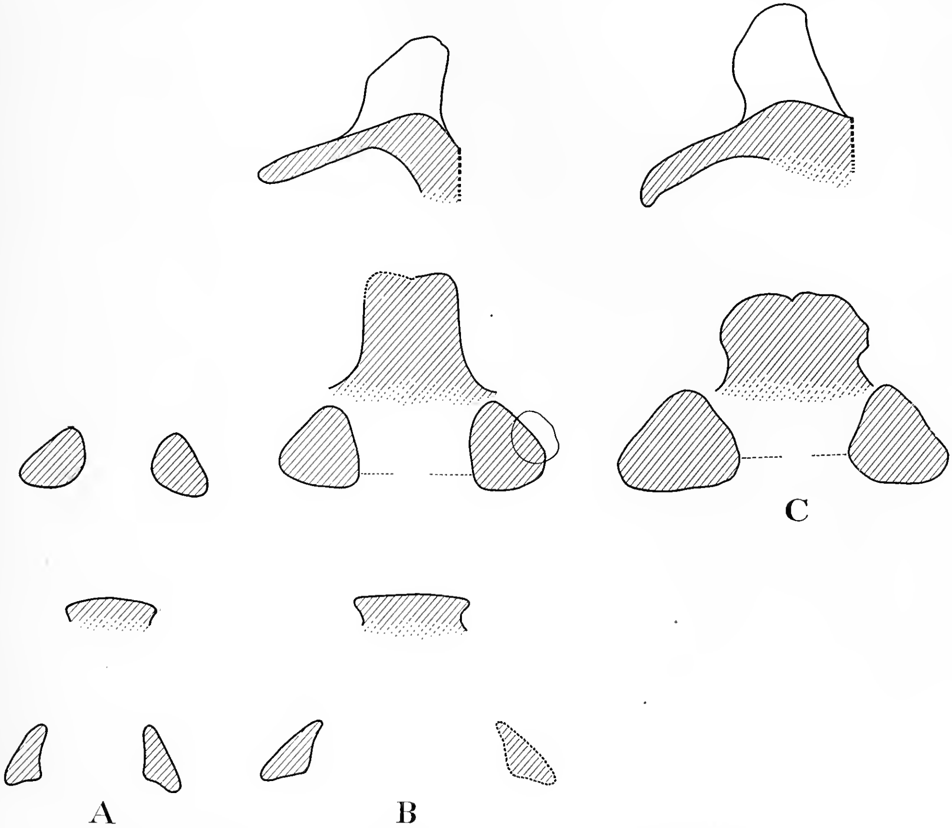

FIGURE 435.—Sections and contours of skulls of *Menodus heloceras* and *M. trigonoceras*

A, *M. heloceras*, Am. Mus. 6360 (type); small horns trihedral in basal section, parietal crest narrow, zygomata very slender. B, *M. trigonoceras*, Am. Mus. 6355 (lectotype or type?); pointed pyramidal horns roundly trihedral in basal section, connecting crest pronounced, nasals long and wide, parietal vertex wide, and zygomata very slender. C, *M. trigonoceras* (or *giganteus?*), Nat. Mus. 1219; horns longer with trihedral section, nasals very wide and distally expanded. One-seventh natural size.

the skull almost equals the giant *Brontotherium*, but in width across the zygomata it is far inferior to this animal; in the length of its grinding series it is far superior to either *Brontops* or *Brontotherium;* in the ratio of its grinding series to the entire length of the skull it is again superior, as well as in the actual measurements both of its premolar and of its molar series. Its fourth premolar is actually longer and narrower than that of *Brontotherium.* The sum of the transverse measurements of its grinding teeth is decidedly less than that in *Brontops* or *Brontotherium.*

The table on page 523 shows that dolichocephaly, a distinctive phyletic character of *Menodus*, is impressed not only upon the skull but upon the teeth.

The horns preserve their triangular or trihedral shape because the connecting crest as seen in the upper view of the type of *Menodus giganteus* (Pl. CXXXVIII, fig. 391) is strongly developed, as well as the anterior ridge which extends downward into the sides of the nasals and the external ridge, the latter extending laterally into the antorbital bar. In the beautifully preserved male skull from the summit of the *Titanotherium* zone in the Field Museum (Pl. CXL) the pointed apices of the horns are clearly displayed. As observed in the side view of the same skull (Pl. CXXXIX) the facial or preorbital portion of the skull is relatively elongate, and there is a broad bridge across the infraorbital foramen as well as a very deep anterior junction of the premaxillaries. The zygomatic arches are strengthened by depth rather than by breadth; it is true that a moderate expansion is observed in this and other old males, such as the type of *T.* "*ingens,*" but the enormous buccal swellings characteristic of *Brontops* and *Brontotherium* are not developed. In the auditory region a highly dolichocephalic character appears—namely, the relatively open condition of the external auditory meatus due to the noncontact or retarded contact of the postglenoid and post-tympanic processes. Similarly, the occipital condyles project widely at the back of the skull. The occiput is relatively high and ascends rapidly above the condyles. The jaw is also highly distinctive, with its long, straight lower border, its backward rather than downward projecting angle, and its well-defined chin. It is totally different from the jaw of *Brontotherium.*

In *Menodus giganteus* the dental series attains the finest proportions known in any member of the order Perissodactyla. The vigorous development of the teeth, exhibited in the large canines, in the pronounced cingula, in the length of the grinding series as a whole, in the height of the crown, in the excess of anteroposterior over transverse measurements of the grinders, and in the progressive dental index, affords one of the most distinctive characters of this phylum as a whole.

Harmonic evolution.—In progressive increase in size all parts of the skull and dentition share alike between the stages *M. heloceras* and *M. giganteus*—namely, about 50 per cent. The horns increase in length 190 per cent as compared with an increase of 250 per cent during the same period in *Brontotherium*—that is, they somewhat more than share the general increase in length of the skull, but they do not dominate in development to the detriment of other features as in *Brontotherium.*

Sexual characters.—The differences between the males and females are very marked, as clearly shown in the contrast between two male and two female skulls in the American Museum. The female skulls are smaller in most of their dimensions, less rugose on the surfaces for muscular attachment. In the males the horns are more robust, more decidedly triangular rather than rounded, the triangular form being sharply defined especially at the base. In their vigorous growth they sometimes exhibit the anterior tuberous branching, as seen in skull Am. Mus. 505. In the females the horns are relatively slender, with less anteroposterior diameter at the base, and more pointed at the summit. While in both sexes the incisors are vestigial and certainly do not pierce the gum, there is marked disparity in the canines. In the males (Pl. CXL) the canines are formidable weapons, the anterior enamel face of one specimen (Am. Mus. 505) being estimated at 70 millimeters in length, whereas in females the canines are far more slender, the anterior face being 45 millimeters. On the grinding teeth the cingulum is equally robust in both sexes—in fact, the most pronounced development of this structure is observed in the female skull (Am. Mus. 1067), which is evidence that development of the cingulum is not a sexual character.

Progressive specific stages.—Three species are definitely distinguishable as characteristic of the lower, middle, and upper zones respectively. There are also two transition species and a closely connected series of "ascending mutations." (See table on p. 523.)

Menodus heloceras (Cope) of Chadron A: The type of *M. heloceras* (Cope) was at first placed as the ancestor of this phylum, but with some hesitation because of its imperfect preservation. So far as known it conforms in skull structure, although in a very primitive stage of development. Its ancestral position in the *Menodus* phylum was confirmed (1910) by Granger's discovery of a second skull at the base of the *Titanotherium* zone.

Menodus ("*Symborodon*") *torvus* (Cope) is an intermediate stage between *M. heloceras* and *M. trigonoceras;* it is known only from the type jaw, which is the genotype of the genus *Symborodon.*

Menodus ("*Titanotherium*") *proutii* Leidy: Leidy founded the genus *Titanotherium* on two specimens, the first was Pomel's type of *Menodus giganteus;* the second specimen, which Leidy fully described and measured, becomes the type of his species *proutii;* it belongs to an animal intermediate in size between *M. torvus* and *M. trigonoceras.*

The Menodus phylum as represented by the Hatcher collection of 25 skulls of species of Menodus from the Chadron formation in the United States National Museum

Species	Catalog No.	Material
M. giganteus Pomel	1220, ♂	Skull. Old male, full size. Nasals typical; also horns.
Do	1212	Posterior part of skull.
Do	8745, ♂	Skull. Nasals and canines typical; also horns. Size medium (="B. ingens" stage).
Do	8741, ♂	Skull. Measurements typical of smaller males; not so large as type.
Do	8735, ♀	Skull. Slender canines.
Do	8761, ♂	Anterior half of skull. Measurement of p^1-p^4 agrees with that in smaller males of M. giganteus. Specific reference uncertain.
Do	8756	Skull. Poor.
Do	8751	Anterior half of upper milk dentition. May be large M. trigonoceras.
Do	8765, ♂	Skull.
Do	8781	Complete left ramus and part of right.
Do	8778	Last half of lower jaw and molars 1, 2, and 3 of upper right.
Do	4745, ♀	Lower jaw.
M. (trigonoceras) giganteus Pomel.	8793	Upper milk dentition (dp^1-dp^4) and m^1, large animal.
M. trigonoceras (Cope)	1219, ♂	Anterior part of skull. An old male, approaching M. giganteus stage.
Do	4291, ♂	Skull. Very fine progressive type; almost at M. giganteus stage.
Do	4707	Skull.
Do	8760, ? ♀	Crushed skull. Inferior specimen.
Do	8768	Skull. Poorly preserved.
M.? trigonoceras (Cope)	1246	Posterior parts of both rami.
M. trigonoceras (Cope)	4257	Skull from level B 3. Long nasals; vestigial incisor and measurements remove it from B. dispar.
M. proutii (Owen, Norwood, and Evans).	4701, ♀	Skull from level C 1 and left fore foot.
Do	8736	Skull.
Do	113	Left ramus of jaw. Type.
M. torvus (Cope)	8799	Pair of lower jaws.
M. heloceras? (Cope)	8744	Skull. Very young, m^1 just protruding; elongate proportions of Menodus. Doubtful specific reference.

Menodus trigonoceras (Cope), of Chadron B: It is interesting to note that Cope's description of *M. trigonoceras* immediately followed that by Marsh of *M. giganteus*. *M. trigonoceras*, which is probably characteristic of B, or the middle *Titanotherium* zone, is distinguished from *M. giganteus*, first, by its inferior dimensions throughout; second, by the shape of the horns, the horn section being an equilateral triangle, as the distance between the malar, nasal, and connecting ridges is practically equal. The skull of *M. trigonoceras* is directly intermediate in size between that of *M. heloceras* and *M. giganteus*.

Menodus giganteus Pomel, of Chadron C: In *Menodus giganteus*, a superb titanothere, specifically equivalent to *Menodus* ("*Brontotherium*") *ingens* Marsh, absolutely determined as characteristic of the upper *Titanotherium* zone, and even of the uppermost levels (Chadron C 3), we reach the climax of this monophyletic series, which is distinguished by the extreme development of all the distinctively phyletic characters as compared with the inferior stages. Its relative abundance indicates that it was capable of holding its own in the struggle for existence between the numerous phyla of *Brontops* and *Brontotherium*.

Remains of species of *Menodus* have been found at the stratigraphic levels indicated below:

Upper *Titanotherium* zone: *M. giganteus* Pomel. Skulls large (type 755 by 553 mm.). Buccal processes of zygomata strongly developed. Tetartocones of p^1-p^4 distinct. Hypocone of m^3 usually separated from cingulum. Horns large, directed obliquely outward and upward. Connecting ridge prominent.

Middle *Titanotherium* zone: *M. trigonoceras* (Cope). Skulls of medium size (type 678 by 490 mm.). Buccal processes of zygomata moderately developed. Tetartocones of p^{1-3} distinct. Hypocone of m^3 sharp and distinct or a sharp cingule. Horns of medium size; basal section equilateral; connecting ridge.

Lower *Titanotherium* zone: *M. heloceras* (Cope). Skulls small (width of type across zygomata 392 mm.; nasals to occiput (estimated) 545 mm.). Horns small, subtrihedral; basal section subtriangular; internal angle rounded; no connecting ridge.

Observations on the measurements of the Menodus series.—The species of this genus constitute an ascending series extending from the lowest to the highest levels of the *Titanotherium* zone. The range in the chief measurements of the successive stages may be epitomized as follows:

Measurements of species of Menodus, in millimeters

	M. giganteus	M. trigonoceras	M. proutii	M. heloceras
P^1–m^3	385–465	333–360	300–313	265
P^1–p^4	141–176	127–136	115–119	--------
M^1–m^3	246–285	203–224	190–192	170
Pmx to condyles	760–825	628–770	?655	603
Zygomatic index	62–70	66–?79	?74	?79
Horn length	150–290	132–214	---------	70

From this it will be seen that in our present collections there are considerable gaps between the successive stages so far as regards the measurements p^1–m^3, p^1–p^4, and m^1–m^3, but that the other measurements overlap. The nasals in this phylum remain very long, whereas in other phyla they are reduced in length.

This is a remarkably consecutive and distinct phylum. Additions to the already large number of skulls may give a continuous series of measurements in each column.

Geologic level.—Unfortunately, the records of the geologic level of members of this phylum are by no means so exact as those of members of other phyla. No member of this phylum is certainly recorded from the lower *Titanotherium* zone of South Dakota, although the primitive characters of the oldest known species, *M. heloceras*, indicate that it belongs on this lower level. In Wyoming one skull of *M. heloceras* (Am. Mus. 14576) has been recorded from the base of the *Titanotherium* zone. Only one skull (Nat. Mus. 4257), belonging to the species *M. trigonoceras*, is definitely recorded as from the middle *Titanotherium* zone (level B). Another skull, referred to *M. proutii* (Nat. Mus. 4701), is tabulated from the lower level of C. This uncertainty ceases, however, in the upper beds, in which we have two positive records—namely, Nat. Mus. 4291, entered as from the upper *Titanotherium* zone (C), and a skull in the Field Museum (P 5927), recorded as found near the top of the upper *Titanotherium* zone, or upper C. It is thus probable that *Menodus* persisted to the very end of the great titanothere epoch.

SYSTEMATIC DESCRIPTIONS OF GENERA AND SPECIES IN THE MENODUS PHYLUM

Menodus Pomel, 1849

(*Titanotherium* Leidy, 1852; *Symborodon* Cope (*S. torvus*, jaw only); "*Titanotherium* Leidy," Osborn, 1902)

Plates XVIII, XX, XXII, XXIV, XLVII, XLIX, LXXXII, CXXIII–CXLII, CLVII–CLIX; text figures 24, 159, 160, 166, 168, 172, 175, 181, 227, 228, 375, 378, 381, 382, 387–389, 391, 393, 394, 396, 398–400, 406, 409, 435–447, 613–619, 630, 639, 640, 642, 701, 708, 713, 715–719, 744, 746

[For original description and type references see p. 204. For skeletal characters see p. 681]

Generic characters.—Characters 3–9, 14, 21, 23, 24, 26 (see below) are expressions of the general tendency to dolichocephaly.

Dentition.—(1) $I\frac{2-0}{2-0}$. Incisors vestigial. (2) Canines, ♂ large, elongate (42–70 mm.), with slight anterior and strong postero-internal cingulum; posterior face rounded; ♀ slender, small. (3) Opposite grinding series rectilinear (not arched). (4) Upward flexure of premolar series, as seen in side view, slight. (5) Length of premolar-molar series about equal to one-half that of the skull, from premaxillary tips to occipital condyles (dental index 48 to 51). (6) Premolar series long. (7) Internal cusps of grinding teeth with sides progressively steep, ectolophs more nearly vertical than in *Brontops*, external crescents of molars more open. (8) Anteroposterior diameter of m^2, m^3 usually greater than transverse diameter. (9) Cingula present between grinders. (10) $P\frac{4-3}{4-3}$; p^1 with worn crown rounded or pear-shaped in outline, outer wall overlapped posteriorly by ectoloph of p^2. (11) Premolar tetartocones exhibiting rapid progressive development. (12) Premolars with pronounced internal cingula, edge rounded to sharp, external cingula sharp, well marked. (13) Molars with partial internal cingula pronounced, external cingula pronounced. (14) Hypocone of m^3 often separate, and surrounded by cingulum.

Skull.—(15) Skull proportions dolichocephalic. (16) Facial portion of skull elongate, with premaxillaries not reduced. (17) Cranial part of skull very elongate. (18) Preorbital malar bridge broad to very broad, with median (malar) ridge low and obtuse (*M. heloceras*, *M. trigonoceras*) or well rounded (*M. giganteus*). (19) Infraorbital foramen very conspicuous in side view. (20) Malar below postorbital process subflat, deep. (21) Free portion of nasals persistently elongate, with parallel sides; but sometimes expanding distally in old individuals. (22) Horns of small to medium size, originating over preorbital malar ridge, shifting forward progressively;[34] basal section progressively trihedral, obliquely placed; summit of horn round to trihedral. (23) Zygomata slightly arched; buccal expansions slight or moderate, in section deep rather than broad. (24) Occiput moderately produced backward behind zygomata; vertex of skull broad posteriorly; pillars flaring slightly to moderately; occiput indented; with median knobs slight or absent. (25) Basisphenoidal rugosity usually present; vomerine septum present. (26) Jaw deep, elongate ramus, pronounced chin; coronoid uniformly broad, elevated, square at summit; angle depressed or backward extended.

The contrasts in proportions of the terminal members of the *Brontops*, *Menodus*, and *Brontotherium* phyla are shown in the following table:

Measurements of typical forms of Brontops, Brontotherium, and Menodus, in millimeters

	Brachycephalic: Brontops robustus, Yale Mus. 12048 (type)	Dolichocephalic: M. giganteus, Field Mus. P 5927 (typical)	Hyperbrachycephalic: Brontotherium gigas elatum, Am. Mus. 492 (typical)
Pmx to condyles	765	825	830
Zygomata, transverse	667	515	740
P^1–m^3	350	425	353
Dental index	46	51	42
P^1–p^4	137	150	126
M^1–m^3	220	270	241
P^4, ap. by tr	40×65	[a] 58×73	47×72
M^3, ap. by tr	81×92	[a]100×78	91×99

[a] Univ. Wyoming Mus.

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[34] A surprising fact is that the horns in the uncrushed *M. giganteus* (Field Mus. P 5927) are almost as far forward as in the uncrushed *B. gigas*. In the uncrushed *B. platyceras* and *B. ramosum* the forward displacement appears extreme.

The dolichocephalic character of *Menodus* in its typical species *M. giganteus* is demonstrated by every measurement of the accompanying table, in contrast with the brachycephalic *Brontops robustus* and the hyperbrachycephalic *Brontotherium gigas*.

Standard measurements of skull, jaw, and teeth in the Menodus phylum, in millimeters

	Upper teeth					Skull							Jaw and teeth					
	P^1–m^3	P^1–p^4	M^1–m^3	Canines, anterior vertical	Canines, anteroposterior diameter	Pmx to condyles	Zygomatic breadth	Cephalic (zygomatic) index	Nasal tips to occiput vertex	Nasals, free length	Nasals, free breadth	Horns, external length	P_1–m_3	P_1–p_4	M_1–m_3	Canines, anterior vertical	Canines, anteroposterior diameter	Symphysis to condyles
M. giganteus group																		
M. giganteus, Univ. Wyo., ♂	465	176	285	60	35	815	----	----	----	----	----	----	----	----	----	----	----	----
M. giganteus Pomel (type)	----	----	----	----	----	----	----	----	----	----	----	----	----	----	[a]280	----	----	----
M. giganteus ("ingens"), Yale Mus. 12010, ♂	428	162	266	----	----	----	553	----	755	125	125	----	----	----	----	----	----	----
M. giganteus, Nat. Mus. 1220, ♂	----	----	----	----	----	798	----	----	755	150	140	178	----	----	----	----	----	----
M. giganteus, Field Mus. P 5927, ♂	425	150	270	52	33	825	515	62	750	175	----	290	400	125	280	47	----	690
"Menops" varians, Yale Mus. 12060, ♂ (type)	410	155	255	----	35	760	555	73	695	105	140	----	----	----	----	----	----	----
M. giganteus, Am. Mus. 505, ♂ (neotype)	393	153	250	[a]70	31	777	545	70	712	120	145	195	----	----	----	----	----	----
M. giganteus, Nat. Mus. 8741, ♂	390	145	245	----	----	800	590	----	----	----	----	----	----	----	----	----	----	----
M. giganteus, Am. Mus. 506, ♀	[a]385	[a]141	[a]246	[a]40	20	[b]805	----	----	[a]770	----	[a]115	----	404	----	[a]260	----	----	[a]651
M. proutii-trigonoceras group																		
M. giganteus (trigonoceras), Am. Mus. 1066	360	135	223	45	27	770	546	70	738	122	----	----	347	109	238	----	----	592
M. giganteus (trigonoceras), Am. Mus. 1007	----	----	----	----	----	----	----	----	----	----	----	----	364	115	242	----	----	590
M. giganteus (trigonoceras), Nat. Mus. 4291, ♂	360	136	224	47	26	770	[a]510	66	----	130	[a]125	150	----	----	----	----	----	----
M. giganteus (trigonoceras), Am. Mus. 1067, ♀	355	133	225	44	25	725	[b]440	60	[a]720	127	[b]135	214	360	126	237	39	----	610
M. trigonoceras, Am. Mus. 6355 (lectotype)	----	----	----	----	----	----	490	----	[a]670	137	135	132	----	----	----	----	----	----
M. trigonoceras, Munich Mus. (mounted skeleton)	[a]355	----	----	----	----	[a]690	----	----	----	----	145	----	----	----	----	----	----	----
M. trigonoceras, Am. Mus. 6356 (cotype)	345	129	220	----	26	----	----	----	----	140	132	----	----	----	----	----	----	----
M. trigonoceras, Brit. Mus. 4447 M	----	----	----	----	----	----	----	----	----	----	----	----	356	[a]120	245	32	----	----
M. trigonoceras, Nat. Mus. 1219	345	136	221	----	[a]21	----	----	----	----	115	----	190	----	----	----	----	----	----
M. trigonoceras, Nat. Mus. 4257	335	127	220	42	----	670	535?	79?	655	120	120	150	----	----	----	----	----	----
M. trigonoceras, Carnegie Mus. 3068, ♀	333	130	203	33	22	628	----	----	----	----	----	----	----	----	----	----	----	----
M. proutii, Am. Mus. 9335	313	119	192	39	----	----	----	----	----	----	----	----	----	----	----	----	----	----
M. proutii, Nat. Mus. 8736	----	----	----	----	----	680	----	----	----	----	----	----	335	----	----	----	----	----
M. proutii, Nat. Mus. 113 (type jaw)	----	----	----	----	----	----	----	----	----	----	----	----	----	----	234	----	----	----
M. proutii, Nat. Mus. 4701, ♀	300	115	190	32	----	[a]655	485	[a]74	----	120	125	----	----	----	----	----	----	----
M. ("Symborodon") torvus, Am. Mus. 6365 (type)	----	----	----	----	----	----	----	----	----	----	----	----	310	100	210	----	----	[a]535
M. heloceras																		
M. heloceras, Am. Mus. 6360 (type)	----	----	----	----	----	----	392	----	[a]545	----	----	----	----	----	----	----	----	----
M. heloceras, Am. Mus. 14576	[a]265	----	170	----	----	[a]603	[a]480	[a]79	[a]620	132	----	70	----	----	----	----	----	----
Percentage of increment from M. heloceras to M. giganteus	75	----	67	----	----	37	7	----	----	33	----	30	----	----	----	----	----	----

[a] Estimated.

Crushed.

Measurements of skulls and jaws associated with and referred to the Menodus phylum, in millimeters

	Skulls and upper teeth				Lower jaws and teeth				
	Interior canine to hypoconulid of m^3	P^1–m^3	M^1–m^3	Symphysis to glenoid	Posterior canine to hypoconulid of m_3	P_1–m_3	M_1–m_3	Symphysis to condyles	Depth below m_3
M. giganteus Pomel (type)							[a] 280		172
M. giganteus, Am. Mus. 506, ♀	[a] 404	[a] 385	[a] 246	[a] 633	[b] 387	[a] 404	[a] 260	[a] 651	176
M. giganteus, Nat. Mus. 4735 (?4745)					385	393	262	625	137
M. giganteus (trigonoceras), Am. Mus. 1067, ♀	370	355	225	543	369	360	237	610	144
M. giganteus (trigonoceras), Am.Mus. 1007						364	242	590	160
M. trigonoceras, Brit. Mus. 4447 M						356	245		
M. giganteus (trigonoceras), Am. Mus. 1066, ♀		360	223			347	238	592	
M. trigonoceras, Am. Mus. 6356 (cotype)	370	345	220	[a] 514					
M. proutii, Nat. Mus. 113 (type)							234		163
M. trigonoceras, Am. Mus. 6345b, ? ♀					[a] 323	[a] 323	[a] 227	[a] 515	120
M. ("Symborodon") torvus, Am. Mus. 6365 (type)					[c] 312	[c] 316	[c] 214	[a c] 535	124
M. ("Symborodon") torvus, Am. Mus. 6365 (type)					[d] 295	[d] 261	[d] 208	[d] 522	124
M. heloceras, Am. Mus. 14576	290	[a] 265	170	443					

[a] Estimated. [b] Crushed. [c] Right side. [d] Left side.

Menodus heloceras (Cope)

(*Megaceratops helocerus* Cope, 1873; "*Titanotherium helocerus*" Osborn, 1902)

Plates XLVII, CXXIII, CXXIV; text figures 168, 378, 399, 409, 435, 436, 613, 639

[For original description and type references see p. 212. For skeletal characters see p. 681]

Type locality and geologic horizon.—Cedar Creek, Logan County, Colo.; lower *Titanotherium* zone.

Specific characters.—Skull small, premaxillaries to condyles estimated about 603 millimeters, tip of nasals to top of occiput about 545. Dolichocephalic (index unknown), width across zygomata 392–425 millimeters. Horns small, "elevation 50 millimeters" (Cope), basal section trihedral (with flattened, subequal external, internal, and posterior faces), tip rounded. Horns above antorbital malar ridge. Nasals squared distally, free length and breadth equal (100 by 100 mm. fide Cope). Buccal swelling of zygoma incipient. Premolar-molar series 265 millimeters (estimated).

Materials.—The type skull was found on Cedar Creek, Logan County, Colo., the same geographic region which yielded the various *Symborodon* skulls. The characters based upon the very imperfect type skull (Am. Mus. 6360) are supplemented by those of the much more perfectly preserved skull (Am. Mus. 14576) found in Wyoming; the latter is in a very primitive stage of development (fig. 436), especially in regard to the small size of the molars, m^1–m^3, which measure 170 millimeters.

Description of the type.—This is the smallest and apparently also the most primitive member of the *Menodus* phylum; it approaches even the Eocene titanotheres in its slender, narrow occiput (Pls. CXXIII, CXXIV) and its slender zygomata. In lateral view we note the well-marked postorbital processes of the frontals and the open condition of the auditory meatus. All these characters point toward affinity with *Menodus*. The specimen, as indicated in Plate CXXIV, A^1, is in fragmentary condition, the facial region being largely wanting. The nasals have been lost, but as measured by Cope they were equal in length and breadth (100 by 100 mm.), a point of significance in the consideration of the affinities of this animal because in *M. trigonoceras* and in the type of *M. giganteus* the breadth also equals the length, whereas in all stages of *Brontops* the breadth exceeds the length. Cope's other measurements are as follows:

Measurements of Menodus heloceras

	Millimeters
Least width of parietal plane	104
Elevation of horn core	50
Length of free nasal bones	100
Width of free nasal bones at base	100

The rudimentary condition of the horns also indicates that this animal belongs in the lower *Titanotherium* zone. The horn section (figs. 399, 435) consists of the relatively acute anterior angle, an external angle, and a gently rounded internal angle, the last attributable to the absence of any connecting crest between the horns; the horn in its subtrihedral shape and the position of its long axis is similar to that in *Menodus giganteus* and is quite distinct from that of the early members of either the *Brontops* or the *Brontotherium* phylum. Similarly the zygomatic section is relatively deep and narrow, agreeing again with that of *M. trigonoceras.* In consonance with dolichocephaly, the postglenoid, post-tympanic, and paroccipital processes are relatively short and simple. We observe a well-defined postmastoid foramen, as in other titanotheres. The posterior nares open between the opposite m^3. The basisphenoid is smooth. Unfortunately the teeth are so fractured that they yield only one important fact—namely, that this is a very old individual, and that its simple characters are not juvenile but specific.

Measurements of two specimens of Menodus heloceras, in millimeters

	Am. Mus. 6360 (type) (Colorado)	Am. Mus. 14576 (Wyoming)
Basilar length	----------	603
Breadth, zygomata	395	[a] 450
Height, temporal fossa	105	110
Width, parietal plane	104	114
Free length, nasals	100	132
Free width, nasals	100	111

[a] Estimated.

Skull referred to Menodus heloceras, from the base of the Titanotherium zone, Wyoming.—The type skull is so poorly preserved that its measurements yield little of interest. A skull which is provisionally referred to this species (Am. Mus. 14576, fig. 436) comes from the very base of the *Titanotherium* zone at Beaver Divide, near Hailey, Wyo. It exhibits the following comparative measurements:

Measurements of Menodus heloceras, Allops walcotti, and Brontops brachycephalus, in millimeters

	M. heloceras, Am. Mus. 14576	A. walcotti, Nat. Mus. 4260 (type)	B. brachycephalus	
			Nat. Mus. 4940	Am. Mus. 1495
P^1–m^3	[a] 265	285	265	288
P^1–p^4	--------	112+	101	118
M^1–m^3	170	169	160	171
Pmx to condyles	[a] 603	640	--------	[a] 560
Nasals, free length	132	105	--------	--------
Horn length	70	100	102	--------

[a] Estimated.

Hence the skull referred to *M. heloceras* is distinguished by small molars, long nasals, and short horns, which are all primitive characters. The form of the horns and nasals suggests ancestral relationship to *Menodus* or *Allops.*

The upper molars, though poorly preserved, appear to resemble those of *Brontops brachycephalus* and differ from those of *Menodus heloceras* in being relatively wider.

Menodus torvus (Cope)

(*Symborodon torvus* Cope, 1873; not "*Symborodon torvus* Cope," Osborn, 1902)

Plates CXXV, CXXVII, CXXXII, CLVIII, CLIX; text figures 166, 396, 437

[For original description and type references see p. 210]

Type locality and geologic horizon.—Northeastern Colorado, *Titanotherium* zone.

Specific characters.—Lower jaw of *Menodus* type, slightly smaller than that of *M. proutii;* p_1–m_3, 310 millimeters; premolars much crowded (p_1–p_4, 100 mm.); incisive border apparently edentulous; an external cingulum on the canines, premolars, and molars; p_1 very small and closely crowded between the canine and p_2.

The jaw (Am. Mus. 6365), chiefly described by Cope, is the lectotype of the species "*Symborodon*" *torvus,* and this species is the genotype of his genus *Symborodon.* This jaw proves to belong to the *Menodus* phylum and to be unrelated to the "*Symborodon*" of previous descriptions.

The measurements of Am. Mus. 6365 given by Cope are more or less inaccurate but serve to identify the type. The following may be substituted:

Measurements of Menodus torvus and M. trigonoceras, in millimeters

	M. ("Symborodon") torvus, Am. Mus. 6365 (lectotype)	M. ("Symborodon") trigonoceras, Am. Mus. 6345, ♀ [a]
Angle to front of canine	545	555
Depth of angle below condyle	225	263
Length of symphysis	155	142
Depth of ramus immediately behind m_3	124	[b] 120
Molar-premolar series	310	[b] 333
P_2–p_4	100	100
M_1–m_3	210	[b] 233

[a] Associated by Cope with type skull of *S. bucco.* [b] Estimated.

Measurements of premolars and molars in Menodus torvus (type), in millimeters

	P_2	P_3	P_4	M_1	M_2	M_3
Anteroposterior	27	37	43	51	67	97
Transverse	20	27	30	36	44	43

Type lower jaw of M. torvus.—The ramus ascends with a gentle curvature to the incisive border, which is absolutely devoid of any traces of teeth or alveoli, being thin and smooth with a small pit on its lower surface (Pls. CXXV, B; CXXVII; fig. 437). The incisor formula is therefore highly distinctive: $\mathrm{I}\frac{}{0}$. The canines were evidently small; the fangs measure 23 millimeters anteroposteriorly, 20 transversely; the crowns are at present broken away but could not have projected much above the level of the other teeth. There is absolutely no space for the first premolar; the second is placed directly behind the canine and has an elevated anterior, noncrescentic lobe and a posterior crescent; the third and fourth premolars exhibit both anterior and posterior crescents, no internal cingula, faint external cingula. The vertical arching of the premolar series is very pronounced. The molars also are devoid of internal cingula but present more or less complete external cingula.

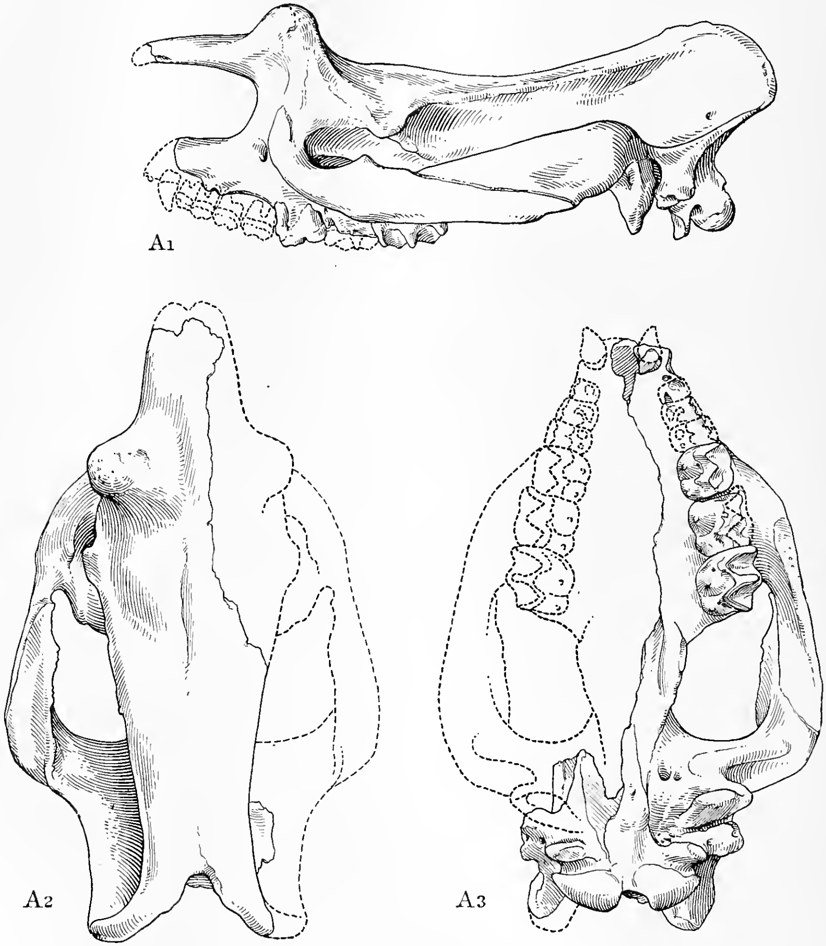


Figure 436.—Skull of *Menodus heloceras*

A1, Side view; A2, top view; A3, palatal view. One-sixth natural size. Am. Mus. 14576; found at the very base of the *Titanotherium* zone immediately overlying beds probably equivalent to Uinta C, Beaver Divide, near Hailey, Wyo. This very primitive skull agrees with the type of *Menodus heloceras* in the trihedral basal horn section, elongate proportions, and slender zygomata. It is also structurally allied to *Allops walcotti* and *Brontops brachycephalus*. The upper molars, though poorly preserved, resemble those of *Brontops brachycephalus* rather than those of *Menodus proutii*.

Menodus proutii (Leidy)

(*Titanotherium proutii* Leidy, 1852)

Plates LXXXII, CXXV, CXXVI; text figures 160, 409, 438

[For original description and type references see p. 205]

Geologic horizon.—Precise geologic level unknown, probably middle level of the *Titanotherium* zone, Chadron A 3 or B 1.

Specific characters.—Size of type jaw slightly smaller (m_1–m_3 234 mm.) than that of jaws referred to *M. trigonoceras*. Referred upper teeth (p^1–m^3 313 mm.) also smaller than in *M. trigonoceras*. Upper and lower premolar-molar series with cingula.

Characters of the type (lectotype) lower jaw.—The reasons for regarding this lower jaw fragment (Nat. Mus. 113) as the type, or lectotype, of this species are given on page 210 of this monograph. The specimen consists of part of the left ramus of the lower jaw containing the posterior alveolus of p_3, both alveoli of p_4, and the three molars, which are much worn and somewhat damaged in certain places. The molars exhibit the strongly developed external cingula that are characteristic of the true *Menodus*, and the measurements show that we have here a small member of the *Menodus* phylum, distinctly larger than the very primitive *M. heloceras* but somewhat smaller than the typical *M. trigonoceras* of the middle *Titanotherium* zone.

Measurements of Menodus proutii.—In the type lower jaw of this species the true molar series (234 mm.) is about 5 to 10 millimeters shorter than in jaws referred to *M. trigonoceras.* The specific name *proutii* is accordingly applied to the smaller members of the "*trigonoceras*" group. If we adopt the trinomial system of nomenclature the specific name *proutii* might include *M. proutii proutii* for the smaller skulls, and *M. proutii trigonoceras* for the larger skulls.

The molars of the type are 20 millimeters longer than in the type of *Symborodon torvus* Cope, which is also a menodont, and the jaw as a whole was considerably larger than those referred to *Allops marshi.*

In a National Museum skull (No. 4701, ♀) referred to *M. proutii* the premolar-molar series is 45 millimeters shorter than in the typical *M. trigonoceras*, the basilar length is also much shorter, and the zygomatic index (74, estimated) is relatively high.

Description of the neotype of M. proutii.—The upper jaw selected by Osborn as a neotype is a specimen (Am. Mus. 9335) from Lance Creek, Wyo., recorded from the middle *Titanotherium* zone.

The upper molars of the neotype are of conformable size with the lower molars of the type. In fact, the well-worn lower premolar-molar series of the type jaw has been found to articulate fairly closely with the less worn upper premolar-molar series of the neotype maxilla (fig. 438). The neotype upper grinders exhibit the characteristic internal and external cingula of *Menodus*, lofty ectolophs, tetartocones strongly developed on p^2, p^3, and p^4, a prominent triangular hypocone on m^3, and molar crowns distinctly elongated anteroposteriorly; they also exhibit rudiments of the crochet and antecrochet.

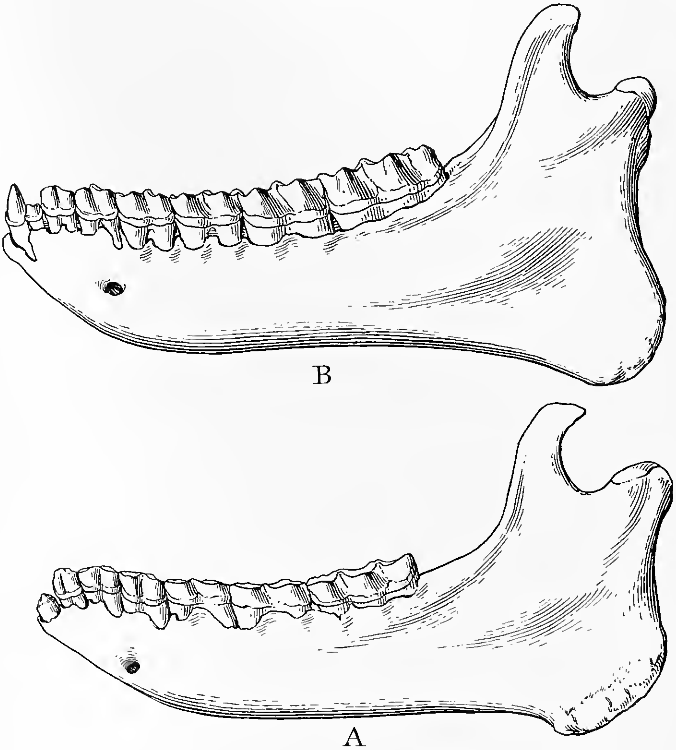


FIGURE 437.—Lower jaws of *Menodus* (*Symborodon*) *torvus* and *M. trigonoceras*

A, *Menodus torvus*, Am. Mus. 6365 (type); a very aged animal with angle very prominent and truncate, cheek teeth with sharply defined external cingula, and incisive border edentulous as in *Menodus*. B, *M. trigonoceras*, Nat. Mus. 4745; a very characteristic jaw, showing rather full symphyseal region, angle produced downward and backward, canines and cheek teeth sharply cingulate and subhypsodont. One-fifth natural size.

Additional measurements of Am. Mus. 9335 (neotype of *M. proutii*) are given below.

	Millimeters		Millimeters
Canine, vertical (estimated)	39	P^2, ap. by tr	26×28
Canine, anteroposterior	24	P^3, ap. by tr	34×41
P^1–m^3	313	P^4, ap. by tr	38×49
P^1–p^4	119	M^1, ap. by tr	59×64
M^1–m^3	192	M^2, ap. by tr	69×62
		M^3, ap. by tr	69×67

Dolichocephaly is strongly marked in m^{1-3}. The measurements show that this specimen is smaller than Carnegie Mus. 3068.

Transitional skulls from M. proutii to M. trigonoceras.—A skull (Carnegie Mus. 3068 or 558?) assigned to *M. trigonoceras proutii* appears to be distinguished subspecifically from the more progressive stage *M. trigonoceras* by the retarded development of the tetartocones of p^4, by the more primitive size and section of the horns, by the hypsodont characters of the external cusps of the molars, and by the correspondingly deep fossettes. This apparently occupies an intermediate position between the *M. heloceras* of the lower beds, *M. torvus*, and the *M. trigonoceras* of the middle beds. The sex is apparently female. To this may be attributed the fact that the horns are somewhat more primitive, elongate-oval in section.

The skull is that of a young animal in the sixth stage of growth, the protocone of m^1 being barely worn. As shown in the comparative measurements, the superior grinding teeth are of strikingly dolichocephalic type, the measurement p^1–m^3, inclusive, being 320 millimeters.

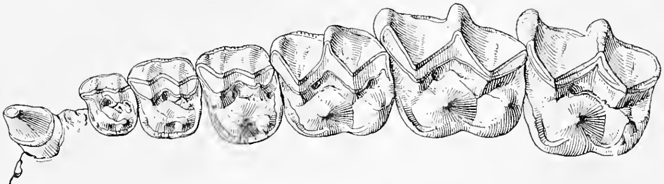


FIGURE 438.—Upper teeth of *Menodus proutii*

Am. Mus. 9335 (neotype); Chadron B, Lance Creek, Wyo.; exhibits the generic characters of *Menodus*. Canines conical with sharply defined cingulum, both external and internal cingula of the premolars and external cingulum of the molars sharply defined, molars elongate anteroposteriorly. Premolar pattern the same as in *Brontops brachycephalus*. The measurements of these teeth indicate reference to *Menodus proutii*. One-third natural size.

In this skull, as in dolichocephalic skulls generally, the bridge over the infraorbital foramen is broad and flat, and the external auditory meatus is widely open below. A wide space separates the postglenoid and paroccipital processes. The dolichocephaly of the dental series is also shown in the spacing of the teeth, which is so considerable that there is a slight diastema between the first superior premolar and the canine; cingula appear between the grinding teeth. P^1 is a large, actively functional tooth, elongate anteroposteriorly. The canines have the highly characteristic form of *Menodus* (*Titanotherium*), being long and pointed, with anterior and posterior cingula; at the same time, their slender section indicates that they belong to a female. Other distinctively *Menodus* characters are the crenulate internal faces of the deuterocones and the crenulate and strongly developed external and internal cingula with sharp edges. In the grinding teeth the hypocones are very prominent, and both the internal cones and the external crescents exhibit deep slopes; this elongate or subhypsodont character of the grinders, distinctive of all true *Menodus* teeth, is very striking.

Menodus trigonoceras (Cope)

(*Symborodon trigonoceras* Cope, 1873; "*Titanotherium trigonoceras*" Osborn, 1902)

Plates XX, XXII, CXXVIII–CXXXII, CXXXIV, CXXXV, CLVII; text figures 172, 378, 382, 396, 399, 409, 435, 437, 439, 440, 613–616, 630, 639

[For original description and type references see p. 213. For skeletal characters see p. 683]

Type locality and geologic horizon.—*Titanotherium* zone, level Chadron B.

Specific characters.—Skull larger than in *M. heloceras*. Premaxillaries to condyles 670 to 725 millimeters, tip of nasals to top of occiput 670 to 738. Mesaticephalic, width across zygomata 485 to 535 (?) millimeters. Index 74 (?). Horns, outside length 132 to 190 millimeters, basal section triangular, tips pyramidal; horns a little in front of preorbital malar ridge. Nasals squared distally, free length 115 to 140 millimeters, breadth 125 to 135 (?). Buccal swelling of zygoma more decided. Premolar-molar series 333 to 360 millimeters, premolars 127 to 136, molars 203 to 225, canines, anterior ♂, 42 to 47. Premolar tetartocones more progressive, tetartocone of p^4 more pronounced.

This animal is directly successive to *Menodus proutii* and connects this species by a series of "ascending mutations" with *M. giganteus*.

Observations on the measurements of Menodus trigonoceras.—In the typical skulls the premolar-molar series is 83 millimeters shorter than in the type of *M.* ("*Brontotherium*") *ingens*. Several skulls (Am. Mus. 1066, 1067, 1007; Nat. Mus. 4291) which were formerly referred to *M. giganteus* have the premolar-molar series over 60 millimeters shorter than in the type of *M. giganteus* and appear to belong rather with *M. trigonoceras*. Between the largest skull now referred to *M. trigonoceras* (Am. Mus. 1066) and the smallest referred to *M. giganteus* there is a marked difference in the length of the true molar series (23 mm.). Hence in our collections at present, with reference to the longitudinal dimensions of the grinding teeth, *M. trigonoceras* does not quite overlap *M. giganteus* but is separated by a small but distinct interval.

M. trigonoceras may be distinguished from *Allops serotinus* by the greater relative anteroposterior measurements of the true molars, by the lesser width of p^4, and by the great length of the nasals, as follows:

Measurements of Menodus trigonoceras and Allops serotinus, in millimeters

	M. trigonoceras, Nat. Mus. 4291, ♂	A. serotinus, Am. Mus. 520
P^1–m^3	360	330
P^1–p^4	136	133
M^1–m^3	224	206
Pmx to condyles	770	720
Zygomatic index	66	78
Nasal length	130	68
P^4, ap. by tr	[a] 41×55	43×65
M^3, ap. by tr	[a] 79×73	78×82

[a] Am. Mus. 6356.

Materials.—This important intermediate stage is represented by the type and paratype skulls in the American Museum (Nos. 6355 and 6356, Cope collection); also by two skulls in the National Museum (Nos. 4257, 1219). Nat. Mus. 4257 is definitely recorded by Hatcher as from the upper level of B, the middle *Titanotherium* zone, a fact of extreme importance, as helping to determine the geologic level of this species. Another skull (Nat. Mus. 4701, ♀) agrees in measurement with *M. proutii* but is recorded from the base of C; it thus may be a female of *M. trigonoceras*. There is no jaw positively associated with *M. trigonoceras*; a referred jaw is Am. Mus. 1007, which is transitional to *M. giganteus* in its measurements.

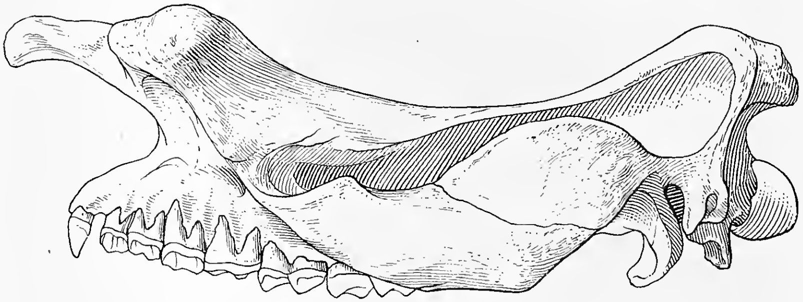


FIGURE 439.—Skull of *Menodus trigonoceras*

Side view. This skull (now in the Munich Museum, formerly Am. Mus. 1066) is vertically crushed, so that the nasals are tilted upward, the horns crushed downward, and the vertical diameters of the orbit and parietal region lessened. One-sixth natural size.

If measurements are reliable as indications of specific affinity we should have to add to this species the skulls Am. Mus. 1066, ♂, 1067, ♀, and the jaw Am. Mus. 1007, which were formerly included under *M. giganteus*.

Characters of the type and paratype of M. trigonoceras.—Cope's type (Am. Mus. 6355) fortunately is a skull in which all the superior portions are fairly preserved, as shown in Plates CXXVIII and CXXIX; the principal missing parts are the premaxillaries, maxillaries, and occipital condyles. A single molar tooth, m^3, shows that this type skull is young or in an early stage of growth, while the paratype skull (Am. Mus. 6356) is entering the seventh stage of growth.

This disparity of age explains some differences between these two specimens, especially in the zygomatic arches, which are wholly attributable to growth or age.

The type skull (No. 6355) belongs to a young individual; the nasals are long and rather thin, with nearly parallel sides, truncate distally. The horns are short, widely divergent, with trihedral section and a well-defined intermediate connecting crest, which is placed at the back part of the horn. The cranial vertex is of moderate width and extends backward into a slightly expanded occiput with lateral pillars, extending into rugose summits; the zygomatic arches are slender in vertical section, but they show marked expansion. The third superior molar bears a small, very sharply defined hypocone, a distinctive phyletic character of this series.

The paratype skull consists of the anterior portion (Am. Mus. 6356) of a fully adult individual in the seventh stage of growth. The more advanced age presents us with the adult characters of this species, especially the thickening and rugose expansion of the nasals distally, the thickening and moderate expansion of the zygomatic arches, the well-developed preorbital and postorbital processes.

Dentition.—The specific identification of the paratype with the type is rendered more positive by the close similarity in the structure of the third superior molar in both skulls. This tooth has a sharp and distinct hypocone. Other dental characters have weighty specific value (Pls. CXXXI, CXXXII). The technical formula, $I^{\underline{2}}$, $C^{\underline{1}}$, $P^{\underline{4}}$, $M^{\underline{3}}$, fails to convey an idea of the vestigial character of the incisor teeth, the crowns of which barely break through the bone of the incisive border and certainly did not cut through the gum; thus the premaxilla of this animal should be described as functionally edentulous. The sex of the paratype is apparently female, the canine being rather slender and elongate. The maxillary teeth are rather progressive in development; the first premolar exhibits a rudimentary tetartocone, or four cusps in all. The tetartocones on p^2, p^4 are well developed but still much inferior in size to the deuterocones; the premolars are further distinguished by pronounced internal and external cingula. Throughout the premolar-molar series we observe a deep pit in the midvalley, just internal to the ectoloph, which is homologous with the medifossette of the rhinoceros and horse molar. Just internal to this pit two ridges enter the median valley. These are apparently homologous with the "crochet" and "antecrochet" of the rhinoceros and horse molars. The molar teeth also exhibit well-developed external cingula; the internal cingula, as in all other titanotheres, are incomplete opposite the protocones.

Skulls of M. trigonoceras.—Of the six skulls in the National Museum collection referred to *Menodus trigonoceras* one (Nat. Mus. 4257) is recorded from the upper levels of the middle *Titanotherium* zone. It belongs to a small male in the seventh stage of growth. The anterior measurement of the canines is 42 millimeters (estimated). Two extremely small vestigial incisors persist upon one premaxilla only. In the first superior premolar the tetartocone is connected by a confluent crest with the deuterocone, as in other species of this genus. The tetartocone cusp on p^3, p^4 is very distinct, especially in p^4.

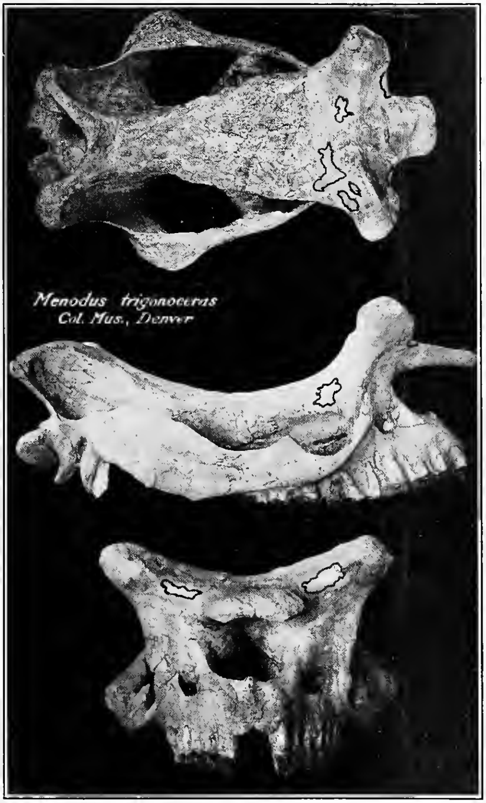


FIGURE 440.—Skull of *Menodus trigonoceras*

In the Colorado Museum, Denver. The nasals and horns were detached when the skull was found, but there is no question as to the association.

From the vertex to the tips of the nasals the skull measures 665 millimeters; the free length and the free width of the nasals are nearly equal, namely, 120 by 125 millimeters. The horns measure 150 millimeters from the edge of the anterior nares to the tips. On the inferior surface of the skull the vomer extends back from the presphenoid as a distinct narrow keel.

In another skull, an old male (Nat. Mus. 1219), as in the more advanced or eighth stage of growth, the horns measure 195 millimeters as compared with 150 in the specimen just described. This is a natural growth increase. It is important to note that the nasals are practically the same length as in the younger specimens, namely, 115 millimeters; but they are greatly increased in breadth (160 mm.), also in the rugose expansion of their tips, which support a pair of lateral tuberosities. This animal is evidently a very old male, and its senescent character is emphasized by the entire disappearance of the vestigial upper incisors. It is also a very large individual. The premolar-molar series measures 345 millimeters.

In contrast with the two skulls described above there is a third skull (Nat. Mus. 4701) belonging to a young female which is recorded by Hatcher from level C 1 of the upper *Titanotherium* zone. The premolar-molar series measures 300 millimeters. The female sex is indicated by the small, pointed canines (34 mm.). Inconsistently with its high geologic level as recorded, the skull exhibits a relatively low stage of development in its premolar teeth, the tetartocones being less clearly separated off than in the old male above described. Although the animal is still young, the incisors have entirely disappeared, as well as all traces of their alveoli. The internal cingulum of the premolars is quite as prominent in this female as in the males, again proving that the cingulum is not a sexual character. There is a large hypocone on the last superior molar, which thus appears to be a specific if not a generic character.

The Ottawa Museum skull from the lower Oligocene of Swift Current River, Assiniboia, Canada.—The fragmentary cranium described and figured by Cope (1891. 2, p. 10, pl. 6) as "*Menodus americanus*" very probably belongs to *M. trigonoceras.*

Menodus giganteus Pomel

("*Brontotherium*" *ingens* Marsh, 1873; "*Titanotherium ingens*" Osborn, 1902)

Plates XVIII, XX, XXIV, XLVII, XLIX, CXXXIII, CXXXV–CXLI; text figures 24, 159, 227, 228, 375, 381, 387–389, 391, 393, 394, 396, 399, 400, 406, 409, 441–446, 617–619, 630, 640, 642, 701, 713, 715–719, 744

[For original description and type references see p. 204. For skeletal characters see p. 687]

Geologic horizon.—Upper *Titanotherium* zone.

Specific characters.—Skull very large, premaxillaries to condyles 770–825 millimeters, tip of nasals to top of occiput 712–755+. Dolichocephalic, width across zygomata 515–553 millimeters, index 62–70. Horns, outside length 150–290 millimeters; basal section triangular, tips pointed; horns much in front of antorbital malar ridge. Buccal swelling of zygoma about as in *M. trigonoceras* (that is, moderate). Premolar-molar series, 360–428 millimeters; premolars 133–162, molars 223–270; dental index 51 (typical). Premolar tetartocones very progressive but still connected with deuterocones by a narrow strip, tetartocone of p^4 very pronounced. Canines ♂ very long (70 mm.).

Menodus giganteus was certainly a contemporary of its long-horned rival *Brontotherium gigas* and probably extended up to the period of the still more specialized *Brontotherium platyceras.* While far inferior in length of horn to those brontotheres, it was certainly superior to them in the possession of a superb series of grinding teeth with connecting crowns and more elevated crests and cones.

The sexual characters of *M. giganteus* are very clearly brought out by comparison of two male skulls, Nos. 1066 and 505, and two female skulls with jaws, Nos. 1067 and 506, in the American Museum collection. A fine skull in the National Museum (No. 1220) also belongs to a male. The skull Nat. Mus. 4291 is recorded from the highest level of the upper *Titanotherium* zone. The male skulls exceed the female in the width of the zygomatic arches, thus proving that, as in the brontotheres, the buccal processes are partly secondary sexual characters. The comparatively slender, pointed horns, and pointed canine teeth of the females are well exhibited in Plate CXXXV, B. This figure shows incidentally the extreme effects of lateral crushing as contrasted with the extreme effects of vertical crushing and deformation of the skull.

The type specimen of the species "*B. ingens*" was erroneously employed by Marsh to complete the characters of the genus *Brontotherium*, but we now know that the genotype of *Brontotherium*—namely, *B. gigas*—is a very different animal in many ways. The type specimen of "*B. ingens*" in the Yale Museum is a fine representative of the species, as described in detail below. The absence of the premaxillary bones in this specimen led to many errors regarding the condition of the incisor teeth; we now have conclusive evidence that in this species, as in *M. trigonoceras*, the incisors are atrophied, vestigial, or entirely wanting. The evidence as to the character of this species afforded by the type specimen is now supplemented by that of an exceptionally fine series of skulls in the American, National, and Field Museums.

Observations on the measurements of Menodus giganteus.—The true molars of the fragmentary type lower jaw agree in measurement and other characters with jaws referred to this species.

In the referred skulls the grinding teeth range from 385 to 465 millimeters in length, a difference of 80 millimeters. The largest skull (in the University of Wyoming) has a longer dentition than any other known titanothere (p^1–m^3 465 mm.).

The extreme contrasts between the narrow mesaticephalic skull and dentition of *Menodus giganteus* and the broad (brachycephalic) skull of *Brontotherium platyceras* are shown in the table below.

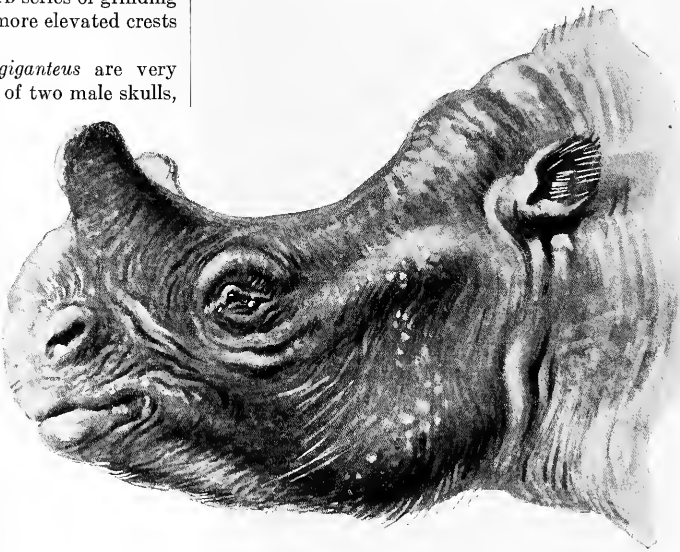


FIGURE 441.—Restoration of *Menodus giganteus*

By Charles R. Knight. About one-ninth natural size.

Measurements of Menodus giganteus, Brontotherium platyceras, and B. gigas, in millimeters

	M. giganteus		B. platyceras, Field Mus. 12161	B. gigas, Am. Mus. 492
	Field Mus. P 5927	Univ. Wyoming		
P^1–m^3	425		340	
P^1–p^4	150		120	
M^1–m^3	270		223	
Molar index	32		25	
P^4, ap. by tr		58×73		47×72
M^3, ap. by tr		100×78		91×99
Pmx to condyles	825		880	
Zygomatic index	62		80	
Nasal length	175		38	
Horn length	290		[a] 390	

[a] Estimated.

From *Allops crassicornis* we observe that *M. giganteus* is distinguished by the greater length of p^1–m^3 and especially of the true molars (*M. giganteus* 246–285 mm., *A. crassicornis* 220), by the greater length of the nasals, and by the much lower zygomatic index.

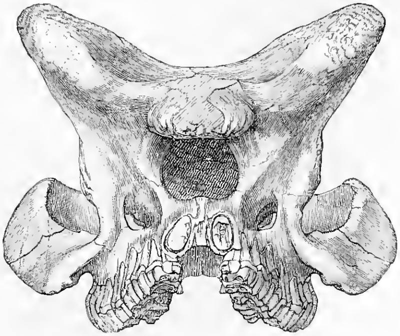


FIGURE 442.—Skull of *Menodus giganteus*

Yale Mus. 12010, type of *Brontotherium ingens* Marsh. Front view. One-eighth natural size. This view shows well certain features of *Menodus*, as follows: Horns trihedral and pointed, nasals distally broad, zygomata deep with small buccal expansions, canines large, cheek teeth with sharp external cingula.

From *Brontops robustus M. giganteus* is readily distinguished as follows:

Measurements of Menodus giganteus and Brontops robustus, in millimeters

	M. giganteus	B. robustus
P^1–m^3	385–465	340–376
P^1–p^4	141–176	139–151
M^1–m^3	246–285	220–236
P^4, ap. by tr.	50×68 to 58×73	43×55 to 46×69
M^3, ap. by tr.	93×89 to 100×78	73×84 to 90×89
Pmx to condyles	777–825	743–813
Zygomatic index	62–73	76–83
Nasal length	105–175	52–90

Geologic and geographic distribution.—The geologic range of this species as recorded by Hatcher is from the summit of B, the middle zone, to the summit of C, the upper *Titanotherium* zone.

Materials.—The species is represented by Pomel's type jaw, which has been destroyed and is known only from Leidy's figure and measurements; also by Marsh's excellent type skull of "*B. ingens*" in the Yale Museum (No. 12010), found in Colorado; by three skulls in the American Museum (Nos. 505, ♂; 1066, ♂; 1067, ♀); by six fine skulls in the National Museum (No. 1220, etc.); and by the superb skull associated with cervical and anterior dorsal vertebrae (Pls. CXXXIX, CXL) in the Field Museum of Chicago (No. P 5927). The largest skull of all is that in the University of Wyoming Museum.

According to the measurements given in the table above, the skulls Am. Mus. 1066 and 1067 and Nat. Mus. 4291, which are all referred here to *M. giganteus*, are much closer to *M. trigonoceras* and are separated from the true *M. giganteus* skulls by a considerable gap.

Characters of Marsh's type of "B. ingens."—The principal characters of the type skull as given by Marsh with measurements are entered in the table above. Additional characters are as follows: This animal is in the eighth stage of growth, advancing toward the ninth. The tips of the internal cusps of m^2 are slightly worn, barely showing the dentine. The top of the skull is uncrushed but somewhat depressed just behind the connecting horn crest. The right horn and right half of the nasals are partly restored, although figured as complete in Plates CXXXVII and CXXXVIII. In the left horn, which is more perfect, the triangular shape is very marked. The anterior angle of the horn runs directly into the nasals. The premolars exhibit very broad internal cingula and pronounced external cingula; the first premolar displays an internal crest formed of the deuterocone and tetartocone. The second and third premolars have the tetartocones more distinct, elevated, and sharply separated off from the cingula; the deuterocones and tetartocones are subequal,

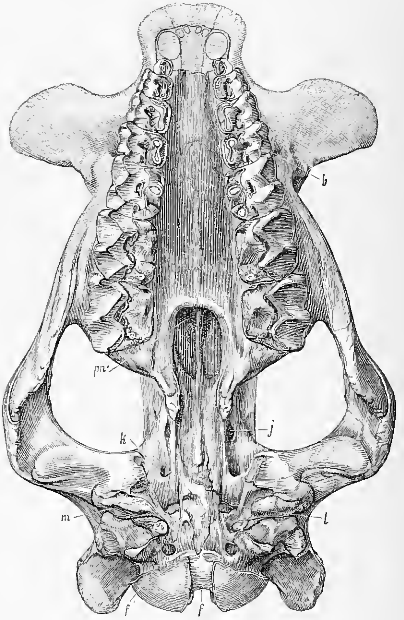


FIGURE 443.—Skull of *Menodus giganteus*

Yale Mus. 12010, type of *Brontotherium ingens* Marsh. Palatal view. One-eighth natural size. Drawing made by Berger under the direction of Marsh. This view shows *Menodus* characters as follows: Skull dolichocephalic, nasals long and distally broad or squarish, horns trihedral in section and pointed, tooth rows rectilinear, cheek teeth with sharp internal and external cingula, premolars with large postero-internal cusps, molars elongate anteroposteriorly, zygomatic expansion moderate.

thus being a progressive advance beyond the *M. trigonoceras* condition. The hypocone of m^3 is tuberculate, with a narrow crest extending off toward the metacone; this tooth exhibits a sessile "crochet" and "antecrochet."

Additional measurements of the type of "B. ingens"

	Millimeters
Summit of occiput to tip of nasals	755
Extreme spread of horns	490
Free length of nasals	125
Width of nasals	125
Molar-premolar series, estimated	428
True molar series	265

Dentition.—The incisors either consist of extremely reduced crowns in depressed alveoli, resembling the vestiges seen in *M. trigonoceras*, or are entirely obsolete. Of the male skulls in the American Museum No. 1066 shows two vestigial alveoli and No. 505 shows one small alveolus; similarly, in the National Museum No. 4291 shows two alveoli partly closed. In one of the female skulls (Am. Mus. 1066) there is a single vestigial incisor on one side, lying in its alveolus below the surface of the jaw.

Canines: Contrasting with this atrophy is the hypertrophy of the canines, which are readily distinguished from those in members of the *Brontotherium* phylum by their long and pointed crowns, circular to suboval in section. Almost completely encircling the base of the crown is a prominent cingulum; this is a very exceptional and distinctive character; in the females the cingulum is perhaps somewhat less prominent. In the males the largest canines measure about 70 millimeters; in the females the canines measure about 40 millimeters. The chief distinction of the female tusks is their much more slender and pointed character.

Premolars: The persistence of the first premolars in both jaws is a general characteristic of this species, although not observed in the specimen in the Field Museum. A peculiarity of p^1 is the presence of a distinct tetartocone, which is even stronger in "*B. ingens*" than in *M. trigonoceras*. In the succeeding premolars, p^2–p^4, the tetartocones are more or less well defined and distinct from the deuterocones, either connected by a low ridge or altogether separate, the proportion between the size of the deuterocone and tetartocone being as 5 to 3. This acceleration of the tetartocone is a progressive character; it is less advanced in the American Museum skulls than in the Yale Museum type of "*B. ingens*," which was probably found on a very high geologic level. As a rule the tetartocones increase in distinctness as we pass backward from p^1 to p^3, but as in all other titanotheres the tetartocone in p^4 is generally less distinct. A mesostyle ridge is faintly developed on p^4 in some specimens of *Menodus*. It is best developed in certain specimens of *Brontotherium* and *Megacerops* in which p^4 is more molariform than in *Menodus*.

Both molars and premolars have deep pits or "medifossettes" in the midvalley, just internal to the ectoloph; this "fossette" is bounded internally by folds homologous with the "antecrochet" and "crochet" of rhinoceros molars. The molars and to a less extent the premolars are proportionately narrower and longer than in the brachycephalic phyla.

Molars: The "fossette" just mentioned is correlated with the vertical elongation of the ectoloph, which now measures 80 millimeters in height, while the protocone measures only 28 millimeters; the outer wall of the tooth is thus between two and three times as high as the inner wall. As in the preceding species of this phylum, the internal cusps also of the grinding teeth have steep slopes.

The hypocone of m^3 shows individual variability: it is either large and distinct (Am. Mus. 1067), or small and distinct (Nat. Mus. 4291), or confluent with the cingulum (Am. Mus. 1066).

The cingulum is certainly the most conspicuous and distinctive character of the grinding teeth; not only does it encircle the canine, but it is sharply defined upon the outer faces of the entire superior and inferior premolar-molar series (Pls. CXXXVI, CXXXVII, CXXXIX). The superior premolars are readily distinguished by the broad shelf-like internal cingulum, unlike that in any other phylum. The superior molars are also cingulate upon the inner sides. The only part of the entire dental series which entirely lacks the cingulum is the inner side of the inferior premolar-molar series, where no titanothere displays a cingulum.

The grinding series as a whole, therefore, is distinguished by its great length, by the proportionate length of the individual teeth, the anteroposterior slightly exceeding the transverse diameter (in the molars), and by the pronounced development of the cingulum.

Skull.—The chief distinction of the skull lies in its proportions; it is relatively long and narrow, the average ratio of two male skulls being, length 773 millimeters, breadth 545 millimeters, and consequent index 69, while in the type of *Brontops robustus* the ratio is 765 to 667, and the index is 87. In all the skulls the nasals are large and quadrate, measuring from 127 to 175 millimeters in length and from 125 to 145 and more in breadth. As in *M. trigonoceras*, advancing age is accompanied by a rugose development of the extremities, with a lateral expansion of the tips and a deepening of the median cleft. Other growth characters of the skull are the increasing length of the horns from 150 to 290 millimeters, the increasing rugosity and breadth of the occiput, the widening of the buccal expansions of the zygomata. These buccal expansions, however, remain limited in extent and do not involve a large part of the zygomatic arch as in *Brontotherium;* immediately below and slightly anterior to the buccal expansion is a very characteristic, slightly downward projection. Other conspicuous characters are the relatively large orbits (as compared with those of *Brontotherium*), the bridge over the infraorbital foramen, the steep slope of the occipital vertex (contrast *Brontotherium*). Additional features of advancing age are the development of the marked supraciliary expansion of the lateral frontal parietal crest (Nat. Mus. 1220), the obliteration of the suture between squamosal and malar.

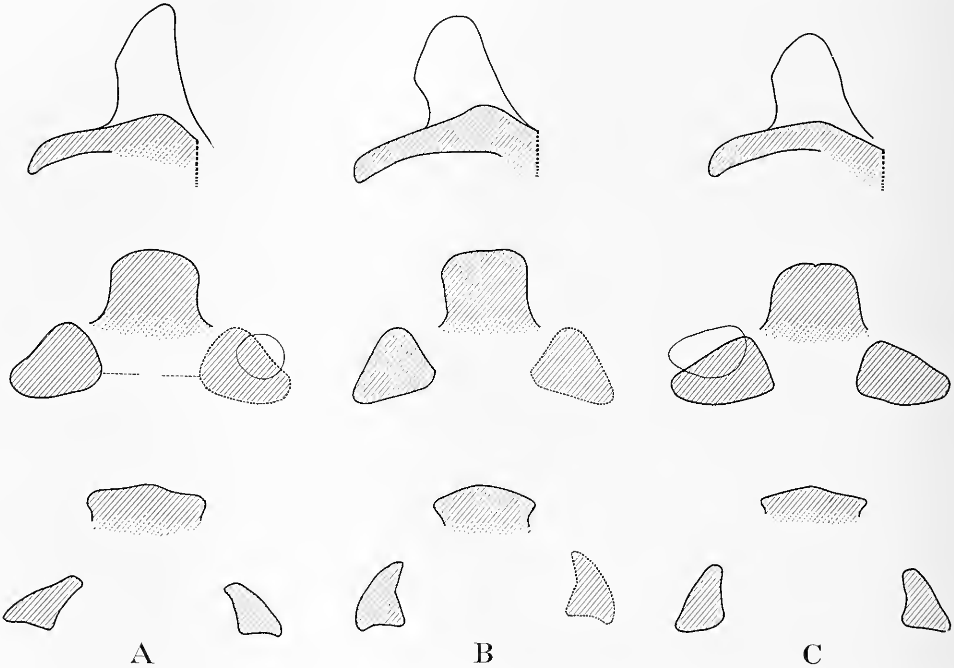


FIGURE 444.—Sections and contours of skulls of *Menodus giganteus* and *M. varians*

M. giganteus: A, Am. Mus. 505, ♂ (neotype), and B, Yale Mus. 12010 (type of *Brontotherium ingens*); relatively long-pointed horns with a prominent anterior swelling suggestive of the accessory hornlet in *Diploclonus*, horns trihedral in basal section, connecting crest near the plane of the posterior face of the horns, nasals long and wide, zygomata little expanded. C, *M. varians*, Yale Mus. 12060 (type); horns thicker (especially at the top), basal section widely trihedral, nasals broad and thick, zygomata somewhat expanded. One-ninth natural size.

Horns.—The distinctive characters of the horns are not only the connecting crest, which, as shown in the section, is situated very far back, but the normal direction, which is chiefly outward and slightly upward. A very distinctive character in front view is the straight inferior contour of the horn (see fig. 442); all members of the *Brontotherium* and *Megacerops* series have a curved or convex lateral inferior contour as seen from in front. Correlated with the lesser strain of the horns and the great breadth of the anterior nares the maxillary pillars on either side of the anterior nares are much thinner than in the stout-horned species. The basal horn section as compared with that of *M. trigonoceras* has already been described and is very distinctive; briefly it consists of an isosceles triangle with the external angle at the vertex. (See figs. 399, 444, 445.) The skull has other distinctive features: First, we observe the width of the bridge over the infraorbital foramen; as in the Palaeosyopinae and also in the related *Brontops* phylum this bridge extends into a thin plate anteriorly, so that the foramen is distinctly seen on the side of the face, whereas in *Brontotherium* and *Megacerops* the malar bridge is narrow and convex and the foramen is not seen in side view. This elongate condition of the infraorbital canal and breadth of the malar bridge is correlated with the dolichocephaly existing throughout the skull. In the midline of the parietal crest there is observed a median ridge clearly shown in the section, there is also occasionally a conspicuous knob in the midparietal region. In the occipital region we observe a mastoid foramen; the postglenoid and paroccipital processes are proportionately narrower and deeper than in the *Brontotherium* series, another fact in keeping with the dolichocephalic structure of the skull. Again there is narrower contact between the postglenoid and post-tympanic, a more open auditory meatus, and a wider space behind the ear than in the brachycephalic types.

Lower jaw.—Dolichocephaly is also influential in the jaw structure, as among the long-skulled rhinoceroses. The rami of the jaw are long and deep, the lower border being carried horizontally forward until it terminates in a well-marked angulation of the chin; from this point it ascends sharply to the incisive border; the angle is broad, with a marked backward extension. This decided angulation of the chin is quite distinct from the convex lower border and shallow, sloping chin in the *Brontotherium* series. Another distinctive feature is the greater size of the mental foramen (Am. Mus. 1067) and its more posterior position beneath the fourth premolar. In the *Brontotherium* series the foramen is usually smaller and more anteriorly placed. The angle has a smooth border, is rather delicate and narrow but none the less prominent, flaring obliquely backward with an even curve at the postero-inferior border, in contrast with the *Brontotherium* angle, which is broader, with a rugose border and truncate apex. The coronoid is broad, has a smooth, rounded anterior edge, and is not strongly curved backward. The smooth backward extension of the angle, the straight lower border, and the definition of the chin are characters exactly paralleled in the dolichocephalic rhinoceroses.

Variation in size.—This is not only distinctive of sex, the females being more slender in all their proportions, but of the stages of growth which are recorded in the measurements of the skulls, and also of the stages of vertical succession or evolution which are recorded in the measurements chiefly of the premolar-molar series, as shown in the tables on page 523.

Final stage of evolution.—In the Field Museum, Chicago, there is a superb skull (No. P 5927), found near the top of the upper *Titanotherium* zone at Phinney Springs, S. Dak. With it were discovered the lower jaws, cervical and anterior dorsal vertebrae. (See p. 686.) The skull is in a beautiful state of preservation and has been very accurately reconstructed by Mr. E. S. Riggs. It belongs to a fully adult animal, with well-worn teeth, and strongly accentuates all the characteristic features of the type of *M.* ("*Brontotherium*") *ingens*. The lateral and anterior views (Pls. CXXXIX, CXL) accordingly give the most perfect idea of the extreme development of this phylum.

Noteworthy peculiarities in the dentition are these: (1) P^1 is present on the left side of the skull but absent on the right. In most other specimens p^1 is constant; this, however, proves that in *Menodus* as in *Brontops* p^1 is a variable tooth. (2) P_1 is also absent in this specimen, the canine being closely crowded against p_2. (3) The third inferior molar exhibits a very small hypoconulid which lacks the internal cup or crescent.

Noteworthy progressive features are the presence of an anterior swelling or incipient hornlet on both the horns, somewhat similar to that observed in the type of *Diploclonus bicornutus*, and the very anterior position of the bases of the horns, which are almost as far in advance of the line of the orbits as in the type of *Brontotherium gigas*. This feature does not, however, interfere with the great length of the nasals, which protrude far beyond the vertical line of the premaxillaries. Notable, also, are the relatively great length of the horns (outside measurement 290 mm.).

The detailed measurements of this important skull are presented in the table on page 523.

Observations on the Menodus giganteus of the University of Wyoming.—The largest dentition among known titanotheres is exhibited in a specimen of *Menodus giganteus* in the University of Wyoming, from the upper *Titanotherium* zone of Bates Hole, Carbon County, Wyo. The premolar series (p^1–m^3) measures 465 millimeters, as compared with 410 in the type. The premolars are very large (176 mm.) and highly progressive. They conform in all details to the *Menodus* type. They show very clearly the enamel folds and ridges which are called "crista," "protoloph," and "metaloph." Their tetartocones, although large, are still connected by a bridge with the deuterocones, as in the Menodontinae generally. The dimensions of the premolars and molars are as follows:

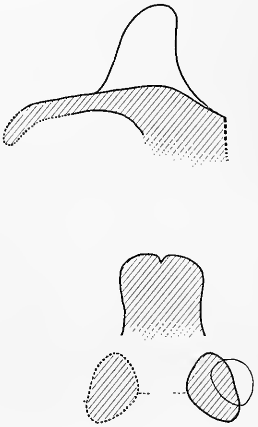


FIGURE 445.—Sections and contours of skull of *Menodus giganteus*

Am. Mus. 506, ♀ (cf. fig. 446). In females of this species the horns are slender but have a relatively high connecting crest, the basal section is obliquely and roundly trihedral, the nasals are long and are decurved at the tip. One-eighth natural size.

	Millimeters
P^1, ap. by tr	25×26
P^2, ap. by tr	40×47
P^3	51×59
P^4 (estimated)	58×73
M^1 (estimated)	81×77
M^2 (estimated)	100×80
M^2, ectoloph, anteroposterior	114
M^2, transverse (across mesostyle) (estimated)	95
M^3, height of ectoloph (paracone)	88
M^3, ap. by tr. (estimated)	100×78
M^3, transverse (across mesostyle)	90

Menodus varians (Marsh)

(*Menops varians* Marsh, 1887; "*Titanotherium ingens* Marsh," Osborn, 1902)

Plate CXLII; text figures 181, 409, 444

[For original description and type references see p. 223]

Geologic horizon.—Geologic level not known, probably upper *Titanotherium* zone.

Specific characters.—The skull is relatively shorter or less extremely dolichocephalic than that of *M. giganteus*. Skull length, premaxillaries to condyles

760 millimeters, nasals to top of occiput 695, width across zygomata 555, zygomatic index 73 (that is, subbrachycephalic). Nasals decidedly shorter than in *M. giganteus* (free length 105 mm., breadth 140). The horns are outwardly directed but of similar section to those in *M. giganteus*. Two vestigial upper incisors retained on each side. Premolar-molar series (410 mm.) relatively very long (dental index 54). Premolar tetartocones very distinct. P^4 with reduplicate tetartocone. Hypocone on m^3 large and distinct from the cingulum.

This animal appears to be specifically distinct from *M. giganteus* and to present a form which tends to bridge over the structural gap between *Menodus* and *Allops*, since while exhibiting all other characters of *M. giganteus*, it possesses the short nasals characteristic of *Allops*. That this skull may be an *Allops* is further indicated by its sub-brachycephaly (index 73) as in *Allops serotinus*, also by the proportions of its horns and nasals.

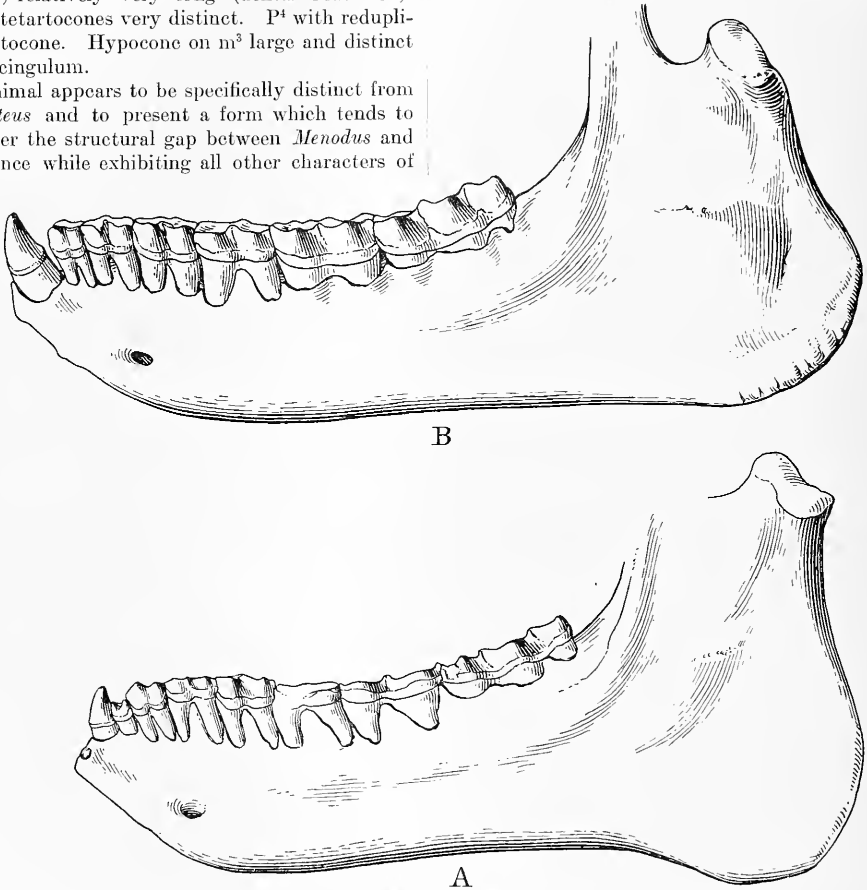


FIGURE 446.—Lower jaws of *Menodus giganteus*

A, Am. Mus. 506, ♀ (cf. fig. 445); B, Field Mus. P 5927, a large male. Both jaws have the ramus elongate, the angle produced posteriorly into a rounded elbow, and the teeth sharply cingulate. One-fifth natural size.

Materials.—The species is known only from the type skull in the Yale Museum (No. 12060), which is represented in Plate CXLII.

Description of the type.—The type skull is that of an old animal in the eighth to ninth stage of growth, both the protocone and the hypocone of m^2 being well worn. In its superior aspect the skull is very similar to Marsh's type of *ingens*, although less dolichocephalic; the horns are connected by the characteristic low transverse crest. In the plane of the posterior faces they are crushed downward and outward in such a manner as not only to change their normal elevation but to decrease the acuteness of the trihedral section and make it difficult to express in cross section (fig. 444, C) their actual form. The nasals had the spread but not the length characteristic of *Menodus*. In inferior aspect of the skull the nares open immediately behind the second molar, as in *M. ingens*. There are traces of a median vomerine keel and a very prominent rugose projection at the junction of the basisphenoid and basioccipital, which is apparently broken away in the type of *M. ingens*. As in *M. ingens* the orbit is directly above the posterior portion of the first molar.

Measurements of Menodus varians

	Millimeters
Length of skull, vertex to tip of nasals	695
Basilar length, occipital condyles to premaxillary	760
Transverse width across zygomata	555
Molar-premolar series	410
True molar series	255
Premolar series	155
Canine crowns, anteroposterior diameter	35
Free length of nasals	105
Free width of nasals	140

Dentition.—The alveoli for two vestigial incisors upon each side persist, with a narrow median diastema between them. There is a vestige of a third alveolus on one side. The alveoli are exceptionally shallow, and these teeth were undoubtedly vestigial. The canines are so robust as to indicate that this was a male animal. The cingulum is continuous around the anterior face; the crowns are broken off. Close behind the canines are the bifanged, well-developed first premolars; these teeth are distinguished as in *M. giganteus* by very broad, crenulate internal cingula and prominent external cingula; in p^2 and p^3 the tetartocones are very prominent. P^4 exhibits an interesting example of correlated bilateral variation in the double conical summits of the tetartocones; this, however, is probably due to the advanced condition of the cingulum. The hypocone is strongly developed and entirely distinct from the cingulum upon m^3, as in Marsh's type *Diconodon montanus* and in several specimens of *M. trigonoceras*.

Relationship to Menodus.—In describing this supposed genus, *Menops*, Marsh observed: "The present genus is most nearly related to *Diconodon* and in its molar teeth agrees with that form. It differs in the presence of two upper incisors on each side." The entirely vestigial character of the incisor teeth naturally forbids our assigning them generic value. This animal presents so many points of close similarity with the type of *M. ingens* that the single decisive specific character which can be selected is the abbreviation of the nasals and the somewhat less extreme dolichocephaly. The nasals are less quadrate than in *M. ingens*, the free length (105 mm.) being less than the free width (140 mm.). Even this character is possibly attributable to individual variation, since some of the typical specimens of *M. giganteus* and *M. trigonoceras* show a relative abbreviation of the nasals. A similar broadening and abbreviation of the nasals occurs in the subgenus *Allops*. The inferior contour of the horns is less straight, and the horns apparently diverge more widely than in *M. ingens*, a condition partly attributable to the downward crushing of the skull or perhaps indicating affinity with the flat, outwardly directed horns of *Allops*.

The reduplication of the tetartocone on p^4 is another feature observed in *Allops serotinus*. A more important difference is that the skull is proportionately shorter and less dolichocephalic than in *M. ingens*, the proportions being, length 760 millimeters, breadth 545, as compared with length 825, breadth 550. The hypocone of m^3 is even larger and more distinct than in most specimens of *M. giganteus*, resembling that in the type of *Diconodon montanus*. This may be a specific or progressive character.

We observe the similarity to *M. giganteus* in many other details, such as the sections of the hôrns, the shape of the zygomatic arches, the presence of small alveoli for the incisors, the antorbital knob on the molars, the comparative length of the face, the apparent exposure of the mastoid bone, the sharp and horizontal shelf of the top of the occipital pillars, the bifanged, well-developed first premolars, the extreme cingulate development of the canines and grinding teeth, the prominence of the tetartocones and of a hypocone on m^3.

Our conclusion is that the genus *Menops* is probably equivalent to *Menodus*, while the species *M. varians* may be regarded provisionally as valid and distinct.

Menodus montanus (Marsh)

(*Anisacodon montanus* Marsh, 1875; *Diconodon montanus* Marsh, 1876; "*Symborodon montanus*" Osborn, 1902)

Text figures 175, 447

[For original description and type references see p. 217]

Type locality and geologic horizon.—Recorded as from "northern Nebraska"; *Titanotherium* zone.

Specific characters.—Nasals narrow, relatively abbreviate, so far as preserved, resembling those of *Allops serotinus*, grinding teeth with transverse diameter exceeding the anteroposterior, thus resembling *Allops*. Incisors reduced or vestigial, as in *Menodus*, m^3 with a distinct hypocone, prominent external cingula on all grinding teeth, and a strong internal cingulum on the premolars. M^1–m^3 218 millimeters.

General characters.—The genotype (Yale Mus. 10022) of *Anisacodon montanus* is an incomplete fragment of a skull, together with the complete molar series of both sides, portions of the left maxillary, of the left zygomatic arch, the extremities of the nasals, and the left superior premolars. There are paired alveoli for p^1. As in *Menodus* the incisive border is narrow, sharp, and functionally edentulous, but it exhibits two vestigial alveoli. The premaxillary contains two canine alveoli. The internal cingulum of the premolars is prominent and rounded; the external faces of both premolars and molars exhibit a sharply serrate cingulum. The third superior molar presents a conical hypocone quite distinct from the cingulum. To this the generic name *Diconodon*, originally applied by Marsh, refers. The grinding teeth are of about the same size as those of *Menops varians*, the molar fossettes are very deep.

Measurements of Menodus montanus

	Millimeters
Canine alveoli, anteroposterior diameter	31
Canine, transverse diameter	19
Nasals, transverse	96
Nasals, longitudinal (so far as preserved)	87
Second superior molar, transverse	88
Second superior molar, anteroposterior	76
Molar series, superior	218

Affinities to Menodus.—As shown in the above detailed description this animal agrees with *M. "ingens,"* and especially with *M. varians*, in the vestigial character of the incisors, the bifanged premolar, the presence of a distinct hypocone on the last superior molar, the marked external cingula on both premolars and molars, and the strong internal cingula on the premolars. It apparently differs from *Menodus* in the narrow nasals and the more transversely extended proportions of the molar teeth.

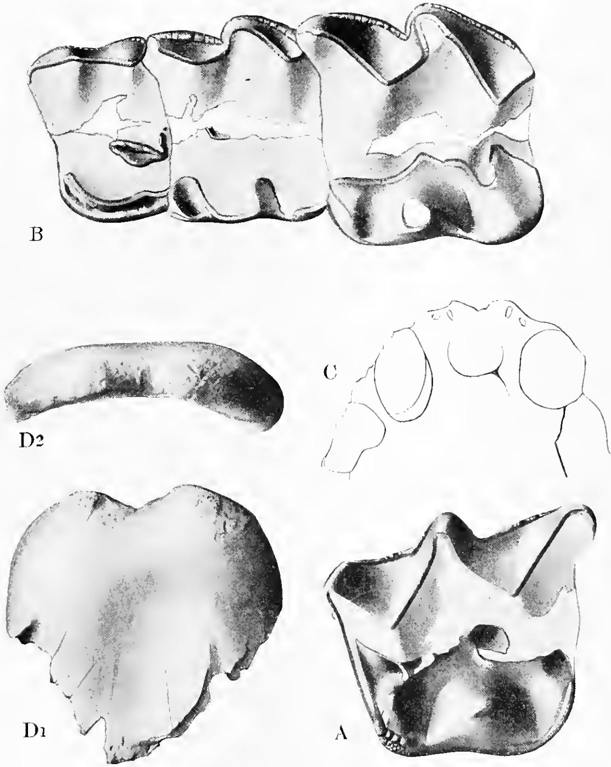


FIGURE 447.—Teeth and nasals of *Menodus montanus*

Yale Mus. 10022 (type of *Diconodon montanus* Marsh). A, Third right upper molar. The elongate proportions and hypocone surrounded by a cingulum are seen also in certain other specimens of *Menodus* (cf. Am. Mus. 1067). B, Fourth upper premolar and first and second true molars of the left side. The elongate proportions and sharp internal and external cingula are seen as in *Menodus*. C, Alveoli of the upper incisors and canines. The upper incisors were vestigial, as in *Menodus;* the canines were large, implying male sex. D_1, Top view of distal portion of nasals. The paired projections are seen as in *Menodus*. D_2, Front view of nasals. One-half natural size.

It seems probable that this fragmentary specimen should be considered provisionally as the type of a valid species, although more perfect material may relate it still more closely or even specifically to *M. giganteus*.

SECTION 6. THE BRONTOTHERIINE GROUP

We now consider the brontotheriine group as distinguished from the menodontine group. It contains two phyla, closely affiliated in their Eocene origin but widely diverging in their Oligocene evolution—namely, the Megaceropinae and Brontotheriinae.

GROUP CHARACTERS

Lower Oligocene titanotheres of medium to larger size. Horns progressively elongating in the males until they attain great size at the expense of the nasals, which are atrophied. Face abbreviated, or brachyopic. Skulls with broadly spreading zygomatic arches and brachycephalic characters in the auditory region, in the occiput, in the broad proportions of the upper grinding teeth, and in the arching of the opposite series of grinding teeth. All grinding teeth devoid of external cingula in males. Premolar grinding teeth precociously becoming more molariform than in other groups. Orbits small.

This group includes all the known long-horned titanotheres, both the smaller megaceropines and the larger brontotheres. Of the two the megaceropines are less formidable animals, without incisor teeth, and with a less powerful action of the horns. The brontotheres are by far the most formidable of all the titanotheres known, animals of gigantic size, with powerful horn action, hence appropriately termed by Marsh "thunder beasts." The anatomical resemblances between these animals are by no means confined to the superficial similarities but extend to all parts of the skull and teeth, as we have seen in the introduction of this chapter, and point to a common ancestry in Eocene time.

The phyletic characters of the brontotheriine group common to *Megacerops* and *Brontotherium* are indicated below:

1. There is a general increase in size of the skull and skeleton.
2. The postorbital region of the skull shows rapid elongation, the preorbital region rapid abbreviation, occiput widely prolonged behind the zygomata, orbits small, and never a prominent postorbital process. In uncrushed skulls the orbits do not appear as if closed posteriorly.

3. The zygomatic arches spread greatly in males, less in females; the zygomatic index becomes very high in extreme forms; the postglenoid unites with the post-tympanic process to inclose the external auditory meatus; the transverse measurements of the superior grinding teeth exceed the anteroposterior measurements throughout; the occiput greatly increases in breadth and slowly in height; the opposite grinding series become arched and strongly bent upward, the opposite canines thus being brought near together. One of the most distinctive and constant features of the skull is the anteroposterior convexity on top of the parietals and the general flatness of the skull top in contrast to the deep concavity of this region in the Menodontinae.

4. The dental index appears to be on the average somewhat lower than in the menodontine group. The variability of the dental index is probably due to crushing. The grinding series does not increase in length so rapidly as the skull but increases greatly in width. The internal cingula tend to disappear or degenerate.

5. The canines are obtuse or recurved, massive in males, small in females, never elongate and pointed.

6. The premolars are distinguished by the accelerated development of the tetartocones, which are placed farther in toward the center of the crown—that is, away from the internal or lingual border, a common distinctive feature; the anterior premolars, $p\frac{1}{1}$, are very progressive, with distinct tetartocones, but nevertheless are thrust inward toward the lingual line and tend to drop out in old age.

7. The internal cingula of the premolars are massive and bluntly crenulate, gradually becoming more or less confluent with the base of the crowns.

8. The dominant feature of the skull is the hypertrophy or elongation of the horns and the corresponding atrophy or abbreviation of the nasals, a compensatory character. The horns are arrested in development in the females, but the nasals are abbreviated in both sexes, though less abbreviated in females than in males.

The brontotheriine group possessing these common characters early subdivided into two very distinct phyla which we term respectively the genera *Megacerops* and *Brontotherium*, animals which enjoyed an independent simultaneous development from the base to the summit of the *Titanotherium* zone. Members of these two phyla inherited a number of ancestral characters and also a number of predispositions to a similar evolution, which are enumerated in the phyletic and family definitions above. Thus in both phyla the horns progressively increase in size, the teeth undergo similar changes.

Megacerops, however, is readily distinguished from *Brontotherium* in many parts of the skull and teeth and probably also in the skeleton, as we shall undoubtedly demonstrate when the skeleton becomes fully known. The most conspicuous points of difference are shown in the accompanying table.

Comparison of features of members of the Megacerops and Brontotherium phyla

Megacerops phylum (subfamily Megaceropinae)	Brontotherium phylum (subfamily Brontotheriinae)
1. Animals of small to medium size, either slowly increasing or arrested in size.	1. Animals of small (*B. leidyi*) to extremely large size, increasing to the largest size.
2. Skulls mesaticephalic to brachycephalic.	2. Skulls dolichocephalic to brachycephalic, finally attaining a high zygomatic index.
3. Horns rounded in section, vertical in position; placed rather above the orbits and not greatly shifting forward, with the connecting crest small or absent.	3. Horns transversely oval to flattened in section, widely divergent, shifting forward and progressively developing a high connecting crest.
4. Narial aperture high and narrow.	4. Narial aperture constricted by the heavy buttresses supporting the horns.
5. Nasals thin and progressively reduced in length.	5. Nasals thick and rapidly reduced to short, obtuse knobs.
6. Incisor teeth usually vestigial; incisive borders edentulous in males and females.	6. Superior incisor teeth invariably persistent, 2–1 in males.
7. Canine teeth small and closely approximating to one another.	7. Canines large, obtuse, arrested in growth, separated from one another.

So far as is indicated by the breadth of the cheek teeth, the curvilinear premolars, the upward flexure of the premolars, and the broad zygomatic arches (for example, *M. bucco*), *Megacerops* appears to be even more brachyopic than *Brontotherium*. *Megacerops* is less extreme in the horns than *Brontotherium* but more extreme in the somewhat closer approximation of the canines and stronger arching of the premolar series.

The grinding teeth of *Megacerops* are of the same type as those of *Brontotherium;* the molars are not readily distinguishable; the premolars of *Megacerops* are smaller with reduced internal cingula. While the incisors are usually absent in the adults there is evidence that they were present in young animals. A skull in the National Museum which resembles *Megacerops* in its horn and nasal structure exhibits large superior incisors.

SEXUAL CHARACTERS

In the females of both series we observe a far more marked distinction from the males than that observed in the menodontine group. Not only are the canine teeth smaller, but there is a pronounced difference in the proportions of the horns. There are certain other detailed characters which so far as our observations are valid seem to separate the females from the males. A summary of these contrasting sexual characters in *Brontotherium* is given below.

Males	*Females*
Horns long; connecting crests large and prominent; nasals decidedly short. Canines larger; incisors more constant, formula $\frac{2-2}{2-2}$ or $\frac{2-1}{2-1}$. Buccal processes of zygomata greatly produced; occiput greatly extended behind the line of the zygomata.	Horns relatively short; connecting crests less prominent. Nasals relatively long. Canines smaller; incisors less persistent, sometimes wanting. Buccal processes of zygomata less prominent; occipnt not so widely extended behind zygomata.

From some specimens it would appear also as if the premolars of brontotheres were somewhat less progressive in evolution in the females than in the males. This would controvert the general principle observed in *Menodus* that the grinding series of the teeth, which are so essential to the nutrition of the females, is the one character in which the sexes do not differ. Specimens of the female sex are smaller in size throughout, as seen in the detailed table of measurements.

SUBFAMILY MEGACEROPINAE

Relatively small, long-horned titanotheres, known chiefly from the middle *Titanotherium* zone. Horns precociously evolved, vertical in position, placed above the orbits, with little or no connecting crest. Incisor teeth much reduced or actually vestigial, canines very small, placed close together, thus tending to contract the premaxillaries.

Geologic horizon and geographic distribution.—So far as known these animals are of medium size or relatively small and are recorded chiefly from the middle *Titanotherium* zone of Cedar Creek, Colorado, and from the lower portion of the upper *Titanotherium* zone of South Dakota, possibly also from Assiniboia, Canada.

Four skulls of *Megacerops* were found in lower Oligocene (Chadron) deposits at the levels indicated below, chiefly according to the records of J. B. Hatcher:

Level C:
  ?*M. acer* (type).
  M. copei, Nat. Mus. 4711 (type).
  M. acer, Univ. Wyo. Mus.
Level B:
  M. bucco, Nat. Mus. 4705, ♀. (Level rather doubtful.—J. B. Hatcher.)

Distinguishing features.—The males develop long horns, which, unlike those of the typical *Brontotherium*, are placed only slightly in front of the orbits, so that, as shown in Charles R. Knight's models and restorations (Pl. XVIII, C; fig. 454), the eyes appear almost directly below the horns. As in the brontotheres the eyes were small. The horns are directed almost vertically upward, with the long basal axis placed obliquely, the basal section never tending to become transversely oval, as in *Brontops robustus* and *Brontotherium*, or triangular, as in *Menodus*. The reason for this is that the horns are supported or braced principally in a fore and aft direction, instead of across the skull by means of the connecting crest, indicating that they were used largely in a vertical or tossing motion of the head rather than in the lateral motion characteristic of the brontotheres.

The narrowness of the chin and premaxillary region and the entire absence of incisor teeth indicates that these animals were provided with a narrow and pointed prehensile upper lip, contrasting with the somewhat broader lips in the brontotheres.

A decided and highly characteristic feature is the marked abbreviation (brachyopy) of the facial portion of the skull, correlated with the cyptocephaly or upward flexure of the anterior grinding teeth.

Materials.—Remains of *Megacerops* are comparatively rare. Their existence was first made known by Leidy in 1871 (see p. 210) through the type species *Megacerops coloradensis;* secondly, by Cope in 1873 from the skulls from Colorado described as *Symborodon bucco, S. acer, S. altirostris.* Cope's specimens are in the American Museum of Natural History. A lower jaw in the American Museum (No. 6364) appears to represent a very small new species of this genus, known as *M. riggsi.* Two exceptionally complete skulls from South Dakota are in the National Museum, one of which is referred to a third species, *M. copei,* related to *M. bucco.* The first (Nat. Mus. 4705, skull O′) is small horned, apparently belonging to a female of *M. bucco,* and is recorded by Hatcher from the top of Chadron B; the second (Nat. Mus. 4711, skull V′), the type of *M. copei,* apparently a male, is recorded by Hatcher from the middle beds and was known by the collectors as the "rabbit skull," because of the resemblance of the flaring horns to the ears of the jack rabbit.

The Megacerops phylum as represented in the Hatcher collection of six skulls and lower jaws from the Chadron formation, in the United States National Museum

Genus and species	Catalog No.	Material
M. bucco (Cope)	4705, ♀	Fine skull. Typical.
Do	4700, ♂	Skull. Close to M. acer Cope. Differs from typical Megacerops in having single upper incisors. Horns and canine of Megacerops type.
M. copei (Osborn)	4711, ♂	Skull. Type.
M. riggsi? Osborn	1236, ♂	Lower jaw.
M. riggsi Osborn	5412, ♂	Right jaw, with symphysis; contains molars.
M. sp	8786, ♀	Lower jaw. Poor.

Our knowledge thus rests chiefly on six skulls and two lower jaws as representing this genus. There are also isolated horns and the top of a cranium in the American Museum collection and fragmentary skeletal material (figs. 625, 629, 638). In the University of Wyoming there is an excellent skull of *Megacerops acer*.

General characters.—These specimens agree in the exceptionally small size of the canines, in both the males and the females. The nasals are thin in two of the species, *M. bucco* and *M. copei*. *M. acer* is somewhat divergent in the thickening of the nasals and in other characters.

It is thus apparent that *Megacerops* is a separate collateral phylum, resembling *Brontotherium* in the elongation of the horns and paralleling *Menodus* in the degeneration of the incisors; but it differs from both phyla in the shape and position of the horns and in the approximation of the canines toward the median line.

Skeleton.—The skeleton is known only from a few portions associated with *M. acer* in the American Museum, which indicate that the animals of that species were rather small.

While generally of smaller size and differing widely from *Brontotherium* in the entire absence or vestigial character of the incisor teeth, the position and basal section of the horns, and some other characters, these animals present many resemblances to *Brontotherium*, especially in the elongate horns—in some cases oval in top section—in the backward prolongation of the occiput, the broad contact between the postglenoid and post-tympanic, the roundness of the malar bones, the suddenly projecting buccal expansions of the zygomatic arches, bluntness of the canines, roundness and bluntness of the internal cusps of the premolars; also the abbreviation of the premolar series and reduction of the cingula, the strongly recurved coronoid, and the general contour of the jaw.

The common characters of these *Megacerops* species are clearly perceived in a comparison of the transverse sections of the horns and of the nasals, which are highly characteristic. The main features of correspondence between *Megacerops copei* and *Menodus torvus* are, first, that the nasals are very thin, even in the portion between the horns; second, that the horns are set widely apart at the base. (This character is obscured by lateral crushing in the male type skull of *M. copei*.) Reference to the detailed descriptions of the skulls in these two species shows that they are closely related but that *M. copei* is more primitive, especially in the retarded condition of the tetartocones, the section of the buccal processes, and the persistence of the reduced incisors.

SYSTEMATIC DESCRIPTIONS OF GENERA AND SPECIES IN THE MEGACEROPS PHYLUM

Megacerops Leidy, 1870

(*Megaceratops* Cope, 1873, in part (*M. acer*); *Symborodon* Cope, 1873, in part (*S. bucco, S. altirostris*); "*Symborodon*" Osborn, 1902)

Plates XVIII, CXLIII–CLX, CLXXXVI; text figures 24, 164, 167, 169, 375, 378, 390, 392–394, 398–400, 434, 448–456, 625, 629, 638, 640, 719, 744, 746

[For original description and type references see p. 208. For skeletal characters see p. 691]

Generic characters.—Incisors typically vestigial. Canines small, obtuse. Grinding teeth without cingula, deflected upward. Premolars with progressive tetartocones. Skull brachycephalic to hyperbrachycephalic (zygomatic index 84), brachyopic. Nasals slender, narrow, decurved, abbreviated progressively. Horns set vertically, typically without connecting crest; placed above orbits; rounded in section.

The genotype of *Megacerops* (1870) is the species *M. coloradensis* Leidy, represented by nasals and horns (fig. 448). The genotype of "*Symborodon*" (1873) is the species *S. torvus* Cope, which is represented by a lower jaw. (See p. 211.) This jaw does not belong to the same phylum as *Megacerops* because it proves to be that of a *Menodus*.

General characters.—Dentition: $I\frac{2-0}{?2-0}$. Incisors reduced, vestigial, or wanting; canines reduced, obtuse; opposite grinding series arched to strongly arched; upward flexure of face and premolar series as seen in side view extreme; length of premolar-molar series generally less than two-fifths that of the skull, from premaxillary tips to occipital condyles; premolar series very short; internal cusps of grinding teeth low, robust, well rounded, ectolophs sharply depressed to the crowns of the teeth; anteroposterior diameter of m^2 and m^3 less than transverse diameter; no cingula between grinders; $P\frac{4-3}{4-3}$; p^1 subquadrangular, outer wall not overlapped posteriorly by ectoloph of p^2; premolar tetartocones exhibiting early and pronounced development; premolars with internal cingula blunt, reduced or absent, external cingula variable; molars without internal cingula, external cingula faint or absent; hypocone of m^3 prominent, triradiate.

Skull: Skull proportions mesaticephalic to brachycephalic; facial portion of skull much abbreviated; premaxillaries contracted; cranial portion of skull elongate; anterior narial aperture high and narrow; preorbital malar bridge very narrow, mainly composed of the median ridge, which is very prominent, subcylindrical, in side view concealing the infraorbital foramen almost entirely; anterior portion of malar stout, rounded; malar below postorbital process strongly convex; free nasals tapering, progressively abbreviated; horns of medium to large size, forward shifting slight or wanting, basal section deep anteroposteriorly, with antero-external or maxillary face flat, oblique, and strongly convex inner face; summit rounded to oval in section; zygomata strongly arched, buccal expansions finally extreme, in section broad rather than deep; occiput moderately produced backward behind zygomata; basisphenoidal rugosity absent, vomerine septum (?) absent.

Jaw: Jaw robust rather than deep, with shallow or concave chin, coronoid strongly recurved. Angle deep, rugose.

Incisors: In most adult specimens the incisors have been shed and are represented only by alveoli. Thus the type of *M. acer* has medium-sized superior incisor alveoli. A specimen (Nat. Mus. 4700) closely resembling *M. coloradensis* in horn structure has persistent superior incisors.

Observations on the measurements of the Megacerops series.—The members of this series are distinguished from *Brontotherium* chiefly by the cylindrical horns and by the feeble development of the connecting crest. The basilar length (pmx to condyles) is shorter than in any species of *Brontotherium* except *B. hypoceras* and *B. leidyi.* The premolars as a rule are shorter and smaller than in *Brontotherium,* as shown below. The molars, however, in proportion to the basilar length of the skull, are sometimes relatively larger than in *Brontotherium,* as shown in the following tables:

Molar index in species of Megacerops and Brontotherium

M. acer, Am. Mus. 6350, ♀ ($\frac{215}{630}$)	34
M. acer, Univ. Wyoming ($\frac{200}{646}$)	29
M. bucco, Am. Mus. 6345a (type) ($\frac{300}{665}$)	30
M. copei, Nat. Mus. 4711 (type) ($\frac{294}{620}$)	30
B. ?tichoceras, Nat. Mus. 8313 ($\frac{196}{695}$)	28
B. platyceras, Field Mus. 12161	25
B. curtum, Yale Mus. 12013 (type)	29
B. gigas, Am. Mus. 492	29
B. leidyi, Nat. Mus. 4249 (type)	28
B. leidyi, Carnegie Mus. 93	28

Anteroposterior and transverse dimensions of p^4 and m^3 in species of Megacerops and Brontotherium, in millimeters

	P^4		M^3	
	Ap.	Tr.	Ap.	Tr.
M. acer?, Am. Mus. 6350 (type of M. altirostris)	43	59	75	82
M. acer, Univ. Wyoming	38	54	78	83
M. bucco, Am. Mus. 6345a (type)	36	54	75	80
M. bucco, Am. Mus. 6353	41	56	65	[a]74
M. bucco, Nat. Mus. (skull A)	----	57	----	----
B. gigas hatcheri, Nat. Mus. 4262	45	57	----	----
B. gigas, Am. Mus. 492	47	72	91	99
B. gigas (hatcheri), Carnegie Mus. 341	45	63	72	84

[a] Estimated.

The internal cingula of the premolars are usually more reduced than in *Brontotherium.*

The close kinship of *Megacerops* to *Brontotherium* is revealed in many details of the incisors, canines, premolars, and molars, in the great expansion of the zygomata, and in the possession of a midparietal protuberance.

Measurements of species of Megacerops and Brontotherium, in millimeters

	Stage 1: B. leidyi		Stage 2: B.?tichoceras, Nat. Mus. 8313 (A)	Stage 3		
				M. acer		M. "altirostris" (type)
	Carnegie Mus. 93	Nat. Mus. 4249 (type)		Type (♂)	Univ. Wyo.	
P^1–m^3	300	290	313	------	------	330
M^1–m^3	190	186	196	------	200	215
Pmx to condyles	665	665	695	------	646	630
Zygomatic index	66	------	76	------	84	------
Nasal length	114	118	90	60	70	44
Horn length	104	107	111	290	242	165,♀?

Standard measurements in the Megacerops phylum, in millimeters

	Upper teeth					Skull							Jaw and lower teeth					
	P^1–m^3 (or p^2–m^3)	P^1–p^4 (or p^2–p^4)	M^1–m^3	Canines, anterior vertical	Canines, anteroposterior diameter	Pmx to condyles	Zygomatic breadth, transverse	Cephalic (zygomatic) index	Nasal tips to occiput vertex	Nasals, free length	Nasals, free breadth	Horns, external length	P_1–m_3	P_1–p_4	M_1–m_3	Canines, anterior vertical	Canines, anteroposterior diameter	Symphysis to condyles
Brontotherium ?tichoceras, Nat. Mus. 8313, ♂	313	[a]126	[a]196	34	33	695	538	76	[b]750	90	126	111	349	122	232	38	33	593
M. coloradensis (type)	----	----	----	----	----	----	----	----	----	[b]110	[b]127	[b]175	----	----	----	----	----	----
M. ("Symborodon") acer, Am. Mus. 6350, ♀ (type of M. "altirostris")	330	127	215	----	----	[b]630	----	----	610	44	117	165	----	----	----	----	----	----
M. ("Symborodon") acer, Am. Mus. 6348, ♂ (type)	----	----	----	----	----	----	----	----	[b]640	60	114	290	----	----	----	----	----	----
M. acer, Univ. Wyoming 2, ♂ (?)	300	99	200	----	----	646	543	84	[b]690	70	115	242	----	----	----	----	----	----
M. ("Symborodon") bucco, Am. Mus. 6345a, ♂ (lectotype)	[b]300	[b]100	200	----	----	[b]665	[c]665	----	750	[c]90	130	[b]185	----	----	----	----	----	----
M. bucco, Nat. Mus. 4705, ♀	315	116	204	22	20	645	[b]520	[b]81	[b]640	80	135	190	----	----	----	----	----	----
M. bucco, Am. Mus. 6353, ♂	317	119	198	29	27	----	----	----	----	----	----	----	----	----	----	----	----	----
M copei, Nat. Mus. 4711 (type)	[c]294	106	195	28	----	[c]620	----	----	[c]601	80	125	[c]300	----	----	----	----	----	----
M. riggsi, Am. Mus. 6364 (type)	----	----	----	----	----	----	----	----	----	----	----	----	282	85	194	----	----	[b]465

[a] Right side.

[b] Estimated.

[c] Crushed.

Sequence of species.—The following summary affords the principal characters by which the chief species so far recognized may be distinguished from one another:

1. *Megacerops coloradensis* Leidy is the genotype. The type is lost and is known only from the figure of the coossified nasals and horns, which indicates an animal about the size of *M. bucco*. *Titanotherium* zone, Colorado.

2. *Megacerops* ("*Symborodon*") *bucco* (Cope) is a more progressive species. It is decidedly brachycephalic. It still retains, however, the long thin nasals. The horns have shifted to a more anterior position. The buccal processes of the zygomata now become very prominent, as in the brontotheres. The occipital pillars begin to expand, the parietal crest is broader, and as a distinctive, progressive character, the tetartocones of the premolars are more developed. It is important to note that this extreme type probably belongs to the upper beds. Colorado and South Dakota. *Titanotherium* zone, level Chadron B.

3. *Megacerops acer* Cope is represented by the male type skull and by a female skull which Cope made the type of his species *M. altirostris*. It is also mesaticephalic and differs from *M. copei* in the thick, short nasals, in the divergence of the horns, in the somewhat more anterior position of the horns, while it resembles *M. copei* in the small size of the tetartocones of the premolars. The occiput (Pl. CLVII, C; fig. 451) is readily distinguished from that of any brontothere by its slender characters, indicating that the muscles of the neck were not so robustly developed in these animals. Colorado and South Dakota. *Titanotherium* zone, upper beds.

4. *Megacerops copei* (Osborn), named in honor of Professor Cope, appears to belong to the middle *Titanotherium* zone (Chadron B). In proportions the skull is mesaticephalic; the horns are vertical, elongate as seen from the front, and their form suggested the unique name "rabbit's ears," which is applied to this skull. They are placed typically directly above the orbits, yet the nasals are very thin, and, as shown in the section (fig. 450), there is no connecting crest. Colorado and South Dakota. *Titanotherium* zone, upper beds (Chadron C).

5. *Megacerops assiniboiensis* Lambe is an animal of small size, known only by the jaw. Saskatchewan, Swift Current Creek. *Titanotherium* zone.

6. *Megacerops riggsi* Osborn is distinguished by its especially short massive jaw. Colorado. *Titanotherium* zone.

Synopsis of specific characters of four species of Megacerops

	M. copei, Nat. Mus. 4711	M. bucco, Am. Mus. 6345a and Nat. Mus. 4705	M. acer, Am. Mus. 6348 (type), and Am. Mus. 6349 [a]	M. altirostris, Am. Mus. 6350 [b] (type)
Skull	Mesaticephalic	Extremely brachycephalic.	Mesaticephalic?	Mesaticephalic?
Nasals	Thin	Thin, ♂ long, ♀ medium.	Thick, short	Thick, short.
Horns	Vertical	Divergent	Divergent	Divergent.
Horns, malar ridge	Prominent	Absent	Intermediate	Faint or absent.
Horns, top section	Strongly oval	Rounded to oval	Oval	Rounded to oval.
Horns, connecting crest	None	None	Well-defined	None.
Horns, position	Over orbits	♂ anterior to orbits ♀ ?intermediate	Anterior to orbits	Intermediate.
Internal flange of buccal process.	Not prominent	Prominent	♂ ? ♀ not prominent	?.
Occiput and pillars	Narrow	Expanding	Narrow	Narrow.
Occiput pits	Absent?	Absent?	Pronounced	Absent?.
Occiput parietal crest	Narrow	Broad	Narrow	Intermediate.
Premolars	Tetartocones smaller	Tetartocones more developed.	Tetartocones smaller	Tetartocones smaller.
Mesostyle p^4	Absent	Present	?	Present.

[a] A small female.

[b] Regarded as the female of *M. acer*.

Jaw characters.—The jaws of *Megacerops* are readily distinguished by the abbreviation of the anterior portion corresponding with the extreme abbreviation or brachyopy of the facial region, with which the abbreviation of the lower premolar series is also correlated. A second distinction is the narrowness of the chin and the small size and approximation of the canines, correlated with the reduction of the lower incisor teeth. The anterior part of the face in *Megacerops* is contracted and the lips were probably narrow and pointed in contrast with the broad, massive lips of *Brontotherium*.

Details of the contrasts in the character of the jaw are as follows:

Jaw characters in Megacerops and Brontotherium

	Megacerops	Brontotherium
Horizontal ramus	Short, massive	Massive, deep posteriorly.
Symphyseal region in side view	Shallow	Very shallow.
Region of angle	Broad, posterior border vertical	Broad, posterior border often vertical.
Incisors	$?I_{\overline{0}}$	$I_{\overline{2-1}}$.
P_1 in fully adult jaws	Absent?	Present or absent.
Diastema in front of p_1	Absent?	Absent.
Canines	?	Swollen at base with massive posterior cingulum.
Upward flexure of premolar series	Pronounced	Typically pronounced.

Megacerops coloradensis Leidy

Text figures 164, 448

[For original description and type references see p. 208]

Type locality and geologic horizon.—Colorado; *Titanotherium* zone. Exact locality and level unknown.

Specific characters.—Nasals long (110 mm., estimated), sharply decurved and tapering distally; horns cylindrical with slightly flattened tips, external length 175 millimeters (estimated). Connecting crest very low.

Materials.—The type specimen, consisting of the coossified nasals and horns, has been lost, and the characters of the genus rest upon Leidy's original description and figures and on the model (Am. Mus. 9018, fig. 448) made from them.

Transitional referred specimen, Brontotherium tichoceras.—In the National Museum there is a beautifully preserved skull (No. 8313, with associated lower jaw) which in horn structure recalls the type of *M. coloradensis*, except that the nasals and horns are somewhat shorter. This skull is of extraordinary interest inasmuch as it combines the nasals, horns, and absence of connecting crest which are characteristic of *Megacerops* with the large incisors and canines which had hitherto been regarded as characteristic only of *Brontotherium*. The premolars are relatively small, and the internal cingula have almost completely disappeared, much more than in *Brontotherium* and even more than in most *Megacerops* skulls. The measurements of this skull approach those of the type of *Megacerops bucco* except that the basilar length is greater, the zygomatic width and horn length are less. It should also be compared with *Brontotherium hatcheri*, but it differs from that type in its shorter horns, absence of connecting crest, and absence of internal cingulum on the premolars.

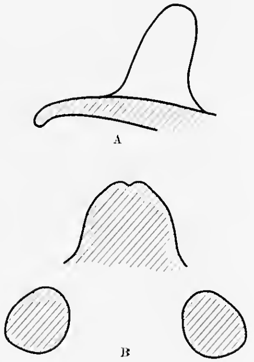


FIGURE 448.—Sections and contours of nasals and horns of *Megacerops coloradensis*.

Am. Mus. 9018, a model made from Leidy's figures and from measurements of his type, which has been lost. One-seventh natural size.

Megacerops bucco (Cope)

(*Symborodon bucco* Cope, 1873; "*Symborodon torvus*" Osborn, 1902)

Plates CXLIV, CXLV, CLIII-CLVI; text figures 169, 170, 378, 392, 393, 399, 449, 719, 744

[For original description and type references see p. 212]

Type locality and geologic horizon.—Cedar Creek, Logan County, Colo.; *Titanotherium* zone.

Specific and generic characters.—I $\frac{?2-0}{0}$, P$\frac{4-3}{0}$. Superior incisors probably absent; premolars with cingula vestigial or wanting, tetartocones nearly as large as deuterocones and more distinct then in *M. copei*, a faint mesostyle upon p^4. Skull shows progressive increase in size over *M. copei*, length nasals to occiput 750 millimeters, premaxillaries to condyles 665 (estimated); extremely brachycephalic, index 100 (estimated); nasals thin, medium in length, broad (90 by 130 mm.); no connecting crest between horns; horns ♂ short (185 mm., estimated); zygomata broadly expanded; occipital pillars expanding, with wide superior rugosities.

Skull and jaw selected by Cope as types of Symborodon bucco.—The type skull of *S. bucco* Cope includes a fairly preserved skull (Am. Mus. 6345a) with enormous zygomatic expansions. The jaw placed with this skull by Cope appears to belong to another phylum. The premaxillaries are wanting. All the maxillary teeth on both sides are preserved with the exception of p^1. The horns and the anterior portions of the orbits have required much restoration but serve to afford some very distinctive characters. The skull is readily distinguished as a *Megacerops* by the entire absence of the connecting crests between the horns, which are set widely apart but so damaged that a perfect basal section can not be made. The nasals are very thin and of medium length. The zygomata arch very widely and exhibit a flattened section which is even more extreme than that of *Brontotherium gigas* and quite distinct from the convex section of the skull Am. Mus. 6346, also referred by Cope to *S. bucco* but regarded by us as pertaining to a species of *Brontotherium*, probably *B. curtum*. Posteriorly the cranium broadens out into the occiput, but it is important to note that this breadth and the peculiar zygomatic section are altered by crushing.

Dentition.—The animal is in the eighth stage of growth, all the internal cones of the teeth being worn except upon m^3. The external cingulum is obsolete throughout the grinding series, as in *M. acer*. The internal cingulum is entirely lacking on p^2 and is very slightly marked on p^4. It is also wanting on the inner sides of the molars. As a marked progressive character, the internal cusps of the premolars are robust and well rounded. The hypocones on m^1, m^2 are prominent and bulge on the lingual side. The hypocone is well developed on m^3, triradiate in form, and connected with the cingulum by only a slight posterior ridge.

Female skull of M. bucco in the National Museum.—The skull Nat. Mus. 4705 is that of an aged female in the ninth stage of growth, the horns of which are set very wide apart (Pl. CXLV, B; figs. 392, E, 449, B). The well-worn canines measure only 25 millimeters anteriorly and are proportionately the smallest we have observed in any species of titanothere. The evidence regarding the incisors is not positive, but there were apparently two vestigial teeth, which certainly could not have been functional. The premolar-molar series measures 315 millimeters. The internal cingula on the premolars is vestigial or entirely wanting. The skull appears to be brachycephalic, the estimated index being 81; the measurement from condyles to symphysis is 645 millimeters, while the width across the zygomata is estimated at 525 millimeters, an excess of length over breadth of only 120 millimeters. The nasals are very broad but at the same time short, the free length being only 80 millimeters. The horns are short, measuring 190 millimeters on the outer side, and exhibit at the base the section so characteristic of this genus, which is due to the flatness of the anterior or maxillary face and the convexity of the posterior buttress.

Megacerops acer Cope

(*Megaceratops acer* Cope, 1873; *Symborodon altirostris* Cope, 1873; "*Symborodon acer* Cope," Osborn, 1902)

Plates XVIII, CXLVI–CLII, CLVII; text figures 167, 170, 375, 378, 390, 392, 399, 400, 450–453, 625, 638

[For original description and type references see p. 211]

Type locality and geologic horizon.—Cedar Creek, Logan County, Colo.; *Titanotherium* zone, level unknown.

Specific and generic characters.—$\mathrm{I}\frac{2-0}{}$, $\mathrm{P}\frac{4}{}$. Incisors greatly reduced but more persistent than in *M. bucco*; canines small; p^1 small, rounded, p^2–p^4 with tetartocones distinct but smaller than in *Menodus torvus*, a prominent mesostyle upon p^4 (No. 6350), narrow internal cingula; hypocones of m^1–m^2 large, projecting on lingual side, hypocone of m^3 triradiate. Nasals thick, short, and moderately broad (60 by 114 mm.); horns ♂ 290 millimeters, ♀ 165, basal section typical, summits transverse oval; cranial vertex dolichocephalic; occiput high, narrow, not deeply indented superiorly. Zygomata ♀ with buccal processes flattened or slightly concave above, size moderate, nasals to occiput 640 millimeters. This differs from *M. copei* in the form and direction of the horns and presence of a connecting crest in the male, in the long, narrow parietal vertex, and in the thickness of the nasals.

Materials.—This was the second species of "*Symborodon*" described by Cope from Colorado in 1870. The type specimen (Am. Mus. 6348) is the skull of a male titanothere of medium size but with long horns, from the *Titanotherium* zone of Cedar Creek, Logan County, Colo. The exact geologic level is not known. Subsequently Cope proposed the name "*Symborodon*" *altirostris* for a skull of the same species (Am. Mus. 6350), a female, as first pointed out by Osborn in 1896. In addition to these two skulls there is fortunately a third (Am. Mus. 6349), probably also a female, in which the right zygoma is preserved.

Relationships to other species of Megacerops.—There can be no question as to the generic relationship of this animal to *Megacerops bucco* and *M. copei*. It presents a number of interesting and significant points of contrast and agreement. The affinity is seen especially in the form and position of the horns in the type, which indicate that they were used in the manner characteristic of other members of the genus. They point upward and slightly outward, and as they are strengthened posteriorly their bases do not lie very far in front of the orbits. This relatively long-horned titanothere was, therefore, a true *Megacerops*, a conclusion which is further supported by the resemblance of the basal horn section to that of "*Menodus torvus*" and by its wide contrast to that of any species of *Menodus*, such as *M. trigonoceras*, or of *Brontotherium*, such as *B. gigas*.

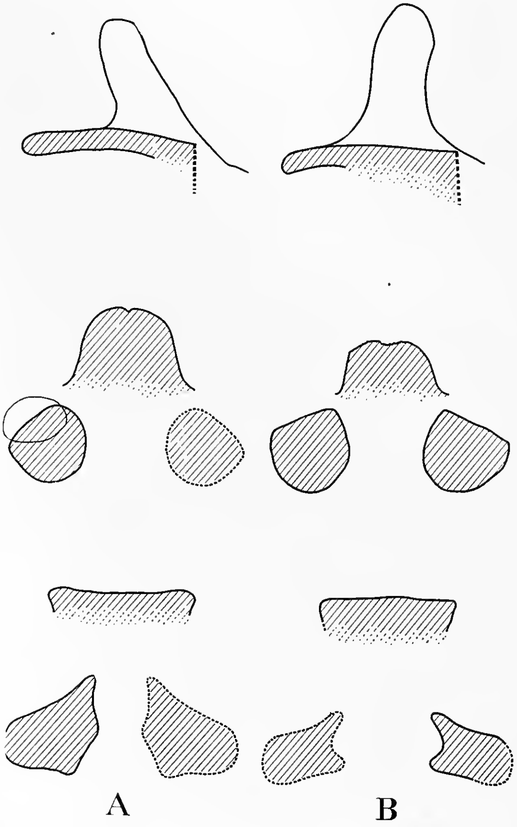


FIGURE 449.—Sections and contours of skull of *Megacerops bucco*

A, Am. Mus. 6345a (type); horns directed upward and forward, their basal section rounded with a flattened external face, the section of the upper part of the horn transversely oval, nasals wide, zygomata widely expanded. B, Nat. Mus. 4705. In this supposed female the horns, as in all other members of this genus, are subcylindrical, their basal section has a flat external face, and the remainder of the section is well rounded; nasals rather short; zygomata moderately expanded. One-seventh natural size.

Seen from in front the horns are placed close together at the base and diverge more at the summits than in the other species, although the divergence is less than in *B. gigas*, for example. That this divergence was correlated with the development of a shallow transverse connecting crest in the males, which was also present in certain females (Am. Mus. 6349) but nearly wanting in the supposed female Am. Mus. 6350 (Pl. CL), proves that it was adapted to resist the lateral strains to which the horns were subjected. Yet in *M. copei* and *M. bucco* the horns are divergent and the nasals are as thin between the horns as toward the tips.

Nasals.—Correlated with the somewhat more anterior position of the horns and partly by compensation of growth there is a very marked abbreviation of the nasals, which now measure only 60 by 114 millimeters and are relatively much shorter than in *M. bucco* and *M. copei*. This stage is therefore parallel to that of *B. curtum* among brontotheres. The crania of these small animals are rather mesaticephalic than brachycephalic. The name *altirostris*, given to the female skull by Cope, referred to the elevation of the nasals above the premaxillae when seen from in front.

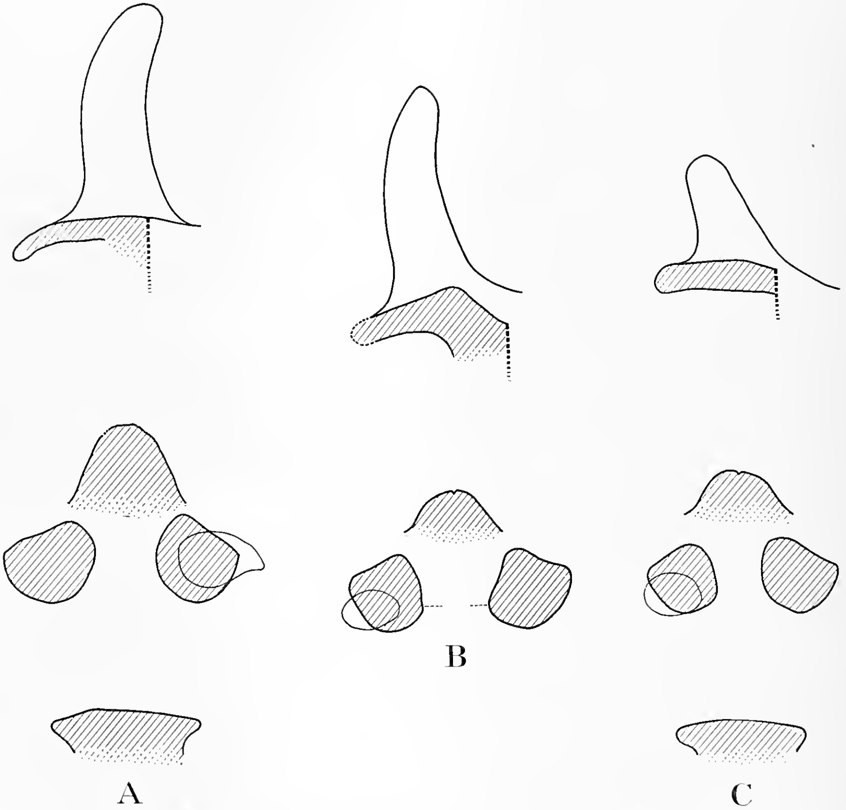


FIGURE 450.—Sections and contours of skulls of *Megacerops copei* and *M. acer*

A, *Megacerops copei*, Nat. Mus. 4711 (type); horns long and subvertical, their basal section thick, the external face flat, and the remainder of the section well rounded; the section of the upper part of the horn widely oval, with a recurved external angle; no connecting crest; nasals larger and broader than in *M. acer* and narrow at the end.

B, *M. acer*, Am. Mus. 6348 (type); horns long and slightly inclined forward, their basal section roundly quadrate with a concave external anterior face; the section of the upper part of the horn transversely oval; a connecting crest; nasals short. C, *M. acer*, Am. Mus. 6350, ♀ (type of *Symborodon altirostris* Cope, now referred to *M. acer*); horns relatively short and directed forward, basal section roundly quadrate, with a long concave external face, section of the upper part of the horn transversely oval, nasals short and thick.

All one-seventh natural size.

Occiput.—The occiput resembles *M. copei* also in the form of the top of the occiput (fig. 451), which is not expanded and, in fact, is peculiarly narrow and simple. Instead of the knobs (fig. 378, F) seen in *Brontotherium* there is a pair of pits (fig. 451) on either side of the center of the occipital crest. The occiput lacks the broad superior flare, which is correlated with brachycephaly and the lateral motions of the skull.

A very distinctive feature is the fact that it is not incurved in the median line superiorly.

The buccal expansion of the zygoma is preserved only in one of the female skulls (Am. Mus. 6349), in which it is seen to be broad and flattened above, as in *M. bucco*, paralleling that of *Brontotherium gigas*. The portion of the malar preserved in No. 6350 is stout and rounded.

Teeth.—That the superior incisors were greatly reduced is demonstrated by the small alveoli in the female skull Am. Mus. 6350, which, however, are not so small as in *Menodus*. The rounded first premolar resembles that of *M. copei*; the slightly defined cingulum on the inner side of the premolars and the rather retarded development of the tetartocones distinguish these teeth from those of *M. bucco*. There is a well-marked mesostyle on p^4. As in *M. bucco* and *M. copei*, the distance from the anterior edge of m^1 to the premaxillary border and the proportionate length of the premolar series are excessively short, compared with *Menodus*, *Allops* and *Brontops*, and even compared with *Brontotherium* (Pls. CLI, CLII, and CLXV). The upward flexure of the premolar series and elevation of the canines and incisors is very marked and in connection with the elevated position of the nasals and perpendicularity of the horns must have imparted a peculiar retroussé character to the face (Pl. CXLVI).

Sexual characters.—The males are well distinguished from the females by the length of the horns, which is 290 millimeters in the male (Am. Mus. 6348) as compared with 177 in one female (Am. Mus. 6350) and 138 in the second female (Am. Mus. 6349). The basal section of the horns is substantially similar, and the summits are transversely oval in section; but in one of the female skulls (No. 6350) the horns project forward without recurvature, while in the other they are recurved as in the male skull. There is a strong convexity of the cranial vertex in the frontoparietal region (a family character) in the male No. 6348 and the female No. 6350, which is feebly developed in the female No. 6349. The horn of the latter has a malar ridge.

Additional observations on skulls of Megacerops acer.—The type of *M. acer* is a relatively long and slender male skull (Am. Mus. 6348) lacking all the teeth, the zygomatic arches, the maxillaries and premaxillaries. The skull is sharply distinguished from any previously described by its obtuse and short but tapering nasals, long, recurved horns with deep anteroposterior basal section and oval tips, a narrow vertex, and narrow, simple occiput. In addition to these characters there appears to be a strong convexity in the central portion of the top of the cranium not altogether due to crushing, which is characteristic of *Brontotherium* and *Megacerops*. The basal section of the horns indicates that they are strengthened not only by a connecting crest but by a posterior ridge passing backward above the orbits, which is separated by a flat surface from the malar ridge.

The skull Am. Mus. 6350 resembles that of *M. acer* in the abbreviation of the nasals and narrowness of the vertex and the occiput and differs from *M. acer* in characters which Cope thought to be specific but which are now found to be sexual. These female characteristics are the relatively short horns and comparatively low connecting crest, as shown in the section (fig. 450); the only difference of note is the convexity between the malar and posterior ridges of the horns.

The anterior teeth of this type have been broken away and lost since the original description. The superior incisors are represented by two small alveoli, placed upon a narrow border, indicating that these teeth were small and disappeared in old age. The formula was, therefore, $I\frac{2-0}{}$, $P\frac{4}{}$. The crowns of the canines have been destroyed. These teeth were of small size, apparently as in *M. bucco*. The first premolar is a small tooth with three cusps (protocone, deuterocone, and tritocone); the second, third, and fourth premolars exhibit four well-developed and distinct cusps, including a convex tetartocone. A feature which may be specifically characteristic is the distinct mesostyle upon p^4. A crenulate and not sharply defined cingulum is observed on the inner side but is entirely wanting on the outer side of the premolars. This more or less vestigial condition of the cingulum is also a distinctive character of the series to which this animal belongs, as well as of the old males of the species of *Brontotherium* of the upper beds. The molars are very broad. On m^3 the hypocone is triradiate, well developed, but not distinct from the cingulum. Another well-marked feature is the prominence and roundly blunt character of the hypocones of m^1–m^3.

FIGURE 451.—Upper part of occiput of *Megacerops acer*

Am. Mus. 6351, showing pits for the ligamentum nuchae and rugosities for the recti capitis laterales. One-fourth natural size.

A female skull (Am. Mus. 6349) fortunately preserves the right zygomatic arch, indicating that this is broad and somewhat flat superiorly, having a section similar to that of *Brontotherium gigas* but less robust. A distinctive character is the breadth of the postglenoid process. The occiput has the relatively slender proportions seen in the type and cotype. The rugosities on top of the occipital pillars are much less extensive than in *Megacerops robustus*.

Referred skull, Megacerops acer, University of Wyoming Museum.—A very fine skull (figs. 452, 453) in the University of Wyoming, collected by Mr. W. H. Reed in the upper *Titanotherium* zone near Alcova, Natrona County, Wyo., has somewhat smaller horns than the type. Its nasals recall those of the type of *S. altirostris*. The premolars, as in other members of the genus, have the internal cingula nearly obsolete and the tetartocones subequal to the deuterocones; the width of the molars exceeds the length. The zygomatic index (84) is high. In addition to the measurements of this skull given above (p. 542), we record also the following:

	Millimeters
Diastema behind canine	20
P⁴, ap. by tr	34×45
M², ap. by tr	73×84
M³, ap. by tr	78×83
Molar index	29

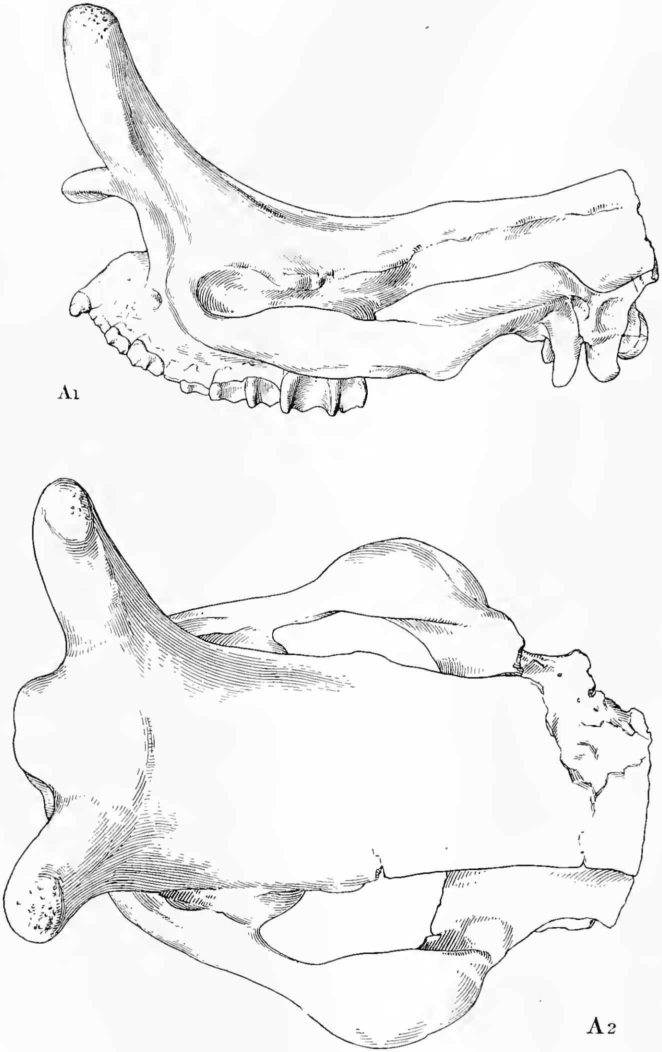


FIGURE 452.—Skull of *Megacerops acer*

Univ. Wyoming Mus. 2. Side (A_1) and top (A_2) views. One-sixth natural size. This skull combines the characters of several supposed species of *Megacerops*. In the form and length of the horns it approaches the type of *M. acer;* in the character of the nasals it resembles the type of *Symborodon altirostris;* in the general form of the skull top it resembles especially the supposed female of *M. bucco* (Nat. Mus. 4705); and in the dimensions of the grinding teeth it agrees with the lectotype of *M. bucco* (Am. Mus. 6345a).

Megacerops copei (Osborn)

(*Symborodon copei* Osborn, 1908)

Plates CXLIII–CXLV; text figures 24, 203, 390, 394, 399, 450, 454, 640

[For original description and type references see p. 235]

Geologic horizon —Middle *Titanotherium* zone, South Dakota.

Specific and generic characters.—$I\frac{2-0}{}$, $P\frac{4}{}$. Incisors (type) persistent but greatly reduced; canines very small, reduced, ♂ 28 millimeters; premolars with cingula reduced or absent; tetartocones connected with deuterocones by a longitudinal ridge. Skull: Nasals thin, short and broad in proportion, 80 by 125 millimeters; horns ♂ 300, no connecting crest, transverse oval near summit; buccal processes of zygomata ♂ stout and convex; malar in front of buccal process very deep, beneath postorbital process stout, convex; occipital pillars medium, not greatly expanded at the summits. Size small, premaxillaries to condyles 620 millimeters.

Materials.—This species is known only from the type skull (Nat. Mus. 4711, skull V′), which is finely illustrated in Plates CXLIV, CXLV. It is from the middle *Titanotherium* zone, probably from the upper levels or even lower, and impresses one with the excessive thinness of the nasals, which in these animals are very broad posteriorly (120 mm.), while not of very great free length. The animal is in the eighth stage of growth and has thus attained its fully adult characters. The small size of the canines (28 mm.) might lead us to regard it as a female, but all the specimens belonging to this genus are characterized by small canines, and the great length of the horns

(301 mm.) proves that it is a male. The incisors were apparently very small and shed early, being indicated solely by a single alveolus on each side.

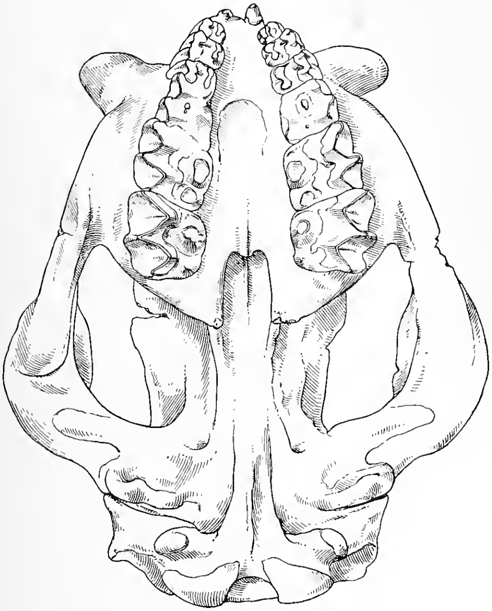


FIGURE 453.—Skull of *Megacerops acer*

Univ. Wyoming Mus. 2. Palatal view. One-sixth natural size. Shows striking resemblance to the supposed female of *M. bucco* (Nat. Mus. 4705) and to the type of *Symborodon altirostris*. Affinity with *Brontotherium* is also indicated in the form of the canines, the highly progressive submolariform premolars, and the broad molars.

The canines are similar to *Brontotherium* canines but of much smaller size. This degeneration of the anterior teeth was shared by the first premolar, which is a small tooth placed close to the canines; in spite of its small size, however, it very probably had a well-developed tetartocone as in all other Brontotheriinae, indicated by the angulate postero-internal border of the much worn tooth. The succeeding premolars, p^2–p^4, exhibit progressive development of the tetartocones (Pls. CXLIII, CXLV); these cusps are still connected with the deuterocones by a low crest, however, and are not clearly distinct; the internal cingula are feebly developed and obsolete opposite the deuterocones. M^3 has a heavy triradiate hypocone. The grinding series as a whole measures 300 millimeters, exactly as in *M. bucco*, but the skull of this specimen is 130 millimeters shorter than in *M. bucco*. It would appear that in this species, as in *Brontotherium*, the dental series does not increase proportionately with the skull.

Skull.—The lateral view of the type male skull (Pl. CXLIII) at first sight strongly suggests that of *B. gigas;* but a close comparison reveals the important difference that the horns are placed very much farther back; they are almost directly above the orbits with buttresses extending backward at the base over the orbits. The horns thus obtained a firm support posteriorly, a mechanical adaptation that compensates for the entire deficiency of a transverse connecting crest. When seen from in front (Pl. CXLIV) the horns are chiefly vertical and parallel, although this is somewhat exaggerated by lateral crushing; they certainly do not flare outward as in *B. gigas*. This unique position correlated with the narrowness of the occiput indicates chiefly a vertical motion of the skull in using the horns and explains the absence of a connecting crest, which would be of great service in protecting the nasofrontal region from fractures occasioned by side blows. The horns differ from those of *M. acer* in the stronger development of the transverse oval section near the summits caused by the sharp development of the malar ridge.

Megacerops assiniboiensis Lambe

Text figures 205, 434, 455

All that is known of this animal is fully stated on pages 239–240. The lower jaw is shown in Figure 455.

Megacerops syceras (Cope)

(*Menodus syceras* Cope, 1889)

Text figures 186, 456

[For original description and type references see p. 226]

This species is known only from the coossified nasals and horn cores. It is probably a member of this phylum.

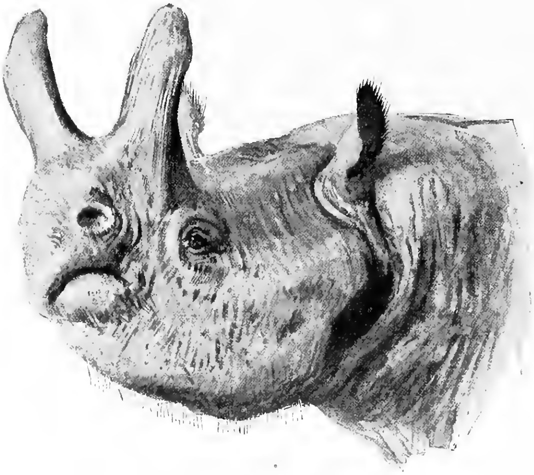


FIGURE 454.—Restoration of *Megacerops copei*
By Charles R. Knight. About one-ninth natural size.

Megacerops riggsi (Osborn)

Plates CLVIII–CLX; text figures 208, 455.

[For original description and type references see p. 242]

Type locality and geologic horizon.—Horsetail Creek, northeastern Colorado; *Titanotherium* zone.

Specific characters.—Of small size, smaller than any known individual of *Megacerops* or *Brontotherium*. A very massive jaw with a small coronoid process and a very short symphysis. Premolar series greatly abbreviated (85 mm.). Premolars and molars with reduced external cingula.

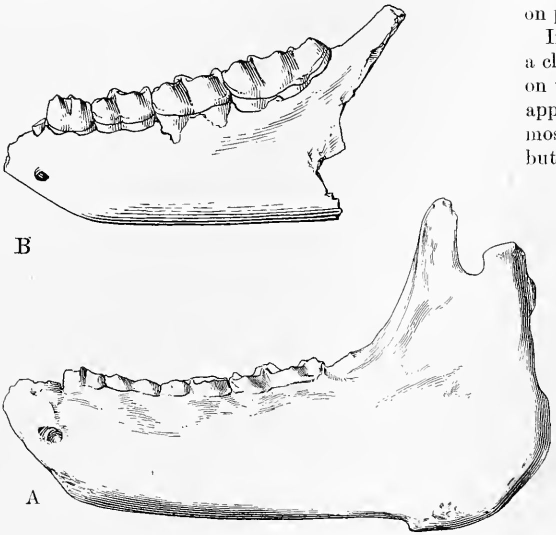


Figure 455.—Lower jaws of *Megacerops assiniboiensis* and *M. riggsi*

A, *Megacerops riggsi*, Am. Mus. 6364 (type). A small titanothere having a massive short jaw, a short chin, and a swollen ramus. (See Pl. CLVIII, A.) The cheek teeth lack cingula. B, *M. assiniboiensis*, Ottawa Mus. (type). A small short jaw provisionally referred to *Megacerops*. The grinding teeth lack external cingula. One-fifth natural size.

The type of this species, named in honor of Mr. E. S. Riggs, of the Field Museum of Natural History, is a jaw in the Cope collection (Am. Mus. 6364) which was wrongly referred by Cope to his species "*Symborodon*" *acer*. It represents a highly specialized and small form of *Megacerops*.

SUBFAMILY BRONTOTHERIINAE

Titanotheres attaining the largest size, chiefly of the upper *Titanotherium* zone, although known from the lower beds upward. The horns progressively longest, most broadly oval, and flattened, shifting forward with the extreme reduction of the free portion of the nasals; very prominent connecting crest, progressively increasing size. Two pairs of persistent superior incisor teeth in males; canines large, obtuse. Brachycephaly expressed in the great horizontal expansion of the buccal processes, in the proportions and arching of the grinding teeth, and in the inclosure of the auditory meatus in the males. Occiput much produced behind the zygomatic arches. Vertex of skull in superior view elongate.

The ancestry of this great Oligocene phylum may possibly be found in the upper Eocene, perhaps in species of *Diplacodon* or of *Eotitanotherium*, described on pages 439, 441.

In these huge animals the titanothere family reached a climax. The generic name "thunder beast," based on the genotype species *Brontotherium gigas*, is highly appropriate because it applies to the most robust and most massively horned not only of the titanotheres but of all the known Perissodactyla.

Marsh mistakenly associated with the type jaw of *B. gigas* the skull of *Menodus*, "*B. ingens*," to define the generic characters of *Brontotherium*, and he assigned the actual skull of *B. gigas* to a different genus, naming it *Titanops elatus*; but we have found that the lower jaw of *B. gigas* is in a stage slightly antecedent to that of *Titanops elatus* Marsh. We have also discovered that this great animal *Brontotherium gigas* (*elatum*) is a central form, whose ancestors (*B. leidyi*) extend down to the base of the *Titanotherium* zone and whose successors (*B. platyceras*) extend up to the very summit of Chadron C (the upper *Titanotherium* zone).

Figure 456.—Sections and contours of skull of *Megacerops? syceras*

Ottawa Mus. (type), provisionally referred to *Megacerops* partly because the basal section of the horns is roundly quadrate and has a flat external face. Nasals of moderate length, connecting crest low. One-seventh natural size.

Thus in the present memoir *Brontotherium* is shown to embrace a most remarkable and nearly monophyletic series or succession of species, eight or possibly nine of which are now known from the lower to the higher levels, presenting certain common generic characters throughout. Modified by a progressive increase in size and by a series of remarkable stages in the evolution of the horns, in the recession of the nasals, and in the expansion of the buccal processes of the zygomata, they culminate in a unique type of perissodactyl skull, that of *B. platyceras*, which appears to be the last of its great race. This species is certainly in the last stage of evolution along its line.

Affinities.—The nearest allies of *Brontotherium* are members of the genus *Megacerops*, but the true brontotheres (the males at least) are readily distinguished by the presence of two pairs of upper and lower incisor teeth, by their robust canines, the flattened oval section of the horns, the progressive connecting crests between the horns, and in general by their superior if not dominant size. The jaw of *B. gigas* (Pl. CLXXI) is very characteristic of the genus, with its recurved coronoid process, shallow chin, robust mandibular section, two pairs of incisor teeth, and obtuse rounded canines. The finely preserved type skull of *B.* (*Titanops*) *elatus* (Pl. CLXXV) enables us fully to characterize the genus. The succeeding and still more advanced stages in the evolution of this phylum were originally named as follows: *Menodus dolichoceras* Scott and Osborn, *Titanops curtus* Marsh, *Titanops medius* Marsh, *Titanotherium ramosum* Osborn.

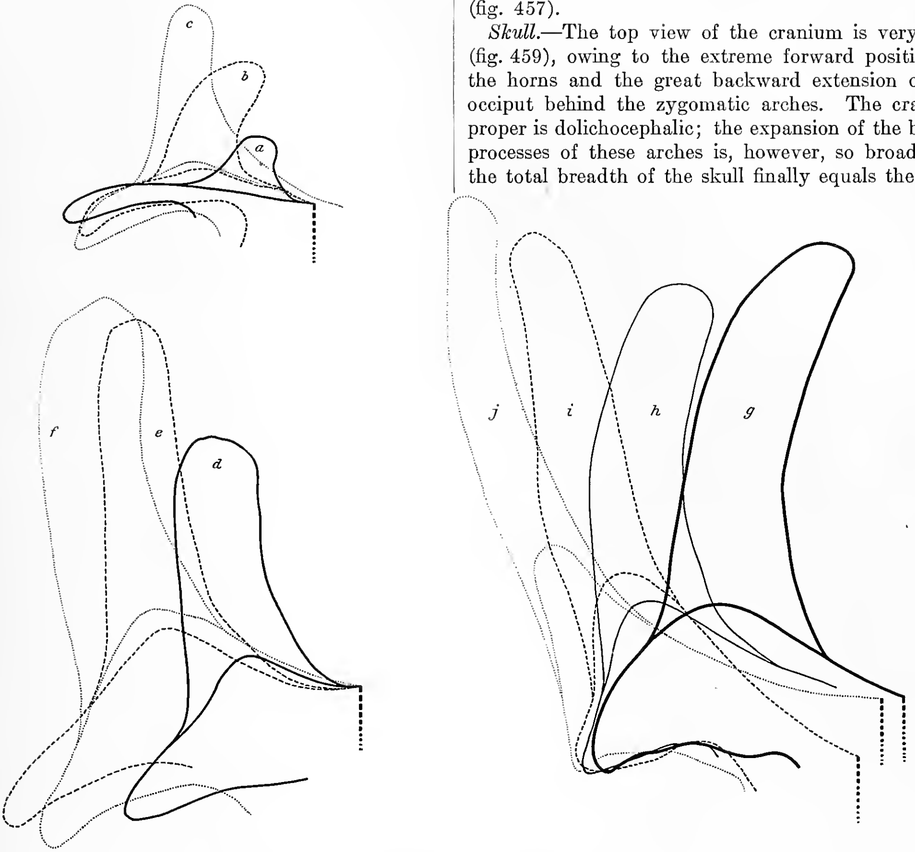


FIGURE 457.—Composite sections showing the evolution of the horns and reduction of the free nasals in the *Brontotherium* phylum

a, *Brontotherium leidyi*, Nat. Mus. 4249 (type), Chadron A 2; *b*, *Brontotherium hypoceras*, Nat. Mus. 4273, Chadron A 2; *c*, *Brontotherium hypoceras*, Nat. Mus. 4702, Chadron A 3?; *d*, *Brontotherium hatcheri*, Am. Mus. 1070, Chadron; *e*, *Brontotherium gigas*, Yale Mus. 12061 (type of *B. elatus*), upper (?) Chadron; *f*, *Brontotherium gigas*, Am. Mus. 492, Chadron C; *g*, *Brontotherium curtum*, Yale Mus. 12013 (type), Chadron C; *h*, *Brontotherium curtum*, Nat. Mus. 4946, Chadron C 3; *i*, *Brontotherium ramosum*, Am. Mus. 1447 (type), Chadron C; *j*, *Brontotherium platyceras*, Am. Mus. 1448, Chadron C. All one-fourth natural size. In the earliest stage, *B. leidyi*, the horns are small and placed near the orbits, there is no connecting crest, and the nasals are long and slender; in the latest and most specialized stage, *B. platyceras*, the horns are extremely long and placed far in front of the orbits, the connecting crest is very high, and the free portion of the nasals is practically vestigial. Between these extremes lie a considerable number of intermediate stages.

Horns.—The males of all these animals exhibit progressively broad and flattened horns, transversely oval from base to summit, diverging widely at the summits, with the great connecting crest rising between them (unlike the typical *Megacerops*), to resist lateral strains, and evolving at the expense of the constantly diminishing free portion of the nasals (fig. 457).

Skull.—The top view of the cranium is very long (fig. 459), owing to the extreme forward position of the horns and the great backward extension of the occiput behind the zygomatic arches. The cranium proper is dolichocephalic; the expansion of the buccal processes of these arches is, however, so broad that the total breadth of the skull finally equals the total length, the zygomatic index in *B. platyceras* being 110, or hyperbrachycephalic. This condition is best understood when the skull is viewed from below (fig. 393). The whole structure of the skull, including the broad and spreading occiput (fig. 378) and the excessive buccal expansion, is adaptively adjusted to the development of the horns, which from their feeble development in the females (as in the type of *Menodus peltoceras* Cope (=?*Brontotherium curtum,* figs. 459, 477, 478) are judged to have been fighting weapons in the males.

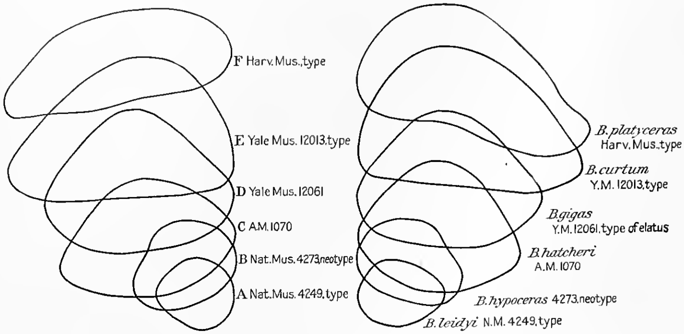


FIGURE 458.—Basal sections of the horns in the *Brontotherium* phylum

A, *Brontotherium leidyi*, Chadron A 2; B, *B. hypoceras*, Chadron A 2; C, *B. hatcheri*, Chadron; D, *B. gigas*, Chadron ?C; E, *B. curtum*, Chadron C; F, *B. platyceras*, Chadron. These sections show the progressive change from the small anteroposterior oval of *B. leidyi* to the very wide transverse oval of *B. platyceras*.

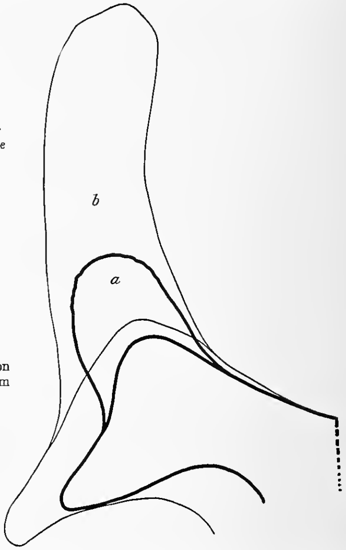


FIGURE 460.—Contrast in contour of horns and nasals between male and female brontotheres

The female (*a*), Am. Mus. 1006 (referred to *B. gigas*), differs from the male (*b*), Am. Mus. 492 (referred to *B. gigas*), chiefly in having short horns and nasals, combined with a high connecting crest.

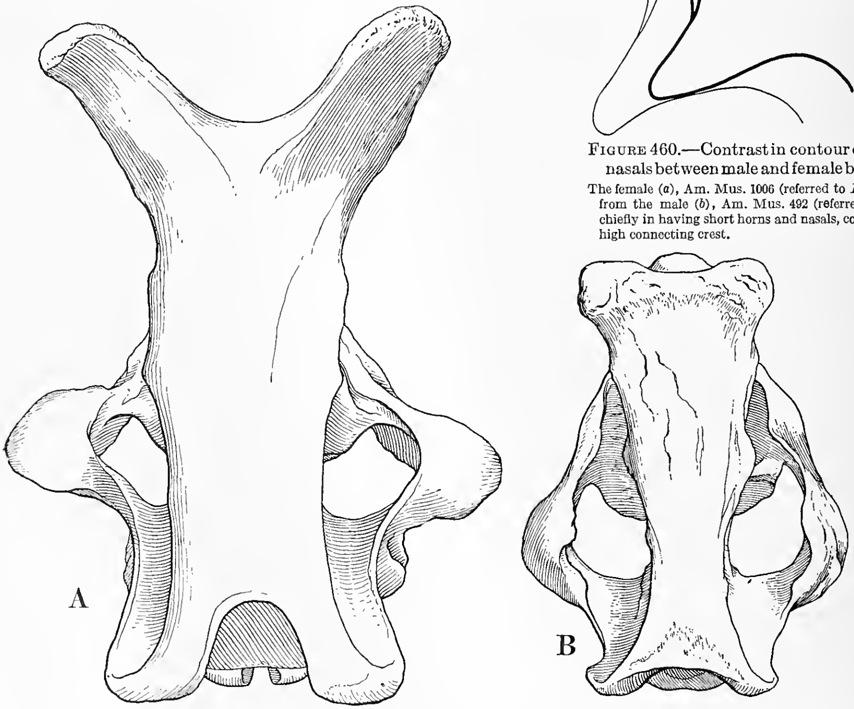


FIGURE 459.—Skulls of male and female brontotheres

Top view. About one-ninth natural size. A, *Brontotherium platyceras*, Am. Mus. 1448 (cotype). In this male skull vertical crushing has emphasized the width of the zygomata. B, *B. curtum* (*peltoceras*), Am. Mus. 1005. This female skull is small, the horns are short, and the zygomata are unexpanded.

Grinding teeth.—The grinding teeth suffered probably from the highly "selective value" placed upon the horns and were retrogressive in many respects; the total increase of length in the grinding series (21 per cent) thus did not fully share in the progressive increase in size of the skull as a whole (24 per cent). The total length of the premolar series diminished, but in *B. gigas* the individual molars are enormous—for example, m^2 (ap. by tr.) 91 by 94 millimeters, as compared with *M. giganteus* (Am. Mus. 505), m^2 87 by 84. The breadth of p^4 was also exceptionally great, and nowhere else do the tetartocones attain such vigorous development as in *B. gigas,* not excepting *Menodus giganteus.*

Sexual characters of brontotheres

MALES	FEMALES
Horns elongate.	Horns abbreviate.
Connecting crest very high.	Crest less developed.
Occiput very robust and backwardly produced.	Occiput less robust and less produced backwardly.
Zygomatic arches very broad.	Zygomatic arches less broad.
Incisors persistent.	?Incisors less persistent.
Canines larger.	Canines two-thirds size of male canines.

The contrast between the males and females generally is well brought out in the accompanying figures of the male and female skulls of *B. gigas.* It is obvious that a number of correlated characters disappear in the nondevelopment of the horns in the females, especially the marked width of the zygomatic arches, which may have been partly defensive structures, and the nonextension of the occiput posteriorly, which was probably designed in the males for the support of the great muscles of the neck.

Standard measurements in the Brontotherium phylum, in millimeters

	Upper teeth					Skull							Jaw and lower teeth					
	P^1-m^3	P^1-p^4 or p^2-p^4	M^1-m^3	Canines, anterior vertical	Canines, antero posterior diameter	Pmx to condyles	Zygomatic breadth	Cephalic (zygomatic) index	Nasal tips to occiput vertex	Nasals, free length	Nasals, free breadth	Horns, external length	P_1-m_3	P_1-p_4	M_1-m_3	Canines, anterior vertical	Canines, antero posterior diameter	Symphysis to condyles
B. platyceras, Am. Mus. 1448, ♂	337	[a]123	221	40	30	[b]728	[b]815	----	[a]693	20	81	[b]433	----	----	----	----	----	----
B. platyceras, Harvard Mus. (type)	----	----	----	----	----	----	----	----	----	----	----	[a]400	----	----	----	----	----	----
B. platyceras, Field Mus. 12161, ♂	340	120	223	36	29	880	710	80	895	38	157	[a]390	----	----	----	----	----	----
B. ramosum, Am. Mus. 1447, ♂ (type)	350	[a]137	216	----	----	741	[b]775	----	665	40	95	[b]399	----	----	----	----	----	----
B. curtum, Yale Mus. 2013, ♂ (type)	350	----	[a]228	34	----	[a]790	[a]610	?78	795	52	[a]105	380	----	----	----	----	----	----
B. curtum, Carnegie Mus.	----	----	----	----	----	----	----	----	----	----	----	365	----	----	----	----	----	----
B. curtum, Nat. Mus. 4946, ♂	348	128	224	----	----	[a]840	620	74	----	65	105	365	----	----	----	----	----	----
B. curtum, Nat. Mus. 1211, ♂	----	----	218	----	----	[a]780	[a]670	----	----	----	----	355	----	----	----	----	----	----
B. curtum, Am. Mus. 1005, ♀	345	130	222	27	20	[a]673	545	[a]80	635	44	101	160	----	----	----	----	----	----
B. curtum, Nat. Mus. 1232 ♂	345	129	228	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----
B. curtum?, Brit. Mus. 5629	----	----	211	34	31	700	563	80	[b]620	34	85	163	----	----	----	----	----	----
B. medium, Nat. Mus. 4256, ♂ (type)	365	138	235	38	----	825	----	----	----	45	110	320	----	----	----	----	----	----
B. medium?, Nat. Mus. 4699	293	117	197	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----
B. medium?, Nat. Mus. 4716, ♀	305	106	197	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----
B. dolichoceras, Harvard Mus., ♂ (type)	----	----	----	----	----	----	----	----	----	49	90	310	----	----	----	----	----	----
B. gigas, Am. Mus. 492, ♂	353	126	241	35	32	830	740	87	793	87	115	365	----	----	----	----	----	----
B. gigas (hatcheri), Carnegie Mus. 341	355	132	218	35	23	773	640	82	----	----	----	----	----	----	----	----	----	----
B. gigas (hatcheri), Nat. Mus. 4262, ♂	343	133	218	33	24	770	----	----	----	70	110	275	350	[a]121	235	33	28	625
B. gigas, Nat. Mus. 4244	348	[a]133	227	----	----	775	657	84	728	67	107	170	----	----	----	----	----	----
B. gigas, Yale Mus. 12061 (type "elatum")	----	----	----	----	----	[a]810	----	----	805	90	105	350	----	----	260	----	----	----
B. gigas, Yale Mus. (type jaw)	----	----	----	----	----	----	----	----	----	----	----	----	365	117	258	34	30	600
B. gigas?, Am. Mus. 1006, ♀	335	127	217	[a]37	22	715	----	----	660	79	88	180	----	----	----	----	----	----
B.? tichoceras, Harvard Mus. (type)	330	----	----	----	----	----	----	----	800?	65	130?	----	----	----	----	----	----	----
B. hatcheri, Am. Mus. 1070, ♂	----	132	----	35	31	----	----	----	----	85	102	265	375	[a]120	263	35	29	600
B. hatcheri, Field Mus. P 5926, ♂	[a]310	118	192	----	----	[a]710	530	----	760	90	----	200	----	----	----	----	----	----
B. hatcheri?, Univ. Wyoming 1 ♂	320	118	198?	----	----	----	546	----	----	100	126	220	[a]330	[a]116	219	37	28	630?
B. hatcheri, Nat. Mus. 1216, ♂ (type)	----	----	----	----	----	----	620	----	700	105	120	250	----	----	----	----	----	----
B. hypoceras?, Nat. Mus. 4702	350	133	212	----	----	715	540	75	----	72	107	143	----	----	----	----	----	----
B. hypoceras, Nat. Mus. 4273 (neotype)	305	[a]123	189	----	----	----	----	----	----	74	----	[a]165	----	----	----	----	----	----
B. leidyi, Carnegie Mus. 93, ♂ (paratype)	300	120	190	34	30	665	440	66	615	114	118	104	335	127	213	33	31	565
B. leidyi, Nat. Mus. 4249 (type)	290	114	186	----	----	665	----	----	625	118	105	107	----	----	----	----	----	----
Percentage of increment, B. leidyi to B. curtum	20	12	22	----	----	26	40	----	27	56	0	250	----	----	----	----	----	----

[a] Estimated.

[b] Crushed.

Measurements, in millimeters, of skulls and jaws associated with and referred to members of the Brontotherium phylum

	Skull and upper teeth				Jaw and lower teeth				
	Anterior canine to hypoconulid of m^3	P^1–m^3	M^1–m^3	Premaxillary to glenoid	Posterior canine to hypoconulid of m_3	P_1–m_3	M_1–m_3	Symphysis to condyle	Depth below m_3
B. platyceras, Am. Mus. 1448, ♂	362	337	221	[a] 483					
B. ramosum, Am. Mus. 1447 (type)	[a] 372	350	216						
B. curtum, Yale Mus. 12013, ♂ (type)		350	240						
B. medium, Nat. Mus. 4256, ♂		365	232						
B. medium, Am. Mus. 1051					450		285	730	?
B. medium, Am. Mus. 1061					400	393	272	632	181
B. gigas, Yale Mus. (type jaw)						365			
B. gigas, Am. Mus. 492, ♂	380	353	241	595					
B. (Titanops) elatum, Yale Mus. 12061 (type jaw)							260		
B. hatcheri, Am. Mus. 1070, ♂					360	375	263	600	179
B. hatcheri, Nat. Mus. 4262					360	358	233	633	125
B. hatcheri, Univ. Wyo., ♂		320	198			[a] 330	219	630	
B. hatcheri, Am. Mus. 1068, ♂					345	332	220	538	166
B. leidyi, Am. Mus. 516					330	338	222	522	133
B. leidyi, Carnegie Mus. 93, ♂ (paratype)		300	190			335	213	565	
Megacerops riggsi, Am. Mus. 6364 (type)					[a] 275	284	195	[a] 465	100
M. coloradensis, Nat. Mus	351	[b] 313	[b] 192	517	353	[b] 352	231	590	116

[a] Estimated.

[b] Left side.

Observations on the measurements of the Brontotherium series.—This phylum is as consecutive and as distinct from other phyla as that of *Menodus*. The separation of certain "ascending mutations" as "species" is very arbitrary. Yet *B. leidyi* is very far removed from *B. platyceras*.

The generic contrasts in measurements which have been given above indicate that in comparison with members of the menodontine group (*Brontops*, *Allops*, *Menodus*) the male individuals of the typical spe cies of *Brontotherium* from the upper beds are distinguished by very short tapering nasals, extremely long flattened horns, long skull top, widely expanded zygomata, very short wide premolars, and massive broad molars.

The progressive allometric evolution from *Brontotherium leidyi* to *B. curtum* and *B. platyceras* may be epitomized as shown in the accompanying table:

Allometric evolution from Brontotherium leidyi to B. curtum and B. platyceras

[Measurements in millimeters]

	P^1–m^3	P^1–p^4	M^1–m^3	P^4, ap. by tr.	M^3, ap. by tr.	Pmx to condyles	Zygomatic index	Nasal length	Horn length
B. platyceras:									
Field Mus. 12161, ♂	340	120	223			880	80	38	390
Am. Mus. 1448				42×67	84×93				
B. curtum:									
Yale Mus. 12013 (type)	350		[a] 228			790	78?	52	380
Carnegie Mus. 341				45×63	72×84				
Nat. Mus. 4946	348	128	224			[a] 840	74	65	365
B. medium, Nat. Mus. 4256, ♂ (type)	365	138	235			825		45	320
B. gigas (elatum), Yale Mus. 12061						[a] 810		90	350
B. gigas:									
Am. Mus. 492, ♂	353	126	241	47×72	91×99	830	87	87	365
Nat. Mus. 4262	343	132	218	45×57		770		70	275
B. hatcheri:									
Field Mus. P 5926	[a] 310	118	192			710		90	200
Nat. Mus. 1216 (type)								105	250
B. hypoceras, Nat. Mus. 4273, ♀	305	[a] 123	189					74	[a] 165
B. leidyi, Carnegie Mus. 93, ♂	300	120	190			665	66	114	104

[a] Estimated.

As thus arranged the skulls form a series in which the horn length and the zygomatic width increase, while the free portion of the nasals becomes extremely abbreviated. But the length of the whole grinding series in the later species does not increase pari passu with the size of the skull and with the length of the horns. From *B. leidyi* to *B. medium* it increases rapidly from 300 to 365 millimeters, but after that, in *B. curtum* and *B. platyceras*, the measurement p^1–m^3 falls to or below 350. Meanwhile the true molars also, which had increased from 190 to 241 millimeters, fall to 223. If this apparent falling off in the increase of the grinding series as a whole shall be confirmed by much more extensive material it may indicate that the excessive increase in the horns was detrimental to further increase in the size of the grinding series (Osborn). The lengthening of the premolar series is arrested by the shortening of the face, but the widening of the premolars as well as of the molars affords a compensatory increase in grinding area. The length of the true molars as compared with the basal length of the skull changed very little, as shown below:

Molar index in species of Brontotherium

B. platyceras:	
Field Mus. 12161 (basilar length extreme)	25
Am. Mus. 1448 (basilar length shortened by crushing)	30
B. ramosum, Am. Mus. 1447 (type)	29
B. curtum:	
Yale Mus. 12013 (type)	29
Nat. Mus. 4946	26
B. medium, Nat. Mus. 4256 (type)	28
B. gigas:	
Am. Mus. 492	29
Nat. Mus. 4244	29
B. "hypoceras," Nat. Mus. 4702	29
B. leidyi:	
Carnegie Mus. 93	28
Nat. Mus. 4249	28

The table of measurements above needs extension from additional material and revision with reference to the length of nasals and of horns.

SYSTEMATIC DESCRIPTIONS OF GENERA AND SPECIES IN THE BRONTOTHERIUM PHYLUM

Brontotherium Marsh, 1873

(*Titanops* Marsh, 1887; "*Brontotherium* Marsh," Osborn, 1902)

Plates XVIII–XXII, XXXIX–XLII, XLVII, LXXXII, CXXIV, CXXXII, CLVII, CLXI–CXCIV, CCXXX–CCXXXV; text figures 10, 18, 21, 24, 25, 27, 29, 33, 87, 165, 174, 177, 178, 182, 191, 193, 194, 198, 199, 202, 212, 229, 372, 375, 377, 378, 382, 383, 388, 390, 392–395, 398–405, 407, 457–481, 515, 519, 620–640, 643, 648, 649, 652, 661, 662, 668, 688, 690, 707–710, 719–727, 740, 744, 746

[For original description and type references see p. 209. For skeletal characters see p. 690]

Generic characters.—Incisors in males persistent, with large posterior cingula, (?) variable in females; canines large, obtuse; grinding teeth with retrogressive cingula; premolars with progressive tetartocones. Skull mesaticephalic to brachycephalic (zygomata). Horns diverging laterally, typically with connecting crest, shifting forward, oval to flattened in transverse section.

General characters.—Characters 3–9, 14, 15, 16, 18, 19, 21, 22, 23, 24, 28, 29, below, are correlated with brachycephaly. (1) I $\frac{2-1}{2-1}$ ♂, incisors ♂ large, flat-crowned, with stout posterior cingulum; ♀ ?one or both pair absent. (2) Canines ♂ short, robust, obtuse, with stout posterior cingulum; ♀ slender, small, with posterior face flat. (3) Grinding series arched (curvilinear). (4) Upward flexure of premolar series as seen in side view decided. (5) Length of premolar-molar series 290–365 millimeters, dental index 42–46. (6) Premolar series short, 114–140 millimeters. (7) Internal cusps of grinding teeth low, robust, well rounded, ectolophs sharply depressed to the crowns of the teeth. (8) P^4, m^{1-3} very broad, anteroposterior diameter of m^2 and m^3 less than transverse diameter. (9) No cingula between grinders, premolar cingula sessile or absent. (10) $P\frac{4-3}{4-3}$, p^1 perhaps more frequently absent than in *Menodus* and *Brontops*, subquadrangular, often with well-developed tetartocone, outer wall not overlapped posteriorly by ectoloph of p^2. (11) Premolar tetartocones, ♂ exhibiting early and pronounced development, ♀ moderate development, tetartocones large and rounded, set well in toward the center of the crown. (12) Premolars with internal cingula, ♂ blunt, reduced or absent, ♀ as in *Brontops*, external cingula variable. (13) Molars without internal cingula, external cingula faint or absent. (14) Hypocone of m^3 prominent, sometimes triradiate. (15) Basilar length of skull, 665–830 millimeters; proportions mesaticephalic to hyperbrachycephalic (index 66–110). (16) Facial portion of skull abbreviated, with premaxillaries reduced. (17) Cranial part of skull elongate. (18) Preorbital malar bridge narrow, with median ridge prominent and well rounded. (19) Infraorbital foramen inconspicuous in side view. (20) Malar below postorbital process subflat to round. (21) Free nasals tapering, progressively abbreviated and finally vestigial. (22) Horns of medium to extreme size, shifting forward progressively, finally extreme, basal section progressively becoming a transverse oval, summit of horn becoming broad, flattened anteroposteriorly, oval in section. (23) Zygomata strongly arched, buccal expansion progressive, in section finally excessively broad and flattened (♂). (24) Midparietal convexity pronounced. (25) Occiput ♂ extremely produced backward behind zygomata, ♀ much less produced. (26) Pillars flaring moderately to extremely, occiput strongly indented, with median knobs. (27) Basisphenoidal rugosity variable, vomerine septum variable. (28) Postglenoid ♂ very broad. (29) Jaw robust with shallow more or less concave chin, coronoid rather slender, tapering, anterior border rounded or square in section, strongly recurved or hooked, pointed at extremity, angle depressed and rugose (♂).

Incisors reduced in females.—There is some evidence for the absence or reduction of the upper and lower incisors in females; this evidence rests chiefly on the supposed female skull referred to *B. curtum* (Am. Mus. 1005). The permanent incisors were protruded very early and have weak implacements in the crowded premaxillae. Hence they are sometimes shed in old animals.

Ancestral brontotheres in the lower Titanotherium zone.—The Eocene ancestry of this subfamily is still in some doubt; its earliest known members may prove to be the species *Diplacodon elatus* Marsh and *Eotitanotherium osborni* Peterson of Uinta C (upper Eocene).

Relatively small and short-horned ancestors of the brontotheres have fortunately been determined by the writer as occurring according to Hatcher's geologic record in the very base of the lower *Titanotherium* zone, definitely proving that the *Brontotherium* phylum early separated from the *Megacerops* phylum and at a much earlier date from the *Brontops-Menodus* phylum. These primitive brontotheres are comparatively rare in the lower beds. They include two species as follows:

Brontotherium leidyi Osborn is a comparatively small animal with short horns, which is determined as a brontothere, however, by two very distinctive characters—first, the transversely oval section of the summit of the horn; second, the very progressive condition of the premolar grinding teeth, in which the tetartocones are well developed. This animal is of extraordinary interest by comparison with *B. platyceras* in showing the extreme transformation in the horn region which took place in the course of the deposition of 200 feet of sediment. It is represented by a number of admirably preserved specimens.

Brontotherium hypoceras (Cope).—This is an animal first named *Symborodon hypoceras* by Cope from the tip of a horn and some other fragments of the skull. He was struck by the transversely oval section of this horn tip. This very imperfect type (Pl. CLXVI, fig. 174) was fortunately compared with the skull in the National Museum and determined by Osborn as a most interesting transitional stage between *B. leidyi* and the species of the higher levels. Like *B. leidyi* it has rounded grinding teeth with low cusps, well-developed tetartocones, and obtuse canines. There is no question as to its phyletic position.

Brontotheres of the middle Titanotherium zone.—*Brontotherium hatcheri* Osborn, from the middle *Titanotherium* zone (Chadron B) includes animals of intermediate size, named in honor of J. B. Hatcher, the chief explorer of the *Titanotherium*-bearing beds, which connect *B. leidyi* and *B. hypoceras* of the lower zone with *B. gigas* and its successors of the upper zone.

Brontotherium tichoceras (Scott and Osborn) possibly belongs geologically to the upper zone, but both its geologic and its phyletic position are somewhat uncertain, although there is no doubt whatever as to its general affinity to *Brontotherium*.

Brontotheres of the upper Titanotherium zone.—*Brontotherium gigas* Marsh, a giant form, was probably characteristic of the lower part of the upper zone, namely, Chadron C 1. The evolution of the special characters of the phylum, the horns, and the zygomatic arches now appears to be accelerated. As shown in the accompanying table six succeeding stages, species, subspecies, or mutations can be distinguished, to which specific names may here be given. While the evolution of the dominant characters of the horns, connecting crests, and buccal processes of the zygomata is progressive, and while the premolars follow the universal law of increasing complication by the development of the tetartocones, the series of grinding teeth as a whole is partly arrested and in some respects retrogressive in development. On account of the shortening of the face the premolar series is shorter than in *Menodus*, but the premolars have the most advanced tetartocones known in any genus except *Megacerops*, and both molars and premolars are extremely broad, so that in basal view the dentition appears enormous. It is true that in *B. platyceras* (Field Mus. 12161) the premolar-molar series is slightly shorter than in *B. gigas elatum* (Am. Mus. 492). The incisors, on the contrary, in the males at least, are remarkably persistent, and one of the readiest means of distinguishing *Brontotherium* is by its reduced cingula on the superior incisors, which are quite different from the smooth, rounded incisors of *Megacerops*.

Stratigraphic horizons of Brontotheres

Lower Oligocene (Chadron formation)	C	3. Upper	Brontotherium platyceras B. ramosum
		2. Middle	B. curtum B. medium B. dolichoceras
		1. Lower	B. gigas elatum
	B	3. Upper	B. gigas ?B. tichoceras
		2. Middle	B. hatcheri
		1. Lower	
	A	3. Upper	
		2. Middle	B. hypoceras B. leidyi
		1. Lower	
Upper Eocene of Uinta Basin		Horizon C 1	Diplacodon elatus
		Horizon B	Eotitanotherium osborni

Geologic succession of lower Oligocene species of Brontotherium

C. OF LARGE SIZE

Upper *Titanotherium* zone:
- Sixth stage, *B. platyceras:* Grinding teeth 337–340 millimeters; nasals vestigial; horns extremely broad and flat.
- Fifth stage, *B. ramosum:* Grinding teeth 350 millimeters; nasals vestigial; horns planoconvex at base, expanding at summits.
- Fourth stage, *B. curtum:* Grinding teeth 345–350 millimeters: nasals shorter; horns slightly convex to plane posteriorly.
- Third stage, *B. medium:* Grinding teeth 365 millimeters; nasals shorter; horns with prolonged malar ridge; concave antero-external faces.
- Second stage, *B. dolichoceras:* Nasals shorter; horns with incipient malar ridge.
- First stage, *B. gigas:* Animals of maximum size; grinders 330–353 millimeters with cingula; horns longer, oval, recurved, 275–360 millimeters in height; nasals narrow, more reduced.

B. OF INTERMEDIATE SIZE

Middle *Titanotherium* zone, upper levels:
- *B. tichoceras* (level unrecorded): Grinding teeth 330 millimeters; horns obliquely oval; phyletic position somewhat doubtful.
- *B. hatcheri:* Grinding teeth 310-320 millimeters with cingula more or less developed; nasals longer than in *B. gigas;* horns 250 millimeters in height.

A. OF SMALL SIZE

Level doubtful, either lower or middle *Titanotherium* zone:
- *B. hypoceras:* Grinding teeth as in *B. leidyi* (305 mm.); nasals intermediate in length; horns longer (140 mm.), more anterior in position.

Upper levels of lower *Titanotherium* zone:
- *B. leidyi:* Grinding teeth 290–300 millimeters, typically smooth and rounded, cingulum faint or wanting; nasals elongate: horns rudimentary, placed above orbits.

The Brontotherium phylum as represented in the Hatcher collection of 44 skulls and jaws from the Chadron formation in the United States National Museum

	Catalog No.	Material
B. platyceras (Scott and Osborn)	8730	Skull.
Do	8729, ♂	Nasals and horns.
B. ramosum (Osborn)	1243, ♀?	Horns.
B. medium (Osborn)	4256, ♂	Skull. Type.
B.? medium (Osborn)	8772	Pair of jaws.
B. curtum Marsh	8726	Fine skull and horns.
Do	4946, ♂	Very fine skull. Right horn broken and healed during life.
Do	1232, ♂	Left upper dental series.
Do	1211, ♂	Skull.
Do	8727, ♂	Anterior half of skull.
Do	8728, ♀?	Skull and jaws.
B.? curtum Marsh	8743, ♂	Skull, nasals, horns (partly destroyed).
B. gigas? Marsh	4244, ♀?	Skull. Horns imperfect. Agrees with B. gigas in dental measurement.
B. gigas Marsh	8752	Upper dentition. Premolars and molars smaller than in large B. gigas.
B.? gigas Marsh	8755	Upper dentition.
Do	8758, ♀	Skull.
B. gigas Marsh	8762, ♀	Skull and parts of lower jaws. Horns small and feeble.
B.? gigas Marsh	4903	Parts of both rami.
Do	8773, ♂?	Pair of lower jaws lacking posterior part of left. Aged individual.
Do	8774	Pair of lower jaws (young).
Do	8783	Left ramus.
Do	8787, ♂?	Pair of lower jaws.
B. gigas? medium?	8791, ♂	Pair of lower jaws.
B.? gigas Marsh	8800, ♀	Left ramus.
B. gigas (hatcheri) Marsh	4262, ♂	Skull, jaws, and part of skeleton.
B. sp	8805	Lower jaws and anterior dorsal (young).
B. medium (?tichoceras)	4699, ♂?	Skull.
B.? tichoceras (Scott and Osborn)	8313, ♂	Skull and jaw (good).
B. sp	1227, ♀	Lower jaw (immature).
?B. sp	8734	Indeterminate skull lacking nasals and horns. Poor.
B. sp	8775, ♂	Pair of jaws (small).
B. hatcheri Osborn	1216, ♂	Skull. Type.
B. medium? (hatcheri)	4716, ♀?	Skull. No canine, horns, or nasals. Genetic reference doubtful; B. hatcheri in measurement.
?B. hatcheri Osborn	4255	Skull with front part of jaw.
B. hatcheri Osborn	4704, ♀	Skull. Small female; horns with connecting crest.
B. (hatcheri) hypoceras (Cope)	8780, ♂	Pair of lower jaws.
B. (hatcheri) hypoceras	8789, ♂?	Right ramus.
B. hypoceras (Cope)	4273, ♂	Skull. Neotype. Important male skull.
Do	4702, ♀?	Skull.
Do	8763, ♀?	Skull.
Do	8757	Pair of jaws; horn cores; nasals.
B. leidyi Osborn	4249, ♀?	Skull. Type.
Do	4250	Part of jaw.
B. (leidyi?) (hypoceras?)	8795	Pair of jaws.

Brontotherium leidyi Osborn, 1902

Plates XIX–XXII, XLVII, CLXI–CLXV; text figures 27, 29, 33, 87, 198, 199, 372, 383, 390, 392, 395, 399, 401–403, 405, 457, 458, 461, 462, 464, 519, 620, 621, 624, 626–629, 635–637, 661, 668, 690, 709, 720, 727

[For original description and type references see p. 234. For skeletal characters see pp. 691, 697]

Geologic horizon.—Lower *Titanotherium* zone of South Dakota, middle level (Chadron B).

Specific characters.—P^1–m^3 290–300 millimeters, m^1–m^3 114–120, dental index 45. Basilar length of skull 665 millimeters, zygomatic breadth 440, index 66 (dolichocephalic or mesaticephalic). Nasals elongate (free length 118 mm.), broad proximally (105 mm.), tapering distally. Horns low (height above narial sinus 107 mm.), placed above preorbital foramen, recurved, with gently sloping anterior contour, summital section a transverse oval. Zygomata with buccal swelling slight.

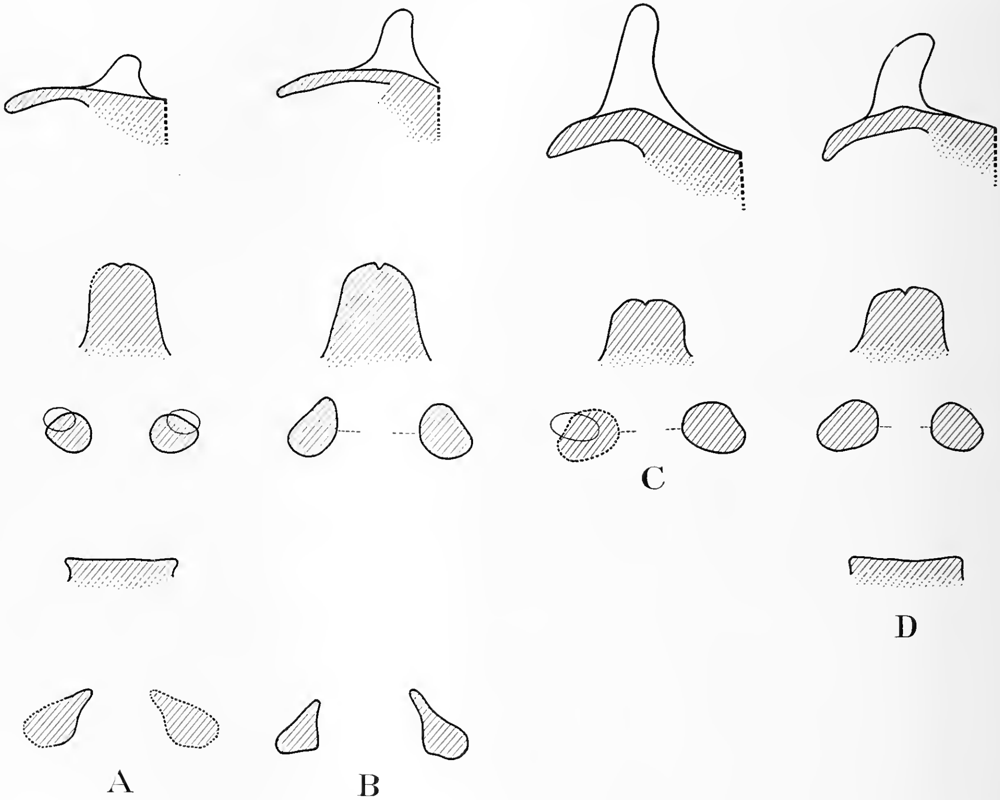


FIGURE 461.—Sections and contours of skulls of *Brontotherium leidyi* and *B. hypoceras*

A, *Brontotherium leidyi*, Nat. Mus. 4249 (type); horns small and placed not far in front of the orbits, their basal section ovoid with the narrow end external, the section of the upper part of the horns roundly oval, connecting crest slight, nasals long and lender, zygomata slightly expanded. B, *B. leidyi*, Carnegie Mus. 93, a referred specimen with horns longer, basal section obliquely oval, zygomata little expanded, nasals long. C, *B. hypoceras*, Nat. Mus. 4273 (neotype), horns much longer than in *B. leidyi* and placed far in front of the orbits, their basal section oval, nasals short. Thus *B. hypoceras* is a much more advanced stage than *B. leidyi*. D, *B. hypoceras*, Nat. Mus. 4702. One-seventh natural size.

Materials.—The species is represented by the type skull (Nat. Mus. 4249, skull R) from the lower *Titanotherium* zone, middle level (B 1), and by a beautifully preserved skull and lower jaws (No. 93) in the Carnegie Museum at Pittsburgh, associated with a humerus, radius, ulna, tibia, and atlas.

General description.—This species is positively recorded from the lower *Titanotherium* zone and is of great interest because *Brontotherium leidyi*, while very primitive and approaching the primitive members of the other phyla in certain respects, is yet readily distinguished from its contemporaries—first, from *Brontops brachycephalus* by the greater length and size of the skull as a whole; second, from the type of *Allops walcotti* (Nat. Mus. 4260) by the more pronounced development of the tetartocones of the premolars, especially of p$_4$, by the reduction or absence of internal and external cingula on the premolars and molars, by the rounded, obtuse contours of the premolars, and especially by the transverse oval section of the horns from base to summit. In all these characters it anticipates the well-marked *B. gigas* and *B. hypoceras* types.

Other features distinguishing *B. leidyi* from *A. walcotti* are no median vertical ridge on occiput; no lateral projections from midtemporal crests; great breadth opposite supraorbital processes; horns slightly more anterior to orbit; no lacrimal knob; broad contact of postglenoid and post-tympanic processes.

Observations on the measurements of Brontotherium leidyi.—The type and hypotype specimens agree fairly well in measurements, and this primitive species is very clearly defined. The zygomatic index is extremely low, owing to the nonexpansion of the zygomata; as compared with *B. platyceras* the nasals are about three times as long, while the elevation of the horns above the nasals is only about one-fourth as great.

The type skull (Nat. Mus. 4249) is in the beginning of the ninth growth stage. The zygomata, although much crushed, give evidence of a sudden flattening and buccal expansion posteriorly, similar to that which we observe on a larger scale in *B. gigas*. The occiput shows narrow lateral pillars; it was deeply cleft above. The nasals are remarkably long, narrowing anteriorly, and decurved. The bridge over the infraorbital foramen is rather broad. The infraorbital foramen is partly exposed on the side of the face. The horns rise a very short distance above the vertex and, unlike those in *A. walcotti*, are markedly recurved and broadly oval at the top. Judging by the alveoli, there is a pair of large lateral incisors with a vestigial alveolus for a median incisor on the right side. The dental formula is thus $I^{\underline{2-1}}$, $P^{\underline{4}}$. The premolars have rounded inner and outer surfaces and vestigial or even no trace of cingula and in this respect resemble those in certain specimens of upper *Titanotherium* zone species of this series. The tetartocones are strongly developed in p^2, p^3, p^4, occupying about two-fifths of the inner surface of the crown in p^2, p^3 and being large and prominent even on p^4. The medifossettes are much deeper than in *Brontops brachycephalus*. The hypocone is cingulate on m^3 and presents a very strong crest or aborted metaloph extending in toward the metacone; m^2 shows the so-called antecrochet and crochet.

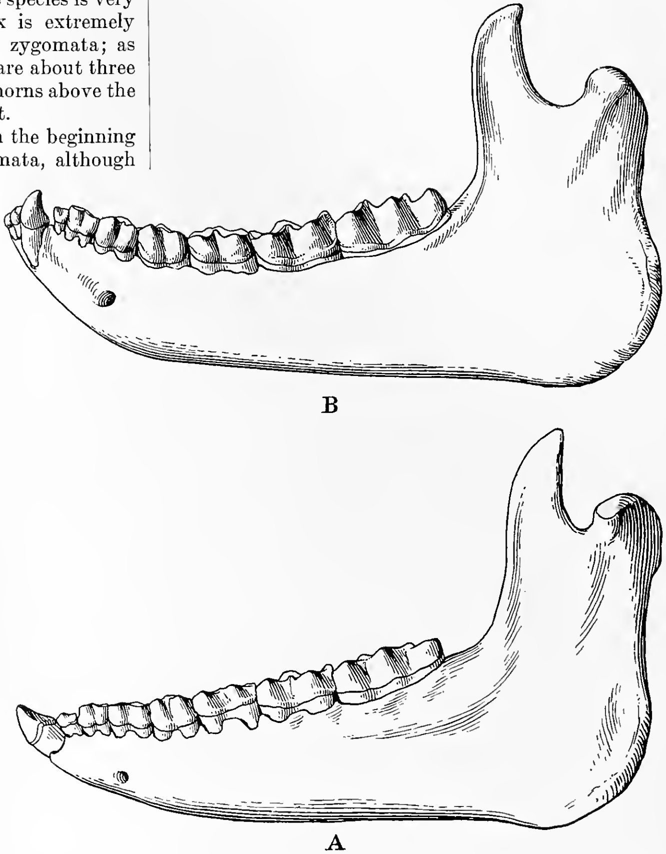


FIGURE 462.—Lower jaws of *Brontotherium leidyi*

A, Carnegie Mus. 93; ramus crushed vertically but teeth well preserved, chin shallow, angle not produced, canine very stout, no diastema in front of p_1, grinding teeth without external cingula. B, Am. Mus. 516; provisionally referred to *B. leidyi* on account of the near agreement in measurements. Incisors stout, canine short and swollen, a small diastema in front of p_1, cheek teeth almost lacking external cingula, premolar series curved upward anteriorly. One-fifth natural size.

The beautifully preserved specimen in the Carnegie Museum (No. 93, Pls. CLXI–CLXV, fig. 462) differs from the National Museum type in the following points: (1) The median incisor is persistent but reduced; (2) the premolars have sessile, crenulate internal cingula; (3) the tetartocones are set even farther in toward the middle of the crown; (4) the preorbital malar bridge is narrower and rounder. It is thus in every respect a characteristic *Brontotherium*. It shows very large, flat-crowned, functional incisors; exceptionally heavy, blunt, posteriorly cingulate canines in the upper and lower jaws; $p\frac{1}{1}$ preserved but small, tetartocones prominent, well rounded; cupped and crenulate hypoconulid on m_3, occipital knobs (Pl. CLXV), inconspicuous infraorbital foramen and rounded malar bridge, nasals thin except along median inferior ridge, chin sloping, coronoid hooked. Taken in connection with the type it proves that *Brontotherium* must have acquired its generic characters very early, especially since both these specimens are from the lower zone.

Jaw of B. leidyi.—The jaw in this stage of evolution is represented by a specimen (Am. Mus. 516) which was formerly (Osborn, 1896.110, p. 181, fig. 5) erroneously described and figured as pertaining to *Menodus trigonoceras*. It exhibits the convex lower border, the small mental foramen below the fang of p_3, the absence of external and internal cingula upon the inferior molar-premolar series, the reduced first lower premolar, the short, obtuse canines, with a postero-internal cingulum, the well-developed pair of lower incisors, the crenulate crest of the hypoconulid on m_3, all characteristic of *Brontotherium*. The chin is a little more decided than in *B. gigas;* the incisors are not evenly rounded but have a posterior cingulum.

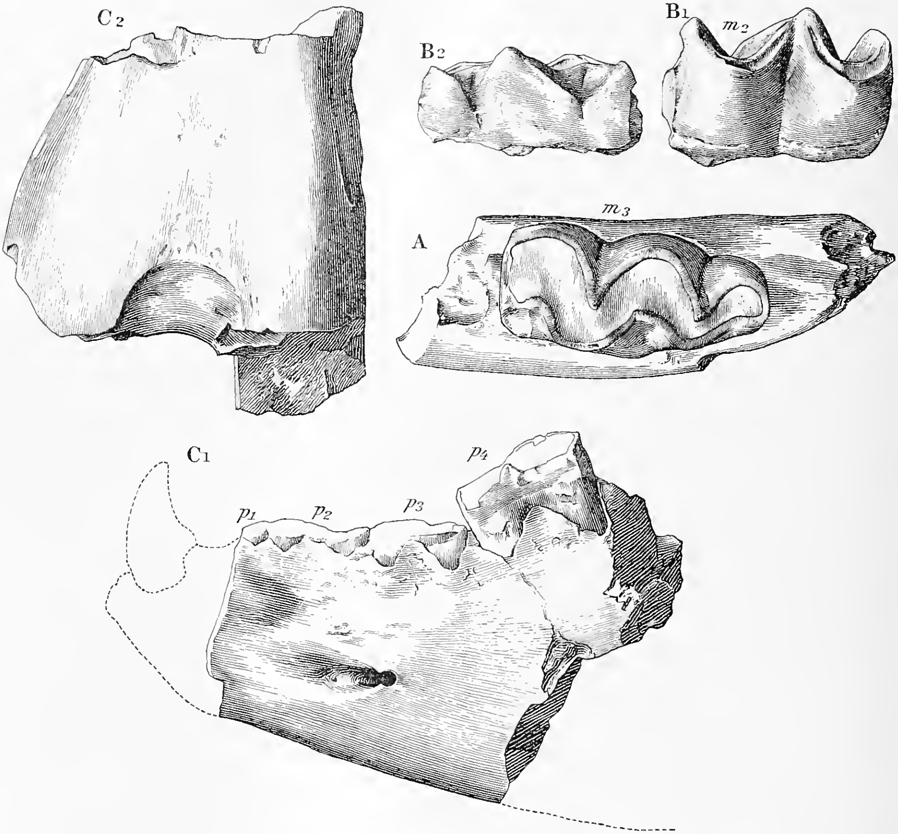


FIGURE 463.—Two lower molars and symphyseal region of *Brontotherium? rumelicum*

Type, paratype, and referred specimen of "*Menodus? rumelicus*" Toula; geologic level, "Belvidereschotter"; locality, Kajali, northwest of Burgas, eastern Rumelia (fide Toula). A, Type, third right lower molar, crown view. B_1, B_2, Paratype, second right lower molar (probably of another animal), external and internal views. C_1, C_2, Referred specimen, symphyseal region (probably of another animal), external and inferior views. One-half natural size. The type offers no very distinctive generic characters, but the referred symphyseal region agrees nearly with *Brontotherium* in general contour and in the proportions and position of the premolars. These specimens, together with the fragment named *Titanotherium bohemicum* and the type lower jaw of *Brachydiastematherium transilvanicum*, are the sole known European representatives of the titanotheres.

Brontotherium? rumelicum (Toula)

(*Menodus? rumelicus* Toula, 1892)

Text figures 193, 463, 464

[For original description and type references see p. 230]

Type locality and geologic horizon.—Lower Oligocene(?) of eastern Rumelia, Balkan Peninsula, Europe.

Generic and specific characters.—Symphyseal region and premolars of paratype approaching *Brontotherium leidyi* in characters and measurements. Premolars with reduced external cingula. Symphysis massive, flattened below.

The second (paratype) and third lower molars seem to offer no decisive specific characters.

Comparative measurements of Brontotherium? rumelicum, in millimeters

	B.? rumelicum	B. leidyi, Nat. Mus. 4249 (type)	B. gigas?, Am. Mus. 1068	Menodus trigonoceras, Am. Mus. 1067	B. robustus, Yale Mus. 12048 (type)
M_3, ap. by tr.	[a] 94×43	96×41	102×48	108×45	110×47
M_2, ap. by tr.	[b] 75×42	68×40	67×48	74×43	77×46
P_1–p_4	[c] 123	119	113	123	133

[a] Type. [b] Paratype. [c] Referred.

These measurements offer no very decisive evidence, but a direct comparison of the cast of the referred lower jaw reveals a strong resemblance to the jaws of *Brontotherium.*

Comparative measurements of third inferior molar of Brontotherium? rumelicum, in millimeters

	B. rumelicum (type)	B. leidyi, (Carnegie Mus. 93)	Menodus trigonoceras	
			Am. Mus. 1007	Am. Mus. 1067
Total anteroposterior	94	96	108	108
Transverse, anterior lobe	43	41	48	45
Transverse, posterior lobe	39		46	
Transverse, third lobe	27		27	

Of the highest importance and interest is the question, How many branches of the titanotheres invaded Europe and Asia? There is no doubt that this family was chiefly North American in evolution, but the presence near the Black Sea of the animal described by Toula as *Menodus rumelicus,* of the previously described *Brachydiastematherium,* and of the newly described *Menodus bohemicus* affords positive proof that at least three branches of the great family of titanotheres actually invaded Asia and eastern Europe. The titanotheres discovered in Mongolia by the Asiatic expedition of 1922–23 are described in the appendix (pp. 913, 942).

Geologic level.—It is a remarkable fact that the geologic records in the present case as well as in that of *Brachydiastematherium* conflict with those in America. The *Brachydiastematherium* is said to have been found in beds of lower Eocene or Ypresian [lower] age. The present type of *M. rumelicus,* on the contrary, is recorded as of extreme upper Miocene age, or as equivalent to Pikermi. Possibly *M. rumelicus* represents a survivor of the titanotheres in western Asia and eastern Europe after the period of their extinction in North America; but this is rendered improbable by the fact that the present type is in a lower Oligocene stage of evolution.

Materials.—Referring to the technical description of Toula (Toula, 1892.1, p. 612) we note that the specimens consist, first, of the type, a portion of a ramus containing m_3 (fig. 463), and secondly of the paratype, an isolated lower molar. This lower molar is certainly a second molar (m_2) rather than a first molar (m_1) as identified by Toula—first, because this tooth is less worn than m_1; second, because it is larger than m_1. Both of these specimens were found at Kajali, north of Burgas, eastern Rumelia, near the Black Sea, northwest of Constantinople. Four years later Toula (1896.1, p. 922) described a portion of a mandibular symphysis which was found in the same locality (figs. 463, 464).

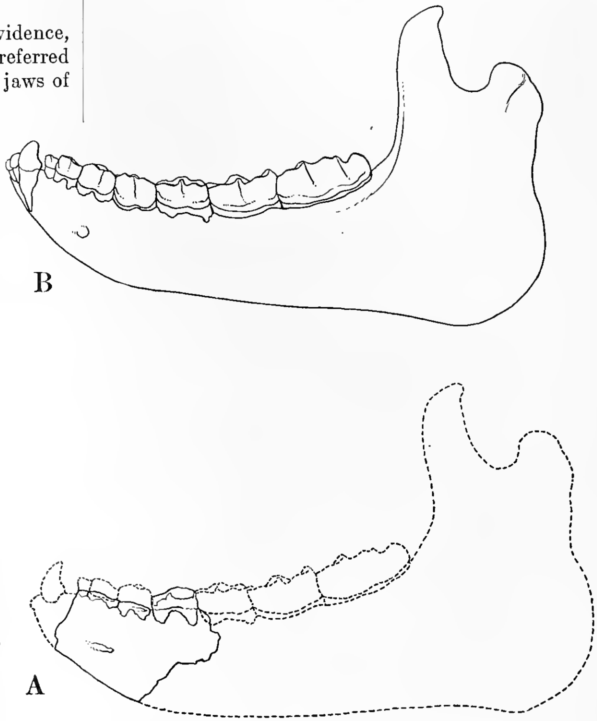


FIGURE 464.—Lower jaws of *Brontotherium? rumelicum* and *B. leidyi*

A, Symphyseal region referred to *B. rumelicum;* B, lower jaw of *B. leidyi.* One-sixth natural size.

Affinities.—The resemblances of these specimens to the Ancylopoda (*Chalicotherium* and *Macrotherium*) were pointed out by Toula, who, however, finally concluded by referring all these specimens to *Menodus.*

We note the following marked differences from the Chalicotheriidae: (1) Presence of a strong third lobe on m_3, which is absent in all chalicotheres; (2) a massive symphysis and chin, which is reduced and degenerate in all chalicotheres; (3) presence, so far as we can judge by alveoli, of large canine teeth, which are reduced in all chalicotheres; (4) absence of the metastylid, in contrast with the presence of the metastylid or reduplication of the metaconid in all chalicotheres.

Thus in spite of the authority of Von Zittel, who also suggested reference of the types to the Chalicotheriidae, the anatomical evidence is absolutely against the affinity to the Ancylopoda. On the other hand, comparison of casts of three specimens kindly presented to the American Museum by the late Professor Toula shows a close resemblance to the large Oligocene titanotheres in the structure both of the teeth and of the jaw. The chief or distinctive characters are as follows:

Symphysis massive, canines probably large, four lower premolar teeth, lower molars without internal or external cingula, hypoconulid m_3 without strong internal crest.

Apparently this type is very similar to *Brontotherium* in its measurements and in the structure of the jaw so far as preserved but especially in the structure of the grinding teeth. The entire absence of internal and external cingula on the grinding teeth forbids reference to *Menodus* and relates the animal certainly to *Brontotherium*, in which the cingula are reduced. The massive symphysis of the lower jaw and the reduced crest of the hypoconulid on m_3 are, it is true, features which suggest a member of the Menodontinae; but on the whole the prevailing characters relate this animal certainly to a branch of the *Brontotherium* phylum.

Brontotherium hypoceras (Cope)

(*Symborodon hypoceras* Cope, 1874; "*Brontotherium hypoceras*" Osborn, 1902)

Plates CLXVI, CLXX, CLXXXIII; text figures 174, 399, 457, 458, 461

[For original description and type references see p. 216]

Geologic horizon.—Middle *Titanotherium* zone (Chadron B); possibly also in lower beds of the upper zone (Chadron C).

Specific characters.—Skull larger than *B. leidyi* (premaxillaries to condyles 715 mm., estimated), free nasals shorter (74 mm.). Horns placed anteriorly, oval from base to summit, outside length 140 millimeters; buccal processes prominent. M^1–m^3 305 millimeters (Nat. Mus. 4273)—that is, somewhat longer than in *B. leidyi*. A single superior incisor in adults(?).

The specific name apparently refers to the erroneous opinion of Cope that there was a second pair of horns, consisting of low protuberances, behind and on a lower level than the first pair.

Materials.—The materials consist of the type and of two imperfect skull specimens in the National Museum. Cope's imperfect type of this species (Am. Mus. 6361) consists principally of a horn tip, the bridge over the infraorbital foramen, and parts of a zygoma, which fortunately offer characters of diagnostic value. The type horn apparently belonged to a young adult or female; it was taken to Washington and closely compared with two relatively complete specimens in the National Museum, with the gratifying result that specific identity was established. These two National Museum skulls are from the upper levels of the lower *Titanotherium* zone, or the lower and middle levels of the middle zone, and are distinguished by short, transversely oval horns, similar in section to those of *B. gigas*, but about only one-third as long and as massive.

The first skull (Nat. Mus. 4702, skull k′) was recorded from the lower beds of upper level C, but Mr. Hatcher regards the record as doubtful. This skull is a *B. hypoceras* in its horn and nasal development, but it has the dental size and development of *B. gigas* (see table above). It is therefore somewhat problematic. Unfortunately it lacks the canines, so we can not determine the sex positively. The very marked development of the tetartocones on the premolars indicates an affinity to *B. gigas;* it also proves that this is a successor to *B. leidyi* or of more recent geologic age. In p^4 the tetartocone is fully as large as the deuterocone and entirely separate; the crowns of the premolars are exceptionally smooth, rounded, devoid of cingulum, with obtuse cusps. The molars are also devoid of cingulum. In m^3 the hypocone is a prominent cingule. The nasals are thin and resemble those in *B. gigas*. The horns are very small and have the characteristic oval *B. gigas* section from base to summit; they are placed remarkably far forward. In superior view the skull resembles that of *B. leidyi* on a larger scale. The top of the cranium narrows gradually, with the occipital pillars apparently slender (although this part is largely restored), the occiput being deeply indented; the zygomata have flattened posterior expansions which recall in contour those of *B. gigas*, although less robust.

The second, the neotype skull (Nat. Mus. 4273, skull l) is correctly recorded from the middle *Titanotherium* zone, level Chadron B 2. The skull (consisting of only the anterior portion) is small, although it belongs to a very old animal in the tenth stage of growth. It corresponds to the preceding skull, but the horns are longer and placed equally far forward; as shown in the section (fig. 461, C) there is a low connecting ridge.

Dentition.—In the neotype skull (Nat. Mus. 4273) the dental measurements are rather close to those of *B. leidyi*, save that the premolar series is longer, but the "free nasals" are much shorter and the horns longer. Extremely valuable evidence is afforded by the short, obtuse canines with strong posterior cingula, which resemble those of *B. gigas* on a small scale. In *B. leidyi* a reduced upper median incisor was observed; but in this specimen no trace of the upper median incisor is found, there being only one pair of well-developed lateral incisors. The loss of

i^1 may be an age character. The crowns are absolutely smooth, oval, and without cingulum. This incisor reduction may also indicate female sex; if not, it would appear to place *B. hypoceras* out of direct ancestry to the *B. gigas-platyceras* line. Since all specimens of *B. gigas* show two well-developed incisors the presence of but a single incisor appears to be a distinctive and specific character in *B. hypoceras.* The characters of the premolars and molars and especially the development of the tetartocones are about the same as in the first skull, except that there is a sessile crenulate cingulum on the inner sides of p_2, p_4, and the tetartocone on p_4 is somewhat smaller.

Brontotherium hatcheri Osborn, 1908

Plates XIX, XXXIX–XLII, CXXIV, CLXVII–CLXX, CLXXII; text figures 202, 395, 399, 400, 404, 457, 458, 465–468, 470, 630, 632, 639

[For original description and type references see p. 235. For skeletal characters see p. 695]

Geologic horizon.—Middle *Titanotherium* zone of South Dakota.

Specific characters.—I$\frac{2}{2}$, P$\frac{4}{4}$. Nasals moderately long (97 mm.), thin at the edges. Horns, 250+ millimeters, two-thirds the length of the *B. gigas* horns. Skull length (premaxillaries to condyles) 710 millimeters (estimated), width (across zygomata) 530 (estimated).

This species was named in honor of J. B. Hatcher, paleontologist and explorer.

Materials.—The species is represented by four specimens, namely, the type skull (Nat. Mus. 1216, skull a) and the referred material, including in the National Museum a second skull (No. 4255, skull Q), in the American Museum the anterior portion of a skull, No. 1070, associated with a lower jaw, and in the Field Museum, Chicago, a complete uncrushed skull (No. P 5926).

The type is the large skull Nat. Mus. 1216, complete except the premaxillaries, recorded by Hatcher from the uppermost levels of the middle *Titanotherium* zone. Although a fully adult animal, in the ninth stage of growth, as compared with *B. gigas* it has shorter horns (250 mm.) of rounded section, a relatively lower connecting crest, and longer nasals (97 mm.). It appears to represent an early phase of evolution of *B. gigas*, the type brontothere. The horns are very round or convex in section and have a well-defined external ridge on the lower outer portion; the connecting crest is relatively shallow, and the nasals are thin; the zygomata are broad and flat. The premolars are well advanced, the tetartocone of p^4 being quite distinct.

A skull in the National Museum (No. 8313) described below under *Brontotherium tichoceras* should also be compared with the type of this species but differs in the absence of a connecting crest.

A second skull of *B. hatcheri* (Nat. Mus. 4255), equally primitive, is also recorded by Hatcher from the uppermost level (Chadron C) of the middle *Titanotherium* zone. This animal, in the seventh stage of growth, exhibits intermediate horns (280 mm.) with a still lower connecting crest than in the type of *B. hatcheri;* the basal horn section has a more prominent nasal angle than in the type. The nasals and horns both in form and in section might be described as intermediate between *Brontops robustus* and *Brontotherium gigas.*

In the American Museum is a skull (No. 1070) which may represent either an earlier stage of evolution, such as *B. hatcheri*, or a variety of *B. gigas*. This skull is that of a bull in the seventh stage of growth and affords valuable supplementary knowledge of the dental and mandibular structure of an advanced *B. hatcheri* (Pl. CLXIX). It proves that the formula is I$\frac{2}{2}$, P$\frac{4}{4}$. P^1 may drop out in old animals, just as in *B. gigas.* The inferior lateral incisors are robust teeth with a crenulate posterior cingulum; the median pair are smaller.

Degeneration of the cingulum.—The premolars of this specimen (Am. Mus. 1070) have an especial interest as showing several stages in the decline of the internal cingulum, which, as we have observed, is very feebly developed in *B. leidyi* and *B. hypoceras.* On p^4, right, the cingulum is a blunt ridge slightly crenulate; on p^3, right, the cingulum is incomplete, the crenulations being much more prominent and more separate; on p^3, left, the line of the cingulum is very faint, the crenulations are very prominent, separate, and apparently in process of being absorbed into the bases of the internal cones. The occurrence of the cingulum in this undoubted bull coincides with other evidence against the hypothesis that the cingulum is a sexual character.

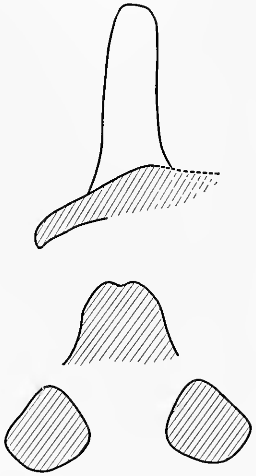


FIGURE 465.—Sections and contours of skull of *Brontotherium hatcheri*

Nat. Mus. 1216 (type). One-seventh natural size.

A peculiar feature of the enamel of the lower and upper teeth is the fine horizontal striation of structure, which is also observed in succeeding members of this series.

In this animal the horns are rounder and shorter than in the type of *B. gigas*, but the connecting crest is much deeper than in the type of *B. hatcheri*. This specimen of *B. hatcheri*, moreover, tends to bridge over the gap between *B. leidyi* and *B. gigas*, because while approaching the latter in the connecting crest between the horns and in its larger size, it resembles the older form of *B. leidyi* in the following respects: (1) The canines, incisors, and grinding teeth are similar, (2) the horns are intermediate in position between those in *B. leidyi* and *B. gigas*, (3) the top view of the skull is similar to *B. leidyi*.

Field Museum skull of B. hatcheri.—In the Field Museum, Chicago, there is a beautiful and nearly uncrushed skull of this species from Phinney Springs, S. Dak., recorded from the middle zone, at a level 75 to 100 feet above the Pierre shale. The skull is a typical *Brontotherium* in every respect and contrasts sharply with the *Brontops-Allops-Menodus* group while agreeing with *Megacerops* and *Brontotherium*, especially (1) in the shape of the nasals, which are gently tapering and distally decurved in both top and side views; (2) in the anterior narial opening as seen in side view; (3) in the upward flexure anteriorly of the tooth rows; (4) in the very narrow, rounded bridge over the infraorbital foramen; (5) in the relatively small orbit; (6) in the shape of the connecting crest and horns; (7) in the midparietal convexity, which is followed by a depression; (8) in the gentle slope of the occipital vertex in side view; (9) in the characters of the cheek teeth, which have very large circular tetartocones set well in toward the middle of the crown, vestigial external cingula, and low, rounded internal cingula and rounded external faces; (10) in the minute p^1. In general this skull also supports the specific separation of *B. hatcheri* as a lower stage of *B. gigas*. Comparative measurements are given above.

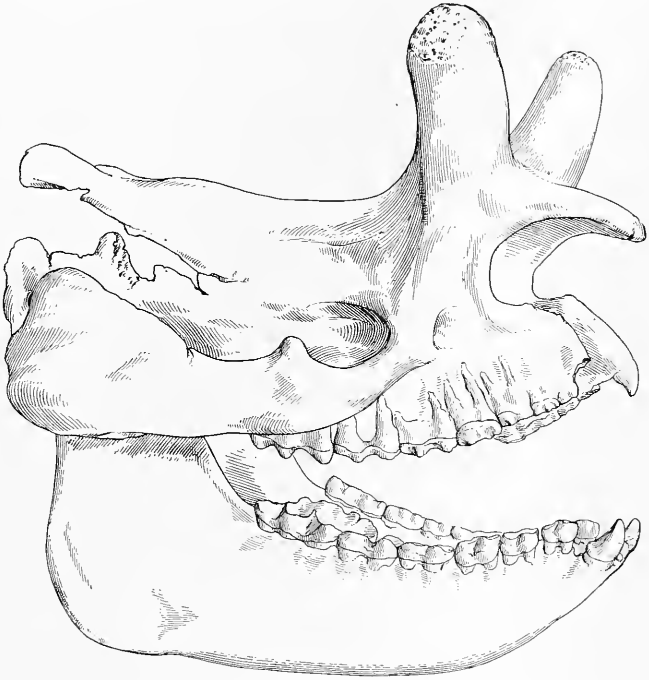


FIGURE 466.—Skull of *Brontotherium hatcheri*

Univ. Wyoming Mus. 1; Chadron C (fide W. H. Reed); northeast corner of Carbon County, Wyo. Side view. One-sixth natural size. The horns and measurements are close to those of *B. hatcheri*, the basal section of the horns recalls *B. tichoceras*, and the associated lower jaw is characteristic of *Brontotherium*.

University of Wyoming skull of B. hatcheri.—A skull (figs. 466, 467) and associated jaw (fig. 468, A) which are provisionally referred to this species are in the University of Wyoming. They were discovered by Mr. W. H. Reed in the upper *Titanotherium* zone in the northeastern corner of Carbon County, Wyo. The absence of a connecting crest, the subcylindrical form of the horns, and the form of the nasals at first suggest the type of *Megacerops coloradensis;* but the skull differs in many points from that of *Megacerops acer*, and the measurements are on the whole closer to those of *B. hatcheri*. The fourth upper premolar measures 41 by 52 millimeters (ap. by tr.); the lower jaw from front of canine to back of angle, 598; other measurements are given above.

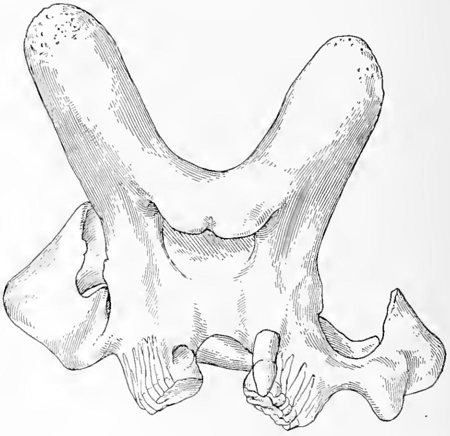


FIGURE 467.—Skull of *Brontotherium hatcheri*

Univ. Wyoming Mus. 1. Front view. One-sixth natural size. This view shows well the resemblances to *B. hatcheri*. (Compare Pls. CLXVII, CLXIX, A², CLXX, B.) The specimen is much crushed and distorted.

Additional observations on B. hatcheri.—This form is not very clearly separated from *B. gigas*, since it was founded on a skull (Nat. Mus. 1216), while *B. gigas* rests upon a lower jaw. The type skull has the nasals longer and the horns shorter and less flattened than in the type of *Titanops elatus*, and the same is true of the other three skulls which stand nearest to the type (Univ. Wyo. Mus. 1, Field Mus. P 5926, Am. Mus. 1070). The range in the principal measurements of these skulls as compared with *B. gigas*, the succeeding stage, is as follows:

Range in measurements of Brontotherium gigas elatum and B. hatcheri (gigas?), in millimeters

	B. gigas elatum, ♂	B. hatcheri (gigas?), ♂
P^1–m^3	348–353	[a] 310–320
P^1–p^4	126–133	118–132?
M^1–m^3	218–241	192–?
Pmx to condyles	770–830	710–?
Zygomatic index	82–87	----------
Nasal length	70–87	85?–105
Horn length	275–365	200–265?

[a] Estimated.

Skull Am. Mus. 1070 has the horns a little longer and more slender than in the type of *B. hatcheri*, but its nasals are as short as in the typical *B. gigas elatum* and its premolars are as long as in that form. Hence it appears to connect these two stages.

Comparative measurements of jaws of B. hatcheri and B. gigas, in millimeters

	B. hatcheri, Am. Mus. 1070	B. gigas, Yale Mus. 12009 (type)	B. gigas (hatcheri?), Nat. Mus. 4262	"Titanops elatus," Yale Mus. 12061 (type)
Symphysis to angle	605	620	623	--------
Condyle to symphysis	600	634	625	--------
Depth, condyle to bottom of angle	300	305	285	304
Depth of jaw below m_1	100	105	101	115
Molar-premolar series	375	365	350	--------
Premolars	[a] 120	117	[a] 121	--------
Molars	263	250	235	260
M_3, transverse	48	47	44	[a] 53
M_3, longitudinal	103	118	100	118
Canine enamel, anterior	35	34	33	--------
Canine enamel, antero-posterior	29	30	28	--------
Length of symphysis	--------	173	182	--------

[a] Estimated.

The lower molar grinding teeth of *B. hatcheri* (263 mm.) exceed in linear dimensions those of either the *B. gigas* type specimen (250) or those of the *T. elatus* type specimen (260); consequently the progressive characters of *B. gigas elatum* are to be seen in the elongation of the horns, the elevation of the connecting crest, and the abbreviation of the nasals (figs. 465, 470), rather than in the increasing length of the grinding series.

The jaws of *B. hatcheri*, *B. gigas*, and *B. elatum* (figs. 468, 471) are influenced so much by age, sex, and individual variation that it is difficult to separate them specifically.

Brontotherium tichoceras (Scott and Osborn)

(*Menodus tichoceras* Scott and Osborn, 1887; "*Megacerops tichoceras*" Osborn, 1902)

Plate CLXXXVII; text figures 177, 469

[For original description and type references see p. 219]

Geologic horizon.—*Titanotherium* zone of South Dakota. Level unrecorded.

Specific and generic characters.—Skull about as large as in *B. gigas.* $I^{\underline{2}}$, $P^{\underline{4}}$. Superior canines and both pairs of incisors well developed; grinding teeth without cingula, premolars with large, distinct tetartocones; nasals of medium length and thickness, contracting anteriorly; base of horns of stout, obliquely transverse section. Buccal processes very prominent, slightly concave superiorly; postglenoid and post-tympanic widely conjoined. Grinding series 330 millimeters—that is, about the same as in smaller skulls of *B. gigas.*

Materials.—The species is known only from the type, in the Museum of Comparative Zoology, Harvard University, a skull which lacks the horns.

The absence of the summits of the horns and of the occiput and the unfortunate loss of the cutting teeth (which has occurred since the original description of this skull was published) prevent us from placing this species phyletically with certainty. It assuredly does not belong to *Menodus* but is rather a member of the brontotheriine group, as shown by the large rounded tetartocones and midparietal convexity. It resembles *Megacerops* in the general aspect of the non-cingulate grinders, the smooth basisphenoid, and somewhat also in the basal horn section and the midparietal protuberance and convexity; it radically differs from this genus in the much greater development of the cutting teeth, or incisors, and the wide separation of the canines. It resembles *Brontotherium* in the form and size of the cutting teeth (so far as the characters of these parts can be judged from the original figures), the wide union of the postglenoid and post-tympanic processes, and the narrowing of the nasals anteriorly. On the whole, therefore, *B. tichoceras* appears to stand closest to the *Brontotherium* phylum, although it lacks especially the characteristic transverse basal horn section, which seems to be merely an exaggeration of the basal section of the type of *B. hatcheri.* If the section were preserved at a little higher point on the horn it might show some of the characteristic flattening.

Additional observations on the type.—A reexamination of the type in 1902 afforded opportunity for additional measurements and sections of the horns and zygomatic arches. The canines in the type, although now lost, were large and indicate that this was probably a male

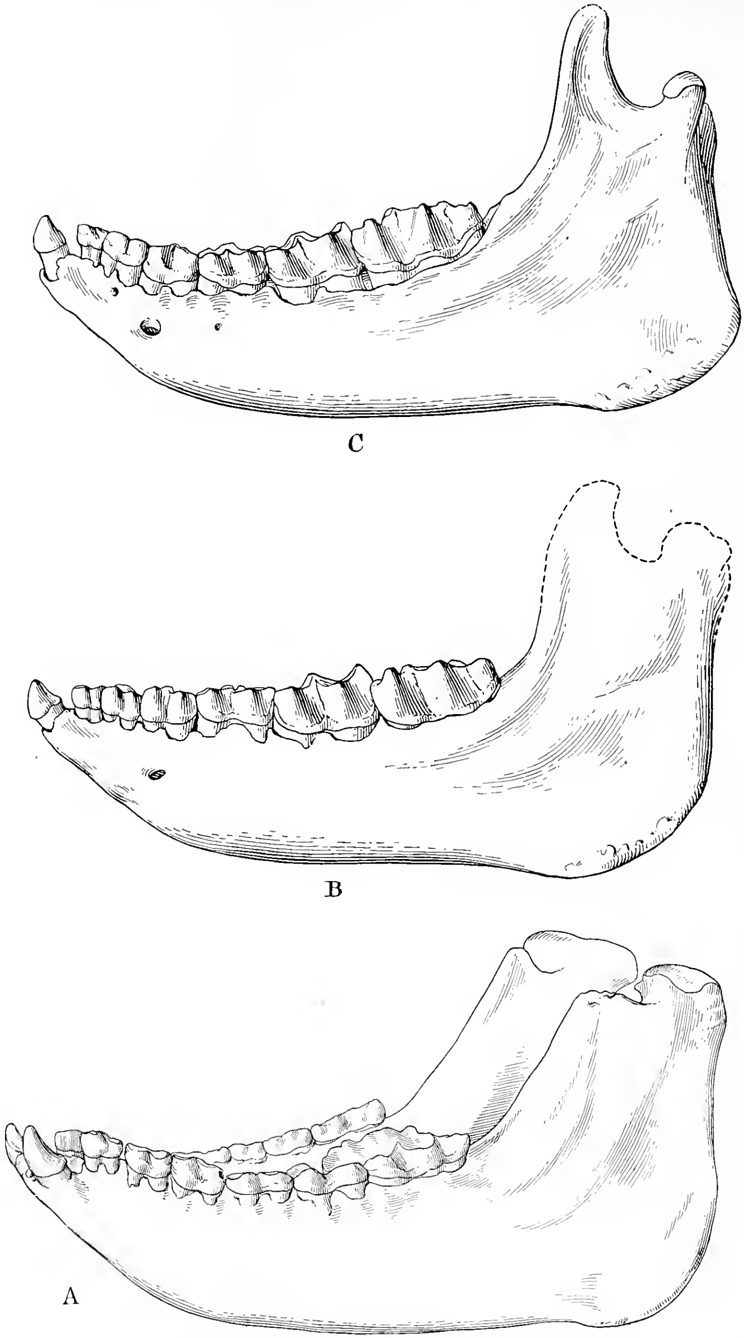


FIGURE 468.—Lower jaws of *Brontotherium hatcheri and B. gigas*

A, *Brontotherium hatcheri*, Univ. Wyoming Mus. 1 (reversed); B, *B. hatcheri*, Am. Mus. 1070; C, *B. gigas*, Yale Mus. 12009 (type). One-fifth natural size. In these jaws the chin is shallow, almost concave, as in typical brontotheres, the ramus stout and massive, the canines spoon-shaped, the incisors well developed, the external cingula wanting, no diastema in front of p_1 (if that tooth is present).

specimen. There are large, distinct tetartocones on the superior premolars. Cingula on all the grinding teeth are wanting. The nasals are of medium length and thickness, contracting anteriorly and decurved slightly at the tip. The horn pillars are stout, contracting the anterior nares, but to a less extent than in *B. dolichoceras*. The postglenoid and post-tympanic processes are widely conjoined. These characters concur with the position of the horns, the relative shortness of the nasals, the breadth of the zygomata, as indicating that this species belongs on the upper levels of the *Titanotherium* zone.

Measurements of Brontotherium tichoceras

	Millimeters
Molar-premolar series	330
Free length of nasals	65
Free breadth of nasals	130
Tips of nasals to connecting crest	130
Occipital condyles to tips of nasals	800?

Transitional skull (Nat. Mus. 8313).—Measurements of this skull will be found under *Megacerops* (p. 542).

Additional observations on the measurements of Brontotherium tichoceras.—The relationships of the type and only known skull of this species are somewhat doubtful. It possibly belongs near *B. gigas* and *B. hatcheri*, although the detailed dimensions of its grinding teeth do not support this view but suggest, on the contrary, possible relationship with *Megacerops*, as follows:

Comparative measurements of teeth of Brontotherium tichoceras, in millimeters

	B. tichoceras		Megacerops (S. altirostris)		B. gigas, Am. Mus. 492		B. "hatcheri," Am. Mus. 1070	
	Ap.	Tr.	Ap.	Tr.	Ap.	Tr.	Ap.	Tr.
P^1	17	20	?19	17	20	19	20	25
P^2	26	34	27	40	30	39	29	40
P^3	37	48	34	48	34	49	39	53
P^4	41	61	43	59	39	60	43	63
M^1	66	64	59	69	57	65	67	70
M^2	76	80	77	79	77	72	-----	-----
M^3	74	85	75	82	81	81	-----	-----

The deep basal section of the horns is also consistent with *Megacerops* affinities.

Brontotherium gigas Marsh, 1873

(*Titanops elatus* Marsh, 1887; *"Brontotherium gigas"*, Osborn, 1902)

Plates XX, LXXXII, CXXXIII, CLXX, CLXXI, CLXXIII–CLXXV, CLXXXIV, CXC, CCXXX–CCXXXV; text figures 29, 165, 229, 377, 378, 382, 390, 394, 395, 405, 457, 458, 460, 468, 470–472, 515, 622, 623, 625–631, 633, 634, 639, 652, 662, 690, 719, 721, 724, 744

[For original description and type references see p. 209. For skeletal characters see pp. 690–694]

Geologic horizon.—Upper *Titanotherium* zone, lower to upper levels.

Specific characters.—P^1–m^3 330–353 millimeters; m^1–m^3 216–241; dental index typically 42, rising to 46. Basilar length of skull ♂ (typical) 830 millimeters, ♀ 760, zygomatic breadth ♂ 740, index 89 (brachycephalic). Nasals rather short, free length ♂ 87 millimeters, free breadth ♂ 115. Horns very large, typical ♂ 330–365 millimeters, ♀ 180 but with high connecting crest as in ♂, basal section in males transversely oval but not flattened, more flattened at top but less so than in succeeding species, horns much in front of orbits and above premaxillaries. Buccal expansion of zygoma very broad in males, slight or moderate in females. Canines, incisors, premolar tetartocones, and cingula much as in *B. leidyi* and other brontotheres.

The characters of *Brontotherium gigas elatum* as determined from the type jaw of *B. gigas* and the type skull and jaws of *B.* (*Titanops*) *elatum* represent the next stage beyond *B. hatcheri*. This advance is seen not in the dimensions of the grinding teeth, which are no greater than in *B. hatcheri* (see table), but in the more advanced evolution of the horns and connecting crest and in the further reduction of the nasals (figs. 468, 470).

General characters of Brontotherium gigas.—With the species *B. gigas*, the "giant thunder beast," we pass to the long-horned titanotheres of the upper *Titanotherium* zone, recorded by Hatcher from the lower, middle, and upper levels. The imposing animal *B. gigas* was apparently in the line of ascent to the still more remarkable *B. curtum*, *B. ramosum*, and *B. platyceras* of the summit. The largest bulls of *B. gigas* (Am. Mus. 492) greatly exceeded those of *Brontops robustus* in size, the skull measuring 32.6 inches (830 mm.) from the premaxillaries to the occipital condyles by 29.1 inches (740 mm.) across the zygomatic arches, as compared with 765 by 667 millimeters in the aged *B. robustus* skull. The expansion of the zygomata renders the brachycephaly, as measured on the palatal surface of the skull, still more marked, the length exceeding the breadth by only 3.5

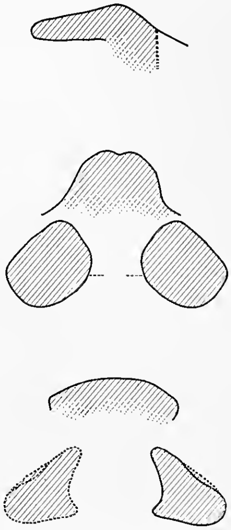


FIGURE 469.—Sections and contours of skull of *Brontotherium? tichoceras*

Harvard Mus. (type of *Menodus tichoceras*). One-ninth natural size. The extremities of the horns are unfortunately missing but must have been massive. The basal section is very large; the external face is flattened, and the internal and posterior faces are well rounded. Connecting crest low, nasals massive and wide, zygomata much expanded, parietal crest wide and convex. The generic reference is uncertain: although these sections suggest those of *Megacerops bucco*, the animal may be related to *Brontotherium hatcheri*.

inches (90 mm.), and the zygomatic index rising to 89 as compared with 62 in a typical *Menodus giganteus*. The proportions of the huge skeleton belonging to the same large bull (Am. Mus. 492) show corresponding increase in the length of the ribs, height of the dorsal hump, and width of the pelvis (see above).

Materials.—Our knowledge of this species is derived from exceptionally rich materials, including especially the type jaw of *B. gigas*, the splendid type skull and jaw of *B.* (*Titanops*) *elatum* in the Yale Museum (No. 12061), and the superb skull of *B. gigas* in the American Museum (No. 492), broadly recorded from the upper *Titanotherium* zone. Associated with the skull of *B. gigas* are a pelvis, forearm, manus, and dorsal vertebra with ribs. There are also two skulls in the National Museum—No. 4262, from the lower levels of the upper *Titanotherium* zone, a young male in the fifth stage of growth, associated with considerable portions of the skeleton, and No. 4244, with imperfectly preserved horns, recorded from the top levels of the upper zone. There is also the skull of a small but aged female (Am. Mus. 1006).

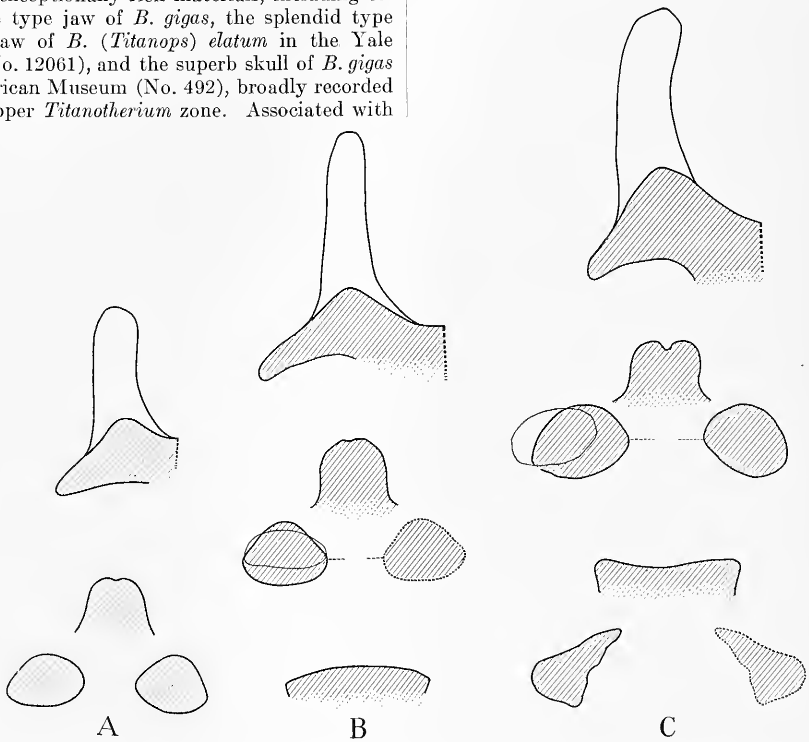


FIGURE 470.—Sections and contours of skulls of *Brontotherium hatcheri* and *B. gigas*

A, *Brontotherium hatcheri*, Am. Mus. 1070; horns shorter than in *B. gigas* and connecting crest lower; basal section of horns roundly trihedral, not so wide as in *B. gigas*. B, *B. gigas*, Yale Mus. 12061 (type of *Titanops elatus*); horns long, erect, and placed far in front of the orbits, their basal section roundly trihedral, section of the upper part of the horn a transversely extended oval, nasals fairly long, parietal crest wide. C, *B. gigos*, Am. Mus. 492; horns stouter, basal section more rounded oval and upper section less flattened, nasals shorter, and zygomata widely expanded. One-ninth natural size.

Relation of Brontotherium gigas and Titanops elatus.—A comparison of the type jaw of *B. gigas* with that of *Titanops elatus* shows that the former represents a younger, the latter a somewhat older and more robust individual of the same species; the type *T. elatus* jaw (see description below and measurements above) resembles the type *B. gigas* jaw in size (allowing for a slight difference of age), in form of jaw, canines, and molars (especially m_3), in the ratio of premolars to molars. It differs only in the presence of p_1, which has dropped out in *B. gigas*, and in the reduction of the cingulum on the premolars. The relation of these species is further confirmed by specimens in the National and American Museums which are described below. The additional generic characters of *Brontotherium* must, therefore, be derived not from the skull which Marsh referred to *B. ingens*, but from the skulls which he referred to *Titanops elatus* and *Titanops curtus*.

Our conclusion is that the type skull and jaws of *B.* (*Titanops*) *elatum* belong to a somewhat larger male animal than the type jaw of *B. gigas* and may represent a more progressive ascending mutation, which might be termed *B. gigas elatum.* The skull and jaws of *B.* (*Titanops*) *elatum* are certainly more progressive than those of *B. hatcheri.*

Observations on the type jaw of Brontotherium gigas.—The type lower jaw was figured by Marsh (1876.1, pl. 12) and is well represented in Plate CLXXI of this monograph.

Measurements of Brontotherium gigas

	Millimeters
Symphysis to angle	620
Symphysis to condyle	600
Depth of jaw, condyle to bottom of angle	305
Depth of jaw below first molar	105
Molar-premolar series	365
True molar series	258
Premolar series	117
M_1, transverse	37
M_1, anteroposterior	59
M_2, transverse	41
M_2, anteroposterior	78
M_3, transverse	47
M_3, anteroposterior	118
Canine enamel, anterior	34
Canine, anteroposterior	30
Length of symphysis	173

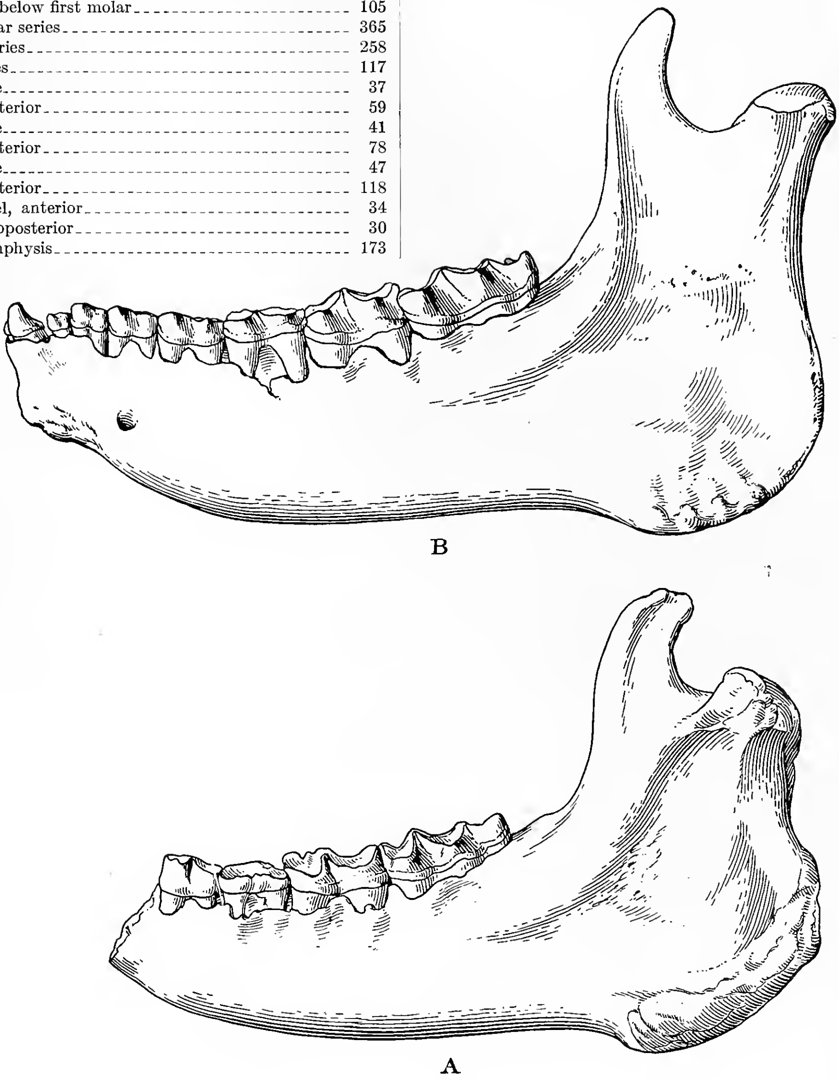


FIGURE 471.—Lower jaws of *Brontotherium gigas* and *B. medium*

A, *Brontotherium gigas*, Yale Mus. 12061 (type of *Titanops elatus*). This animal has the measurement of m_1-m_3 longer than in the type of *B. gigas* and may represent a slightly higher stage. The angle is very prominent and rugose, as in old animals. The molars have reduced external cingula. B, *B. medium*, Am. Mus. 1051; the largest known titanothere jaw. It conforms in all important respects to the *Brontotherium* type. One-fifth natural size.

The jaw is of the true brontothere type. The mental foramen is at a point vertically below the posterior fang of the third premolar. Above and behind it are two smaller foramina. The jaw is swollen beneath the fourth premolar and then ascends rapidly to the incisive border with a slightly convex chin, but there is an interval between the chin and the canine that is concave and somewhat hollowed out beneath. The coronary process as figured is restored at the tip; the anterior border presents a smooth, rounded ridge antero-externally, which is brought into further prominence by a depression running just back of and parallel with it.

Teeth: The incisors are represented by two pairs of rather small alveoli with a slight diastema between; the lateral alveolus is slightly larger than the median; the canines are low-crowned, obtuse, flattened, and cingulate on the postero-internal surface and probably indicate a male; there is a narrow diastema (11 mm.) between the canines and second premolars and no indication of p_1. The premolars exhibit no external or internal cingula; there is an external crenulation only on the valleys of the molars; the grinding teeth therefore are decidedly noncingulate. M_2 and m_3 exhibit a rudimentary metastylid; m_3 has a broad-cupped hypoconulid with a slightly crenulate internal crest.

The presence of lower incisors and the shape of the canines differentiate this jaw from that of the animal later described by Cope as *Symborodon torvus.* The looped structure of the hypoconulid of m_3 is different from that in the *Menodus* series. The closest resemblances in the jaw, canines, absence of cingula, and in m_3 are to the animal later termed by Marsh *Titanops elatus.*

Observations on the type skull of B. (*Titanops*) *elatum considered as pertaining to B. gigas.*—The cranial vertex is somewhat crushed and moderately broad, with a rugose crest overhanging the orbital and temporal fossae; the nasals are rather narrow, of medium length; the external auditory meatus is completely coalesced below, the angle of the jaw is slightly depressed, and also extended backward. The age of the skull is determined as in the ninth stage, all the internal cusps of the grinding teeth being worn except upon the last superior molar.

It should be noted that the zygomatic arches, the premaxillaries, and the anterior portion of the jaw of this skull are wanting.

Teeth: The superior premolars exhibit a distinct internal cone, the tetartocone, which is well marked off and separate from the deuterocone on p^3, p^4. P^4 also apparently exhibits a mesostyle. The hypocone is fairly prominent but partly connected with the cingulum on m^3. The internal cingulum of the superior premolars is sessile and crenulate. The lower premolars and molars exhibit a vestigial or basal cingulum except on m_3, in which the cingulum, as in the type of *B. gigas,* is slightly more decided. M_3 exhibits a broad hypoconulid and crenulate internal crest, a characteristic phyletic character.

Measurements of the type jaw are given above.

The type skull is unfortunately incomplete, so that the chief dental measurements are lacking, but the basilar length and the dimensions of the nasals and horns are approached by a finely preserved skull in the American Museum (No. 492). This is remarkable for its very large true molars (241 mm.), its great basal length (830 mm.), and its high zygomatic index (87). The horns are less flattened than in *B. medium* and *B. curtum* but more flattened than in *B. hatcheri.*

Two other skulls provisionally referred to this stage (Carnegie Mus. 341, Nat. Mus. 4262) agree closely in measurements with each other but have the true molars (218 mm.) and the horns (275 mm.) considerably shorter than in Am. Mus. 492; another skull (Nat. Mus. 4244) has much shorter horns (170 mm.). Thus these skulls seem to connect *B. gigas elatum* with *B. hatcheri* and serve to illustrate the variability in length of the horns and of the nasals.

The female skull (Am. Mus. 1006) which is referred to this species approaches the male skulls in the dimensions of the cheek teeth as well as in the sections of the horns and nasals. But it differs from all typical *Brontotherium* skulls in having well-defined internal cingula and retarded tetartocones in the premolars; so that relationship with *Brontops robustus* might be suspected were it not for the much closer agreement in dental measurements with *B. gigas.*

Fine male skull (Am. Mus. 492).—The fully adult characters of the males are admirably shown in the nearly perfect American Museum skull No. 492, which is in the seventh stage of growth. Two smooth, rounded incisors are preserved on one side above; the canines measure 35 millimeters anteriorly as compared with 41 in *B. robustus;* they are shorter and obtuse (Pls. XX, B, CLXXIII, CLXXIV). There is no diastema behind the canine. The greatly reduced first premolar is pressed close to the canine and tends to drop out; the premolars can readily be distinguished from those of *B. robustus;* the tetartocones although low and obtuse are about two-thirds as large as the deuterocones and quite distinct throughout. The premolar cingula, however, have retrogressed as in *B. leidyi,* being practically vestigial on the outer side and less distinct on the inner side than in *B. robustus;* the molar cingula also are nearly obsolete. On m^3 is a sessile hypocone connected with the cingulum.

The grinding teeth, considered so important to the welfare of large herbivorous quadrupeds such as this, are in certain respects in a condition of retrogression. In the type of *B. gigas* the bluntness and crenulation of the internal cingula precede degeneration. In this very large skull (Am. Mus. 492) they measure 353 millimeters, only 3 millimeters more than in the type skull of *B. robustus.* This contrast between the arrested development of the teeth and the pronounced evolution of the dominant protuberances of the skull has its parallel among the Dinocerata.

The inverse relations of the nasals and horns illustrate the law of compensation of growth, the free nasals being here absorbed and reduced in compensation for the great elongation and expansion of the horns, which are now strengthened by a very prominent crest, attaining a vertical thickness of 140 millimeters as compared with 78, the maximum thickness in *B. robustus.* Behind the horns the skull slopes into a broad saddle shape, more uniform in width anteroposteriorly than in *B. robustus*, partly owing to lateral crushing, but the vertex is much longer, especially as seen in the backward extension of the occiput behind the zygomata.

The parietal vertex is very wide, with overhanging supraorbital and supratemporal crests, terminating in a powerful rugose occiput which is broader and more shelf-like superiorly than in *M. robustus*. The buccal processes are flatter superiorly, though the area of the section is not greater than in the large specimen Am. Mus. 6346, which is provisionally referred to *B. curtum;* as in *B. leidyi* there is a flange extending inward from the center of the zygoma (fig. 470, c). The pillars of the occiput are very powerful, with a pair of tuberosities (fig. 378, F, k, k) projecting upward on either side of the median line. We have seen these tuberosities in *Megacerops* and in prophetic form in *B. leidyi*. They represent the development of special muscular fasciculi or tendons for the semispinalis capitis muscles and the ligamentum nuchae; these tuberosities are rudimentary or absent in certain skulls of *Menodus* and are replaced by two pits in *Megacerops acer*. There is a wide union between the post-tympanic and post-glenoid processes; each pterygo-alisphenoid wing is cleft on its extreme lower border for the insertion of the pterygoid muscle; the pterygoid wings are somewhat shorter than in *Brontops robustus*. As in *B. leidyi* and in contrast to *B. robustus*, there are no paired protuberances at the junction of the basioccipital and basisphenoid for the attachment of the recti capitis antici majores. The vomerine ridge is reduced.

Juvenile stage of growth.—A relatively young male skull in the fifth stage of growth (Nat. Mus. 4262), with which are associated the backbone and limbs (see above), illustrates the form of the horns, nasals, and zygomata of this species in the young condition and serves to strengthen the identification of *Titanops elatus* with *B. gigas*. It was found at Hat Creek, Wyoming, and is recorded by Hatcher as from the lowest level of the upper *Titanotherium* zone (Chadron C). The horns measure 275 millimeters. The formula is $\mathrm{I}\frac{2}{2}$, $\mathrm{P}\frac{4}{4}$; the upper incisors are small and conic without posterior cingulum; the lower incisors, of which the outer one is preserved, have a crenulate posterior cingulum; the superior canines measure 33 millimeters and are short and obtuse, with a characteristic posterior slope and cingulum; the inferior canines have a postero-internal, less prominent cingulum. The tetartocones on p^2–p^4 are very distinct; p^4 has a mesostyle as in the type specimen. The jaw resembles that of the type of *B. gigas* in the chin and angle; the chin is extremely shallow.

Character of the female skulls.—The determination of a small skull (Am. Mus. 1006) as a female of this species is rendered probable by its discovery on the same level as the large *B. gigas* (Am. Mus. 492), as well as by the sections of the nasals, horns, and zygomata. The disparity in size between this female skull and the male skull is very marked. The animal is well advanced in the seventh stage of growth. The deep connecting crest and shape of the nasals resemble those of *B. gigas*, but the horns are very short and obtuse, and the buccal processes are much less robust. The malar bridge is broader than in the male skull, as in *B. curtum* female, and the median ridge is obtuse and low. The post-tympanic has a characteristic broad, flattened union with the post-glenoid; the palatine aspect also resembles that of *B. gigas* on a small scale, with a smooth basisphenoid.

Sexual characters are observed not only in the extremely small canines but apparently also in the reduction of the incisors, so far as we can judge from the alveoli and fangs. Careful examination reveals the reduced fang of a lateral incisor on the right side. The canines differ from those of the male not only in the much smaller size but also in lacking the swollen appearance; they are, in fact, recurved, conic. The premolars differ from those of the male in the lesser size of the tetartocones and in the pronounced non-crenulate cingulum.

A very large skull in the National Museum (No. 4244), in the fourth stage of growth, either a large female or a juvenile male with imperfectly developed horns, is recorded by Hatcher from the top level of the upper zone. The horns measure 195 millimeters, with the anterior ridge more prominent than in the type. Other characters conform closely to the type—namely, $\mathrm{I}\frac{2}{}$, distinct tetartocones on p^4, m^3 with a small but distinct hypocone, buccal processes flattened. A variation is the loss of p^1.

Female characters in general.—A comparison of the supposed female skulls of *Brontotherium gigas* and of *B. curtum* shows that since the male progressive characters are largely correlated with excessive size and horn development the females actually appear to be more primitive—namely, the horns are shorter, the zygomata are slighter, the occiput is less extended backward, the malar bridge is wider, the orbit is larger, the external auditory meatus is somewhat more open.

The apparent loss or reduction of the incisors, the somewhat retarded condition of the tetartocones, and the pronounced development of the internal and external cingula are, however, very difficult facts to explain as sexual characters.

Additional observations on the supposed female of Brontotherium gigas.—A female skull in the American Museum (No. 1006) which has been referred to this species presents a very puzzling specimen. The sections of the horns and nasals offer resemblances and differences to those of the type of *B.* (*Titanops*) *elatum* which have been assumed to indicate a female of this species.

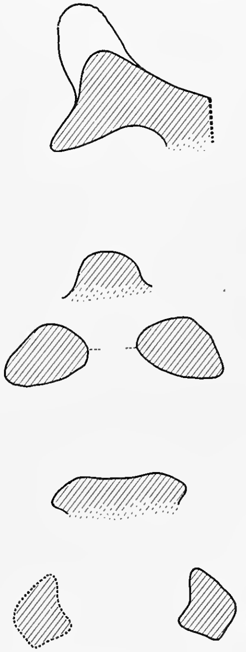


FIGURE 472.—Sections and contours of skull of *Brontotherium gigas?*

Am. Mus. 1006, ♀, referred to *B. gigas* on account of the characteristic form of these sections. It seems, however, to be too small to be a female of that species (W. K. Gregory). One-eighth natural size.

On the other hand, the specimen differs from male brontotheres and resembles the Menodontinae, especially *Diploclonus amplus*, in the following features: (1) The narrow well-defined internal cingula; (2) the dimensions of p^4 (ap. by tr., 40 by 61 mm.) and m^3 (84 by 82) are closer to those of a skull referred to *Diploclonus amplus* (Nat. Mus. 4710), which are respectively 42 by 61 and 82 by 81 millimeters, than they are to those of male brontotheres, which usually have larger p^4 and wider m^3; (3) the canine (Pl. CXC) is not of the swollen *Brontotherium* type; by analogy with *Menodus* the female canine in *Brontotherium* should be somewhat like that of the male, only much more slender; (4) the cranial vertex lacks the midparietal convexity or eminence of *Brontotherium* and *Megacerops*. The anteroposterior measurements of the dentition (see above) do not offer decisive evidence of relationship with *Brontotherium*. In brief, the systematic position of this skull at present appears doubtful and it may possibly belong near *Diploclonus amplus*. (See fig. 472.)

Brontotherium dolichoceras (Scott and Osborn)

(*Menodus dolichoceras* Scott and Osborn, 1887; "*Brontotherium dolichoceras*" Osborn, 1902)

Plate CLXXXVI; text figures 177, 473, 474

[For original description and type references see p. 220]

Geologic horizon.—*Titanotherium* zone of South Dakota, level not recorded.

Specific characters.—Nasals, free length 49 millimeters, breadth 90 millimeters—that is, more reduced than in *B. gigas*, less reduced than in *B. curtum*. Horns elongate (310 mm.), about as in *B. gigas*; horn section transversely oval, more progressive than in *B. gigas*, with anterolateral depression and incipient external ridge. Size of skull about as in *B. hatcheri*. Premolar cingula reduced, which perhaps is an individual variation.

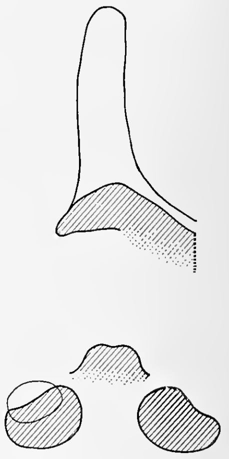


FIGURE 473.—Sections and contours of skull of *Brontotherium dolichoceras*

Harvard Mus. (type) elongate horns suboval in basal section, nasals short. One-ninth natural size.

As described the type of this species is an adult, not aged male preserved in the Museum of Comparative Zoology at Harvard. It is in the seventh stage of growth, with the internal cones of p^3 completely worn and the protocone and hypocone of m^1 worn. As shown by the measurements given below, the skull was of medium size, or about as large as the type skull of *B. hatcheri*.

This species, named "the long-horned brontothere" by Scott and Osborn, represents a next higher stage in the evolution of the brontothere phylum, although it appears rather as a collateral branch than as a member of the main line of ascent. The type skull is the only material that can be referred certainly to this species. The nasals now project only 49 millimeters in front of the anterior bases of the horns, and in sagittal section (fig. 473) there is a uniformly convex curve from the summit of the connecting crest to the tips of the nasals, as in the fine specimen of *B. curtum* (Nat. Mus. 4946) described below. The horn section on the right side is the more perfect, that on the left being crushed laterally; the horns are crushed in upon the antero-external faces, a feature which exaggerates

FIGURE 474.—Skull of *Brontotherium dolichoceras*

Harvard Mus. (type). The right horn is longer and more slender than the left, possibly an effect of crushing. (See Pl. CLXXXVI, C.) One-eighth natural size.

the flatness of the anterior face of the horn section (fig. 473). At the sides of the horns there is a short extension of the external crest, and in this individual the malar, anterior, and internal angles are not very sharply defined. Characteristic of the horns are the external ridge extending from the sides of the nasals upward and the very marked hollowing out of the maxillary face. As observed in the original description the great size of the maxillary horn pillars reduces the opening of the anterior nares to a narrow aperture. The connecting crest is fairly prominent. The vertex of the skull has the very characteristic longitudinal uniform breadth. The occipital crests are wanting, but the paired knobs (fig. 378, F) are preserved. As in *Brontotherium* and *Megacerops* the basisphenoid is without rugosity. As in brachycephalic skulls generally the postglenoid and post-tympanic processes are widely conjoined, the auditory meatus being very small.

Teeth.—The upper premolars are distinctly of the *Brontotherium-Megacerops* type, with well-rounded, distinct tetartocones and reduced cingula.

Conclusion.—This skull differs from the type of *B.* (*Titanops*) *medium* (Marsh), in its smaller size and in the absence of the basisphenoid rugosity. It exhibits some resemblances to *Megacerops acer* but is distinguished by the more marked divergence of the horns. In the absence of knowledge of the occiput and of the condition of the cutting teeth, incisors, and canines, the phyletic position of this species can not be considered as absolutely determined at present.

It appears possible, however, that in spite of its somewhat smaller size (compare the range in size in skulls referred to *B. gigas*) this species may be the same as that later termed *B. medium* by Marsh.

Brontotherium medium (Marsh)

(*Titanops medius* Marsh, 1891)

Plates XIX, XX, CLXXII, CLXXVI, CLXXX; text figures 25, 191, 395, 407, 471, 475

[For original description and type references see p. 228]

Geologic horizon.—Upper *Titanotherium* zone of South Dakota.

Specific characters.—Size about that of a large *B. gigas;* basilar length of skull 825 millimeters; grinding series elongate (365 mm.), dental index 43 (about as in *B. gigas*); nasals more reduced (free length 45 mm., free breadth 110); horns long (320 mm.), becoming flattened in section, connecting crest in type shallower than in *B. gigas* or in *B. curtum*.

So far as we can observe this species appears to be in a stage of evolution very similar to that of the previously described *B. dolichoceras*.

The name *"medius"* was probably assigned by Marsh in reference to the intermediate length of the nasals between those of *B. gigas* and *B. curtum*.

Materials.—Our knowledge of this evolution stage is afforded by the type specimen of *B.* (*Titanops*) *medium*, a large and finely preserved male skull in the United States National Museum (No. 4256). It is recorded as from the top levels of the upper *Titanotherium* zone. The grinding series in the type specimen of *B. medium* is exceptionally elongate, namely, 365 millimeters; consequently we have associated with this species a very large lower jaw (Am. Mus. 1051).

Skull.—We notice especially the persistence of two upper incisors and the prominence of the well-rounded tetartocones on the premolars, that upon the right, p^4, being sharply distinct. The incisors differ from the typical brontothere form in exhibiting smooth, rounded crowns, apparently noncingulate. The canines are short (38 mm.), heavy, and blunt, as in *B. gigas*, with robust posterior cingula. The anterior premolar, p^1, is triangular and exceptionally small, with a single much-worn internal cusp. The hypocone of m^3 is small and cingulate, but from this cusp there extends completely across the crown the abortive metaloph so characteristic of many members of this and other phyla. The animal is still young, being intermediate between the fifth and sixth stages of growth; the only internal cones which are worn are those of m^1, yet the horns attain an outside measurement of 320 millimeters, proving the rapid individual development of these important organs. The horns are distinguished by the sharp carrying up of the external and anterior ridges to a high point. Thus the outer or maxillary face is concave below and flattened above. This feature is also seen in a less conspicuous manner in the type of *B. dolichoceras*. The nasal section and the length of the nasals (45 mm.) are also identical in the two specimens.

Lower jaw.—Possibly belonging to this species is the enormous jaw in the American Museum collection (No. 1051). As shown in Plate CLXXII, B, and in Figure 471, B, this has the characteristic form of the canines, the posterior molar, angle of the jaw, etc., of *B. gigas*, but the lower incisors show some reduction and lack the decided development of the cingulum observed in No. 1070 (*B. hatcheri*). Moreover, the great length of this jaw (730 mm.), measured from the condyle to the symphysis, favors its reference to *B. medium* rather than to *B. ramosum* or *B. platyceras*, in which the jaw is relatively shorter.

Conclusion.—*B. medium* is one of several stages of the upper zone resting on a single type and tending to connect *B. hatcheri*, *B. gigas*, *B. dolichoceras*, *B. medium*, *B. curtum*, *B. ramosum*, *B. platyceras* in a more or less continuous phylum.

Additional observations on Brontotherium medium.—The type skull is remarkable for the large size of the premolars and molars and for the shortness of the nasals. The other two skulls provisionally entered under this species above (p. 553) have much smaller dental measurements, about as in *B. gigas* or *hatcheri*, and may belong in either species. The female skull in the British Museum, referred provisionally to *B. peltoceras*, approaches the female skull referred to *B. curtum* (Am. Mus. 1005) except that the nasals are smaller. Future investigation may settle whether *B. medium* is distinct from *B. gigas elatum.*

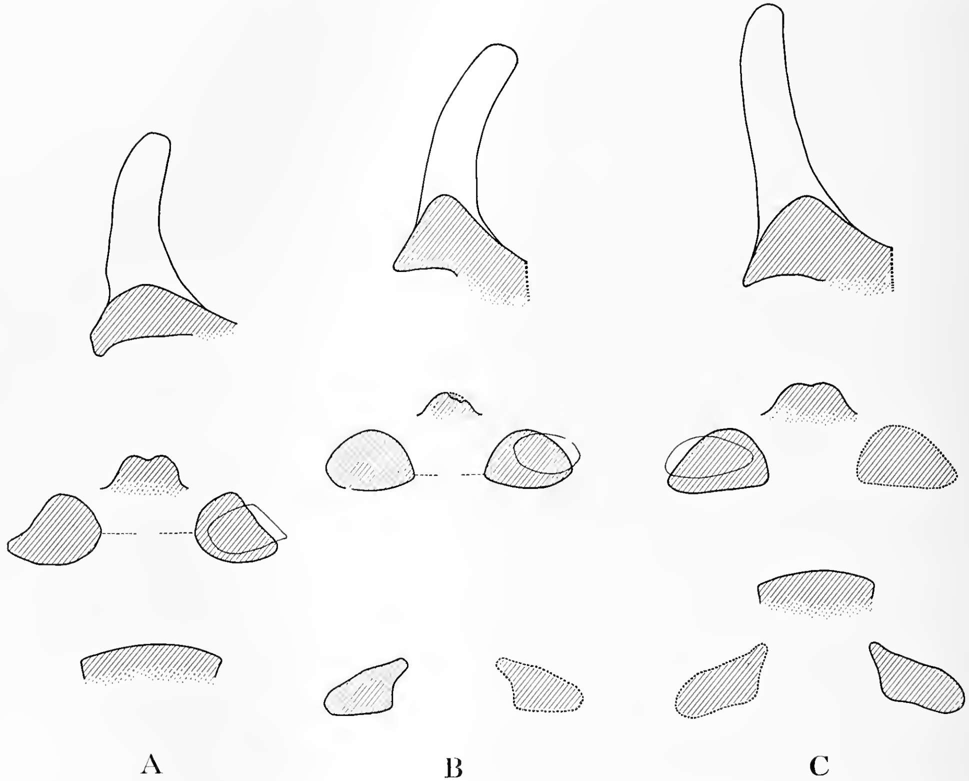


FIGURE 475.—Sections and contours of skulls of *Brontotherium medium* and *B. curtum*

A, *Brontotherium medium*, Nat. Mus. 4256 (type), short nasals approaching in form those of *B. curtum*, but horns not so long; basal section of horns has a flattened external face. B, *B. curtum*, Nat. Mus. 4946. C, *B. curtum*, Yale Mus. 12013 (type). In *B. curtum* nasals are very short, horns long, basal section well rounded externally and flat posteriorly, zygomata well expanded. One-ninth natural size.

Brontotherium curtum (Marsh)

(*Titanops curtus* Marsh, 1887; ?*Menodus peltoceras* Cope, 1891; "*Brontotherium curtum*" Osborn, 1902)

Plates XX, XLVII, CLVII, CLXXVII–CLXXX, CLXXXIII–CLXXXVI, CXC, CXCII–CXCIV; text figures 182, 390, 392–394, 399, 457–459, 475–478, 709, 719, 744

[For original description and type references see p. 224]

Geologic horizon.—Upper *Titanotherium* zone of South Dakota.

Specific and generic characters.—Molar-premolar series 350 millimeters (estimated). Premolars with very distinct tetartocones; external cingula feeble; internal cingula reduced. Nasals greatly abbreviated, free length 52 millimeters. Horns greatly elongated in males (355–380 mm.), in females abbreviate (160 mm.); basal section of horns strongly convex anteroposteriorly, slightly convex to plane posteriorly, breadth moderate. Zygomata with buccal expansions broad, plane above, bulging at the sides, plane below. Skull mesaticephalic, basal length ♂ 790–840 millimeters, zygomatic breadth ♂ 620 millimeters; zygomatic index 73–77. Vertex of skull elongated by expansion of occiput back of the zygomatic arches and by forward shifting of the horns. Female skull much smaller (nasals to top of occiput 635 mm.).

The chief advances in this stage beyond *B. gigas* and *B. medium* are in the still further abbreviation of the nasals, the more flattened posterior face of the horns, the more backward extension of the occiput, all progressive characters which are bridged over more or less fully by transitional types. The disparity between the males and females is now still more marked, the latter being apparently represented by specimens referred to the species *B.* (*Menodus*) *peltoceras* Cope.

Materials.—Besides the noble type skull of *Titanops curtus* in the Yale Museum (No. 12013) this species is represented by a pair of horns in the Harvard Museum and by a large, fully adult skull (Nat. Mus. 1211) and the skull of an old bull (Nat. Mus. 4946) in the National Museum. Both these skulls in the National Museum are recorded from the top level of the upper *Titanotherium* zone (Chadron C). In the American Museum there is fortunately a small female skull, No. 1005. Cope's type of *Menodus peltoceras* (Am. Mus. 10719) consists simply of the great connecting crest supporting a pair of low horns.

Detailed description of the type skull.—The type male skull (Yale Mus. 12013, Pls. CLXXVIII–CLXXX) is in the seventh stage of growth. The horns have therefore not attained their maximum length, and the connecting crest is comparatively low and rounded. The horns are placed well forward and vertically overhang the canines. The external ridge has increased, while the anterior ridge has practically disappeared (Pl. CLXXIX; figs. 457, G; 475–478). The section of the horns is now almost planoconvex, the inferior face being strongly convex and the posterior face almost plane; at the summits the horns exhibit a rugose lateral expansion suggestive of that which is so strongly marked in *B. ramosum.* Another progressive feature is the very sudden expansion of the zygomatic arches into a broad and relatively shallow convexity (Pls. CLXXVIII, CLXXX). The vertex of the cranium is bounded by a lateral crest with a rugose border overhanging the temporal fossa.

Dentition.—The superior canines are short, recurved, with a broad posterior cingulum. The premolars exhibit well-separated internal cones, especially on p^3 and p^4, there being a distinct cleft between the deuterocones and the tetartocones. The first superior premolar is indicated by an alveolus on the left side. In the molar-premolar series the enamel is crenulate on the sides of the internal cones. On m^3 the hypocone is fairly prominent but not separate from the cingulum.

Age and growth characters.—As above noted the type male skull, being in the seventh stage of growth, does not exhibit either the maximum length of the horns or the maximum development of the connecting crest. In the fully adult male skulls in the National Museum (Nos. 4946 and 1211), which are in the eighth stage of growth, we have finely illustrated the skull characters of the old bulls. The connecting crest of No. 1211, which is the oldest and most progressive skull, is now extremely deep and descends by an almost straight line to the tips of the nasals, which are now only 40 millimeters in length. The horns are very long (355 mm.), recurved, with the characteristic strongly convex section in front and slightly convex section behind. The second old bull in the National Museum (No. 4946) is somewhat less progressive, the horn section (fig. 475, B) being very convex anteriorly and less convex posteriorly. The horns are relatively broader and more flattened posteriorly, and the nasals are still more abbreviate (65 mm.). The horn of this specimen has been broken off and partly regenerated during life, a fact which appears to show the value of the horns in contests between the males.

A specimen in the Harvard Museum (No. 1004) represents a much smaller animal in an earlier stage of evolution, in which the horns are still convex on the posterior surfaces. All these specimens agree with *B. gigas* in the backward extension of the occiput behind the zygomata, in the inward flange of the zygomata, and in numerous other details of character.

Other features in the National Museum skull (No. 4946) are the following. It appears that skull growth continued even after the teeth were much worn down. Added to the progressive feature of the lengthening and flattening of the horns and the abbreviation of the nasals, marked in this bull, is the incipient development of a narrow ridge on the outer side of the horns, an exaggeration of the "external or malar ridge"; it does not extend very far but is marked in old individuals. This "malar ridge" is prophetic of the continuous external ridge down the entire side of the horn in the higher phyletic stage, *B. platyceras.* The structure of the zygomatic arch is especially interesting; immediately behind the orbit it consists of a vertically compressed plate. A variation of interest is the small tuberosity on the inner side of the horn, suggestive of the internal hornlet of *Diploclonus.*

Carnegie Museum specimen.—A fine pair of horns in the Carnegie Museum (No. 560) which are referred to this species have an external height of 365 millimeters and a basal anteroposterior diameter of 103 millimeters. They are of special interest as showing a pair of secondary horns or hornlets, which consist of elongate oval swellings 78 millimeters long at the base and about 22 millimeters high, located on the internal border of the main horns.

Male skull referred by Cope to "Symborodon" bucco (Am. Mus. 6346).—As we have seen above, the actual type of "*Symborodon*" *bucco* is a skull (Am. Mus. 6345) which belongs to *Megacerops bucco.* Another specimen described and figured by Cope as "*Symborodon*" *bucco* (Am. Mus. 6346) is probably referable to *B. curtum.* The buccal processes are very broad (656 mm., estimated), arching suddenly outward, deep and biconvex in section. The occipital crest is backwardly extended. There is a median vertical ridge over the foramen magnum, and a pair of rugosities on either side of the median line. The basisphenoid is smooth.

It is probable that this skull belongs to *Brontotherium* and not to *Megacerops,* because it has prevailing *Brontotherium* characteristics. There are, however, some differences. The zygomatic buccal section is somewhat more convex than that in the type of *B. curtum,* which is flatter. From the evidence now at hand we might regard this skull as representing an intermediate or connecting stage between *B. gigas* and *B. curtum,* and we should expect that if complete it would be found to possess horns and nasals also intermediate between those of the two species. We shall await subsequent discoveries with great interest.

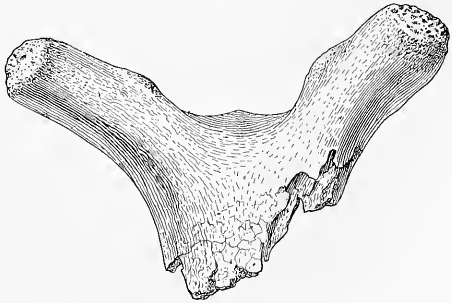


FIGURE 476.—Horns of *Brontotherium curtum*

Carnegie Mus. 560. Posterosuperior view of horns showing rugose tips and accessory swellings or hornlets. (After Peterson.) One-eighth natural size.

Female skull of B. curtum.—A small skull in the American Museum (Am. Mus. 1005) was formerly referred by the present author to a female of *B. gigas;* but the nasals are so excessively short and the sagittal section so strongly resembles that of *B. curtum* that this small female skull is more probably referable to this species. Like the female originally referred to *B. gigas*, it illustrates afresh the great disparity in size between the cow and bull titanotheres at this period of evolution. The apparently primitive but actually sexual characters exhibited in this skull have been noted already. As in the female skull of *B. gigas* the premolar tetartocones are less distinctly circular than in the males. The internal cingulum is less reduced, the occiput is not so greatly prolonged back of the zygoma, and the canines are short and recurved rather than bulbous. This list of sexual characters appears like a summary of primitive characters. The premaxillaries are edentulous, or toothless, confirming the evidence afforded by the *B. gigas* female skulls, that in the brontotheres the upper incisors were reduced or wanting in the females—a conclusion, however, which requires final substantiation by additional evidence. The malar bridge over the infraorbital foramen is broader than in the male. While the frontal section closely resembles that of *B. curtum,* the sexual disparity is illustrated not only by the light zygomata and narrow occiput, but by the irregularly osseous summits and by the form of the horns, which are less flattened posteriorly than in the male type of this species (Pls. CXC, B; CXCII; figs. 459, B; 477, B).

Of interest is the vertical septum extending from the under surface of the nasals to meet a similar septum rising from the premaxillaries, which is seen also in other skulls in the different phyla. While incomplete, this septum illustrates a tendency toward the formation of an intranarial septum similar to that in the rhinoceroses.

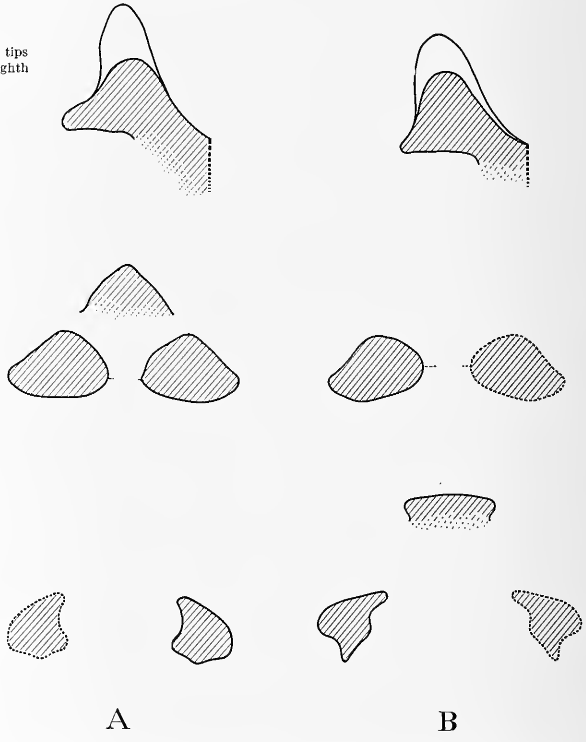


FIGURE 477.—Sections and contours of skull of *Brontotherium curtum*

A, British Mus. 5629. One-eighth natural size. This specimen has short horns, a high connecting crest, and moderately expanded zygomata, as in the supposed females of *Brontotherium,* but the canines are larger than in females and suggest that this is a male. It resembles Cope's type of "*Menodus peltoceras.*" The basal section of the horns is flattened to concave posteriorly and has a flattened external face. The nasals are small and pointed. B, Am. Mus. 1005, ♀. The horns are even shorter than in the preceding specimen, and the connecting crest is equally high. The basal section of the horns is wide, flattened posteriorly and antero-externally; the zygomata are moderately expanded.

Another character which parallels especially the brachycephalic rhinoceros is the flattening out of the lower lateral portion of the occiput.

Additional observations on the supposed female of Brontotherium curtum.—The female skull described above (Am. Mus. 1005) has been referred to this species because of the abbreviated nasals, high connecting crest, and flattened horns. The shortness of the horns has been assumed to be a female character. The systematic position of this skull, however, is hardly free from doubt, and the remarks made above with reference to the supposed female of *B. gigas* may possibly apply here, especially in view of the dimensions of p^4 (ap. 40 mm., tr. 61) and m^3 (84 by 82), which suggests reference to the Menodontinae rather than to the Brontotheriinae. However, the premolar external cingula in the present specimen are obsolete, the tetartocones are better developed, and the anteroposterior measurements of the dentition are also close to those of male skulls of *B. curtum*, with which species this skull may be left for the present.

Female skull, Cope's type of Menodus peltoceras (Am. Mus. 10719).—This type, described in detail in Chapter III, page 230, confirms the evidence afforded by the American Museum specimen No. 1005 as to the shortness of the horns in the females of these upper-level brontotheres. It resembles Am. Mus. 1005 in the extreme abbreviation of the nasals, in the steepness and size of the connecting crest, and in the marked prominence of the vertical ridge on the outer side of the horn. In sagittal and basal section the specimen agrees best with the female skull referred to *B. curtum*, but the still more extreme reduction of the nasals is equaled only in the species *B. platyceras*, to which this fragment may possibly belong.

Conclusion.—The type specimen of *M. peltoceras* probably represents a female of one of the long-horned species of brontotheres, probably *B. curtum*.

A finely preserved skull in the British Museum, (No. 5629) is represented in Plates CXCIII, CXCIV and Figure 477, A.

It presents a puzzling character in the large size of the canines, which resemble those of a male; in all other measurements it agrees with the male specimens of *B. hatcheri* and *B. gigas*, but in the conformation of the peculiar shield in front of the skull and of the abbreviated nasals this certainly resembles the supposed female of *B. curtum* (Am. Mus. 1005). It also exhibits a still stronger resemblance to the type of *Menodus peltoceras* Cope just described. The canines and grinding teeth in form are those of a true *Brontotherium*. It is difficult to interpret this specimen satisfactorily. If it is actually a male it may indicate that *B. peltoceras* was a distinct, peculiar species of brontothere with short horns; or this may be an aberrant specimen, either a female in which the canines are exceptionally large, or an aberrant male in which the horns are exceptionally short.

This specimen certainly raises some doubt as to our interpretation of the female sex of the skulls described above.

Brontotherium ramosum (Osborn)

(*Titanotherium ramosum* Osborn, 1896; "*Brontotherium ramosum*" Osborn, 1902)

Plate CXCI; text figures 194, 457, 479

[For original description and type references see p. 231]

Geologic horizon.—Upper *Titanotherium* zone of South Dakota.

Specific characters.—$I^{\underline{1}}$, $C^{\underline{1}}$, $P^{\underline{4}}$, $M^{\underline{3}}$. Premolars with obsolete external and reduced internal cingula; with two distinct internal cones. Molar-premolar series 350 millimeters. Skull brachycephalic. Horns elongate, in males 399 millimeters; gently planoconvex at the base. Very broad, gently biconvex and laterally expanded at the summits, with a very deep connecting crest. Nasals greatly abbreviated. Zygomata expanded into two wide, flat plates.

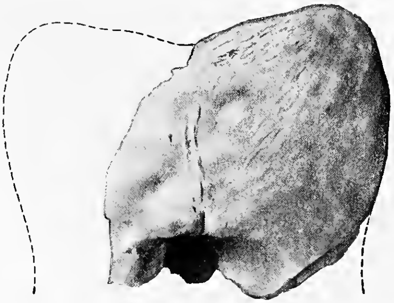


FIGURE 478.—Left horn and nasals of *Brontotherium curtum? (female)*

Am. Mus. 10719 (type of "*Menodus peltoceras*"); White River, Colo. Front view. One-fourth natural size. This fragment represents the left horn and coossified nasals of a brontothere allied in form to British Mus. 5629. It may have been a female of one of the long-horned, short-nosed types (*B. curtum*, etc.).

This species or ascending mutation appears to be a further evolution of the *B. gigas*, *B. curtum*, *B. medium* phylum. It is related in many characters to *B. curtum* and, on the other hand, is transitional toward *B. platyceras*, as shown in the sections of the horns, nasals, and zygomatic arches (fig. 479).

This "branching" or "spreading-horned" brontothere is represented only by the type skull of a very old bull in the American Museum collection (No. 1447) in the tenth stage of growth, and by a pair of horns with connecting crest in the National Museum (No. 1243).

From this somewhat scanty material the validity of the stage entitled *B. ramosum* awaits confirmation. As a proof of extreme age even the cingulate hypocone of m^3 is well worn, a rare occurrence. Note also that the skull is covered with exostoses, which are partly age or even senescent characters and may represent extreme development of the *B. curtum* type of skull. Among these exostoses are the branching internal expansions of the tips of the horns, to which the name *ramosum* refers. Remarkable exostoses are observed on the outer and inner portions of the buccal zygomatic processes and on the rugose tips of the occipital pillars.

The type skull is vertically crushed; this interferes with the natural position of the horns, which are pitched strongly forward, whereas in life the horns must have been vertical or even slightly recurved, as in well-preserved specimens of *B. gigas* and *B. platyceras*. Zygomatic expansion has now reached a still more extreme stage; the total length of the skull along the basal line is closely estimated at 741 millimeters, while the breadth across the zygomatic arches now attains 775, the breadth thus actually exceeding the length. The appearance of breadth is, however, greatly increased by crushing. The molar-premolar series is now shortened to 350 millimeters, which is less than in *B. medium*. The horns are still longer than in the preceding types, measuring 399 millimeters (15.7 inches) as compared with 355 in the oldest male of *B. gigas* and 380 in the type of *B. curtum*.

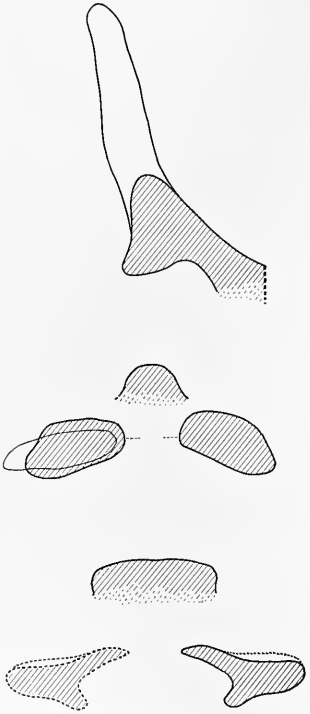


FIGURE 479.—Sections and contours of skull of *Brontotherium ramosum*

Am. Mus. 1447 (type). One-ninth natural size. The marked forward pitch of the horns, the extreme flatness of their basal section, and the extreme width and flatness of the zygomata have all been emphasized by crushing, but even before crushing the anterior face of the horns was probably convex, the nasals were extremely short, and the zygomata were much expanded.

A clear separation from the *B. gigas* type is seen in the frontonasal or sagittal section, which resembles very closely that of the aged *B. curtum*, attaining a vertical depth of 160 millimeters. The horn section near the base is, however, quite different from that of *B. curtum*, being relatively broader, less convex anteriorly, and quite as flattened or even slightly concave posteriorly. The apical section of the horns is far more flattened and broadened, being very slightly convex on both sides, whereas the apical section of the *B. curtum* type is more similar to the basal section. The external ridge, unlike that in *B. platyceras*, extends down two-thirds of the side of the horn but does not reach the malars in front of the orbits. The nasals are of about the same length as in *B. curtum*. The buccal processes are extraordinarily broad and flat; they exhibit the internal projection toward the temporal fossa, also seen in *B. gigas*. At the back of the skull the post-tympanic forms a broad and close union, practically a synostosis, with the postglenoid, narrowing down the auditory meatus to a small tube. In the median upper portion of the occiput we do not observe the small pair of tuberosities (fig. 378, F) which characterize *B. gigas*. The tops of the occipital pillars are grooved by the upgrowth of the rugosities.

Unfortunately the premaxillaries are broken, and the maxillaries lack the first premolars, which are represented by alveoli. A very striking progressive feature is the complete separation of the tetartocones from the deuterocones in p^2–p^4, so that although well worn down an enamel isthmus still separates the two areas of dentine. The external cingula of these teeth are obsolete; the internal cingula are ill defined.

B. ramosum therefore represents a very advanced stage of evolution but does not reach the climax attained in this remarkable series of skulls by the succeeding stage known as *B. platyceras*.

The type skull is badly crushed, giving a false appearance of extreme width. In dental measurements it is closer to certain specimens of *B. hatcheri* than it is to *B. platyceras*.

Brontotherium platyceras (Scott and Osborn)

(*Menodus platyceras* Scott and Osborn, 1887; "*Brontotherium platyceras*" Osborn, 1902)

Frontispiece; Plates XVIII, XIX, CLXXXI, CLXXXII, CLXXXVII–CLXXXIX; text figures 10, 18, 24, 27, 33 178, 375, 388, 399, 457–459, 480, 481, 620, 640, 643, 648, 649, 661, 707, 725, 726

[For original description and type references, see p. 221]

Geologic horizon.—Upper *Titanotherium* zone of South Dakota.

Specific characters.—Dental formula in males $I^{\underline{2}}$, $C^{\underline{1}}$, $P^{\underline{4-3}}$, $M^{\underline{3}}$. Incisors with rounded, smooth, oval crowns, long axis of crowns anteroposterior, canines ♂ 42 millimeters. Premolars with external cingula, obsolete, internal cingula reduced; tetartocones fairly distinct. Premolar-molar series 337 millimeters. Skull brachycephalic, 730 by 850 millimeters. Nasals vestigial, 20 millimeters. Horns extremely flattened transversely, slightly convex posteriorly; deep connecting crest, continuous malar ridge. Zygomata with broad, deep buccal processes.

Materials.—This grand stage, the "flat-horned" brontothere, which represents the climax of the evolution of the long-horned titanotheres, is comparatively rare. It is represented by the type horns in the Harvard Museum, also by another pair of horns in that museum. The well-preserved skull of an old male in the American Museum (No. 1448) was discovered by one of the expeditions under Mr. J. B. Hatcher; it agrees closely with the type and may be taken as a neotype. The finest skull known is that in the Field Museum (No. 12161), discovered by an expedition under Mr. E. S. Riggs.

Brontotherium platyceras is one of the most remarkable and exceptional ungulates known to science. Both in front and in side view the head presents a unique and extraordinary appearance.

The connecting crest between the horns has grown to such a height and the horns to such a breadth that in front view the head terminates in a great vertical plate 6.75 inches deep and more than 18 inches broad at the widest part. From the sides of this plate the horns extended upward and were gently recurved backward. The nasals are now mere pendent tuberosities from the base of this plate and the external nares open directly forward. At the sides of the head there were the great cheek processes. As this was the face of an animal in the seventh stage of growth, we may imagine the grotesque appearance of an old bull in the tenth stage. The breadth of the skull has now reached its extreme, the width of the zygomatic arches being about 32 inches (815 mm.), exceeding the length (distance from tips of the premaxillaries to the occipital condyles) by 3.35 inches (85 mm.).

It is evident when we compare these correlated progressive characters of the skull with the comparatively stationary characters of the teeth that the chief force of evolution or of selection was directed toward the development of the horns and buccal processes; while the teeth, so essential to the vitality of this species, were stationary. It is difficult to account for the sudden extinction of this apparently prosperous and numerous race of brontotheres; but the mechanical imperfection of the teeth may have been one of the factors in the extinction as fully discussed in a subsequent chapter.

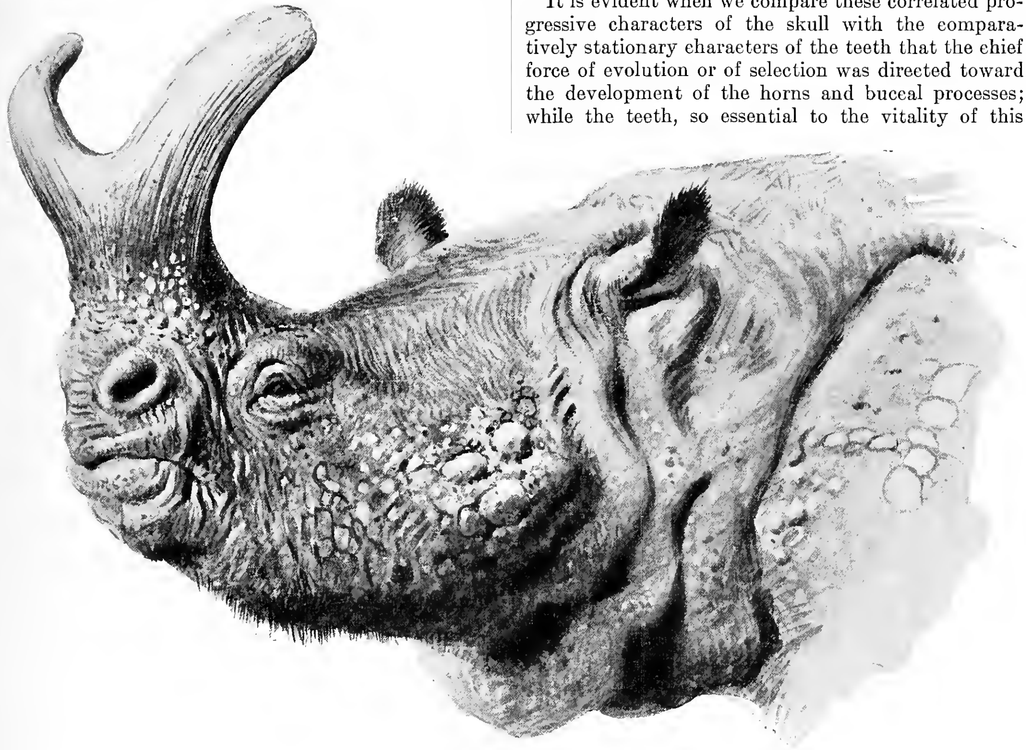


FIGURE 480.—Restoration of *Brontotherium platyceras*

By Charles R. Knight. About one-ninth natural size.

Teeth.—An exception to the general retrogression of the teeth is the persistence of the two upper incisors, as in all previously described males of the *Brontotherium* phylum. As preserved in the neotype skull (Am. Mus. 1448) the summits of the superior incisors are smooth and oval, with the long axis anteroposterior. It is difficult to imagine of what service these small incisors could have been to the animal and why they should have been preserved in this phylum while they have degenerated in the others. But the fact of their persistence proves that they were used in some manner, at least in the males. The canines have degenerated; they are smaller than those of *B. gigas* and very much smaller than those of *B. ramosum.* The premolars have less distinct internal cones than in *B. ramosum* and are seen to correspond rather with those of *B. gigas.* The cingula on the posterior molars are obsolete.

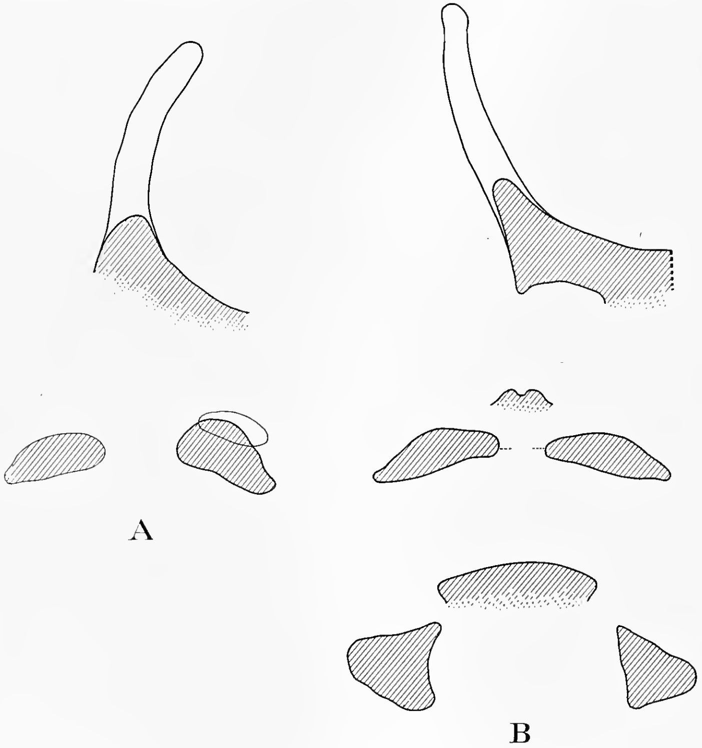


FIGURE 481.—Sections and contours of skull of *Brontotherium platyceras*

A, Harvard Mus. (type); B, Am. Mus. 1448 (neotype). One-ninth natural size. In this species the very long horns have a much flattened section and are placed far in front of the orbits. The free portion of the nasals is almost vestigial, and the zygomatic expansions are very massive.

Skull.—As we have seen in the type the elevation of the connecting crest between the horns is so great that it now connects them at the base, forming a broad, continuous crest (Pl. CLXXXVII) subconcave posteriorly, with sharp edges.

The sections of the horns in the American Museum skull (No. 1448, fig. 481, B) were taken just above the crest. They are extremely broadened, with the anterior faces slightly convex and the posterior faces plane or slightly concave. The posterior concavity of the horns, observed in the Harvard type specimen (fig. 481), is here rendered plane by crushing. This plane section is carried nearly to the summits, which do not expand as in *B. ramosum.* A comparison of the sagittal sections with those of the previously described species also illustrates the extreme thinning, anteroposteriorly, and the vertical face of the connecting crest. The fact that this crest and the horns incline forward is probably due to vertical crushing.

The nasals are reduced to 20 millimeters, one-half the length observed in *B. ramosum* and *B. curtum.* The entire outer edges of the horns are now composed of the sharp external ridges, which reach from the summit to the anterior superior rim of the orbit, where they are grooved horizontally by the lacrimal ducts. The completion of this sharp outer face is the fulfilment of a growth tendency which we have seen in various degrees of development from 2 to many inches in length in preceding stages.

The entire anterior portion of the neotype skull is distorted by pressure; the posterior portions are entirely wanting and have been restored in plaster. The external auditory meatus was entirely closed by a deep union of the postglenoid and post-tympanic processes. The enormous zygomata were fortunately preserved, especially that upon the right side, which is accurately represented in the section. The mass of this buccal process is as great as in *B. curtum* and apparently exceeds that of *B. ramosum.* This section and the less progressive structure of the premolars furnish two reasons for regarding *B. platyceras* as derived from the *B. gigas elatum* and *B. curtum* types rather than from the *B. ramosum* type. According to this view *B. ramosum* would represent a contemporary or collateral species rather than one in the direct line of ascent.

Additional observations on the measurements of Brontotherium curtum and B. platyceras.—The five male skulls referred to *B. curtum* exhibit the following range in measurements as compared with *B. platyceras:*

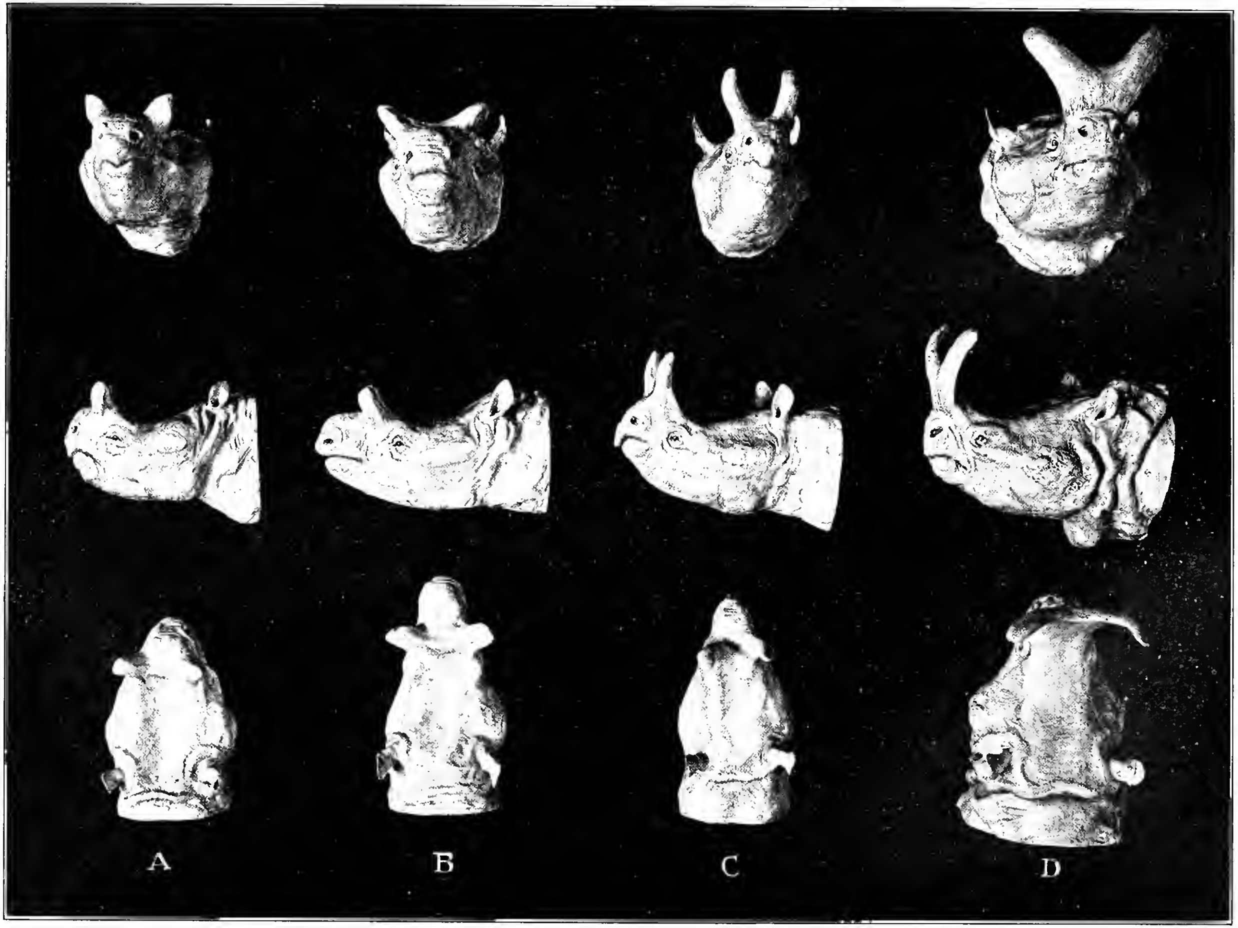
Measurements of Brontotherium curtum and B. platyceras, in millimeters

	B. curtum	B. platyceras
P¹–m³	345–350	337–340
P¹–p⁴	128–130	120–123
M¹–m³	218–228	221–223
Pmx to condyles	780–840	728–880
Zygomatic index	74–?78	80
Nasal length	52–65	20–38
Horn length	355–380	390

Thus *B. curtum* is a little larger than *B. platyceras* in the dental measurements but has longer nasals and shorter horns.

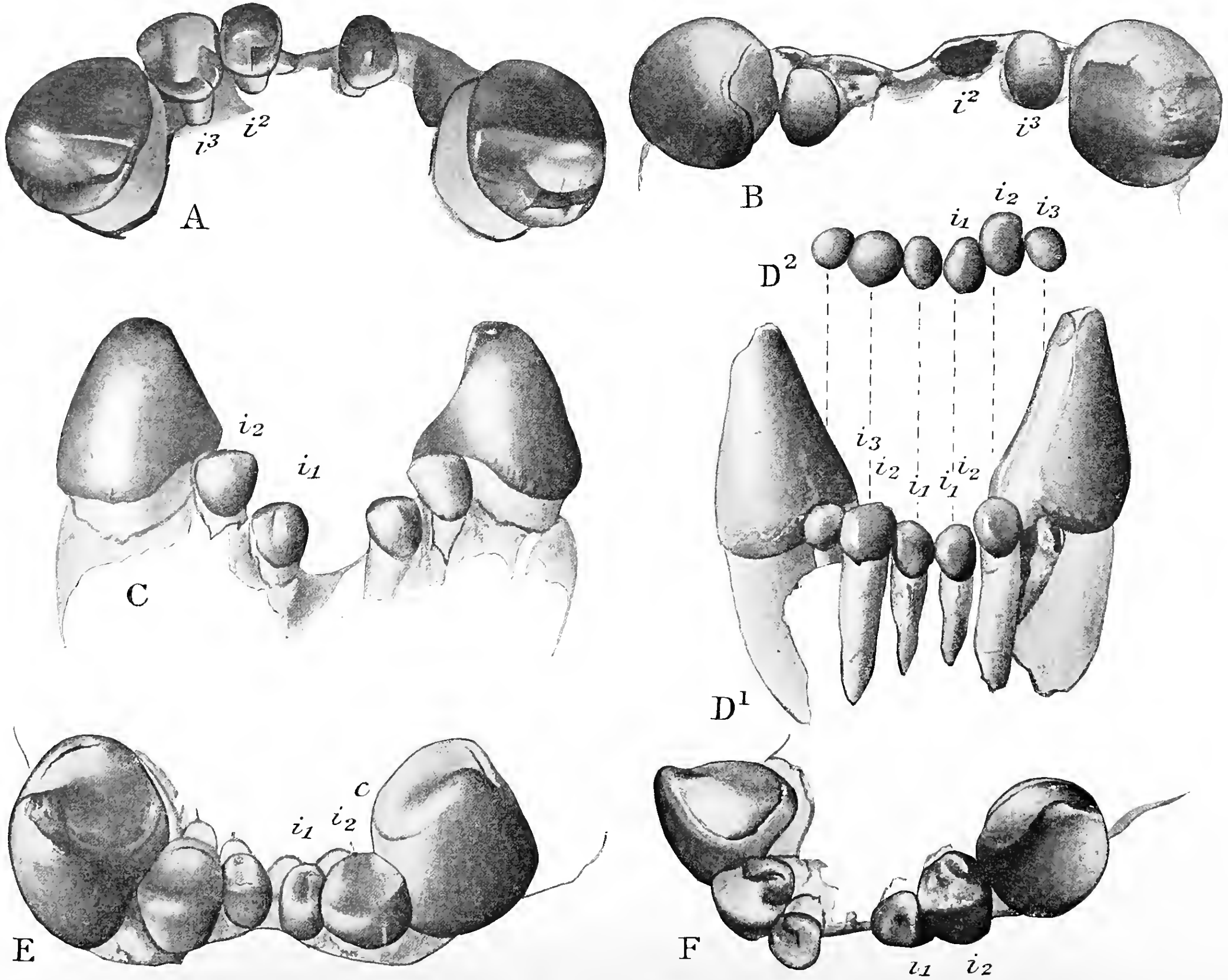
In *B. platyceras* the type consists only of a pair of horns and hence affords no dental measurements. The first referred skull (Am. Mus. 1448) is crushed, so that the length of the horns has probably been increased, the basilar length perhaps lessened. The true molars are not as large as in certain specimens of *B. gigas*, but the ratio of molar length to the basal length of the skull is at least not less than in other brontotheres. In basilar length the first specimen of *platyceras* is smaller than *curtum*, the second specimen is much larger.

The second referred skull in the Field Museum of Chicago (No. 12161) is the largest titanothere on record and is superbly preserved (Pls. CLXXXI, CLXXXII). Its flattened spreading horns combine features of *B. platyceras* and *B. ramosum.* Its molar index (25) is lower than in typical brontotheres (28–29). The premolar series is short.



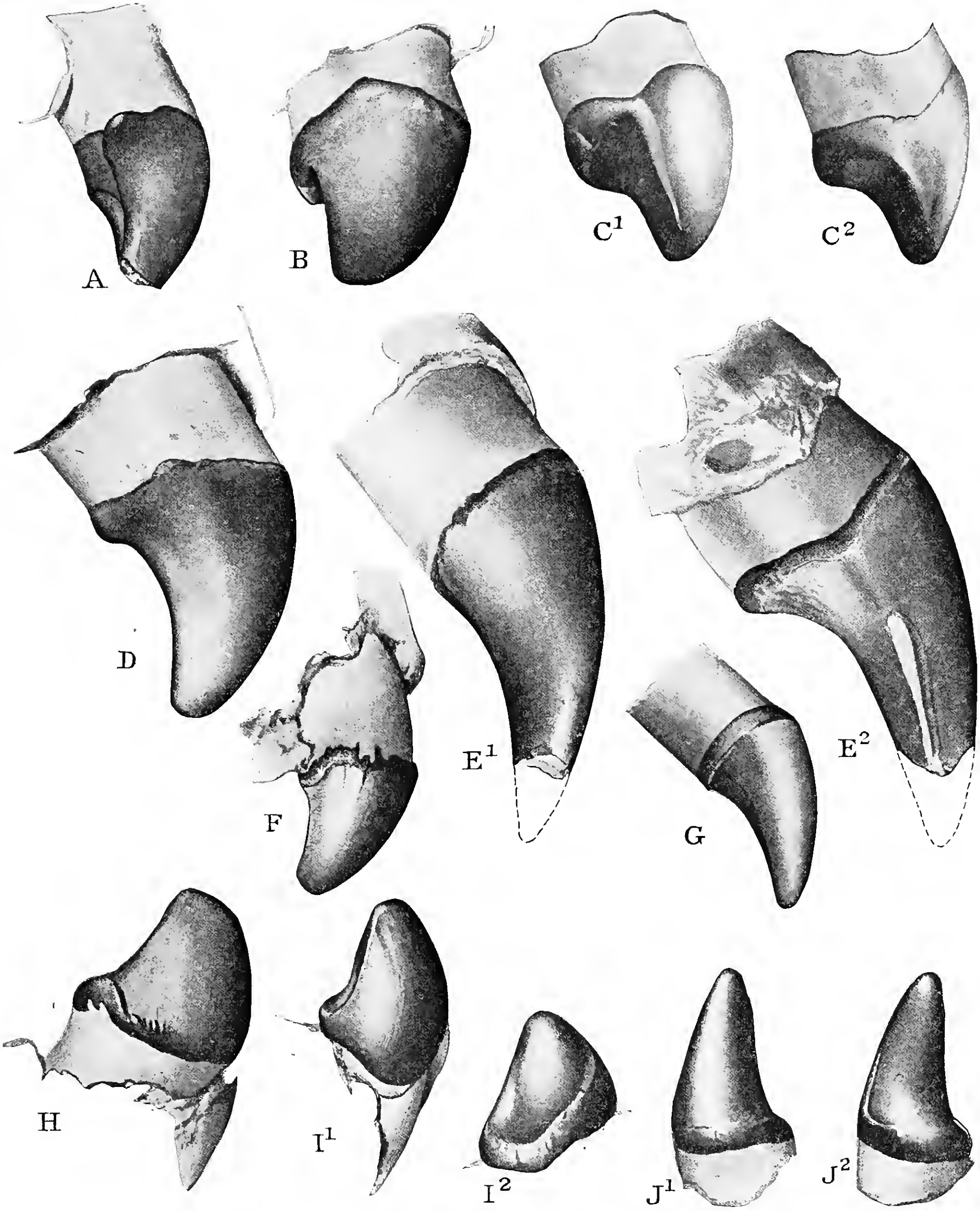
RESTORATIONS OF THE HEADS OF FOUR GENERA OF OLIGOCENE TITANOTHERES

Modeled by Charles R. Knight. A, *Brontops robustus*, brachycephalic. B, *Menodus* (*Titanotherium*) *giganteus*, mesaticephalic, stenocephalic. C, *Megacerops* (*Symborodon*) *acer*, brachycephalic. D, *Brontotherium platyceras*, hyperbrachycephalic



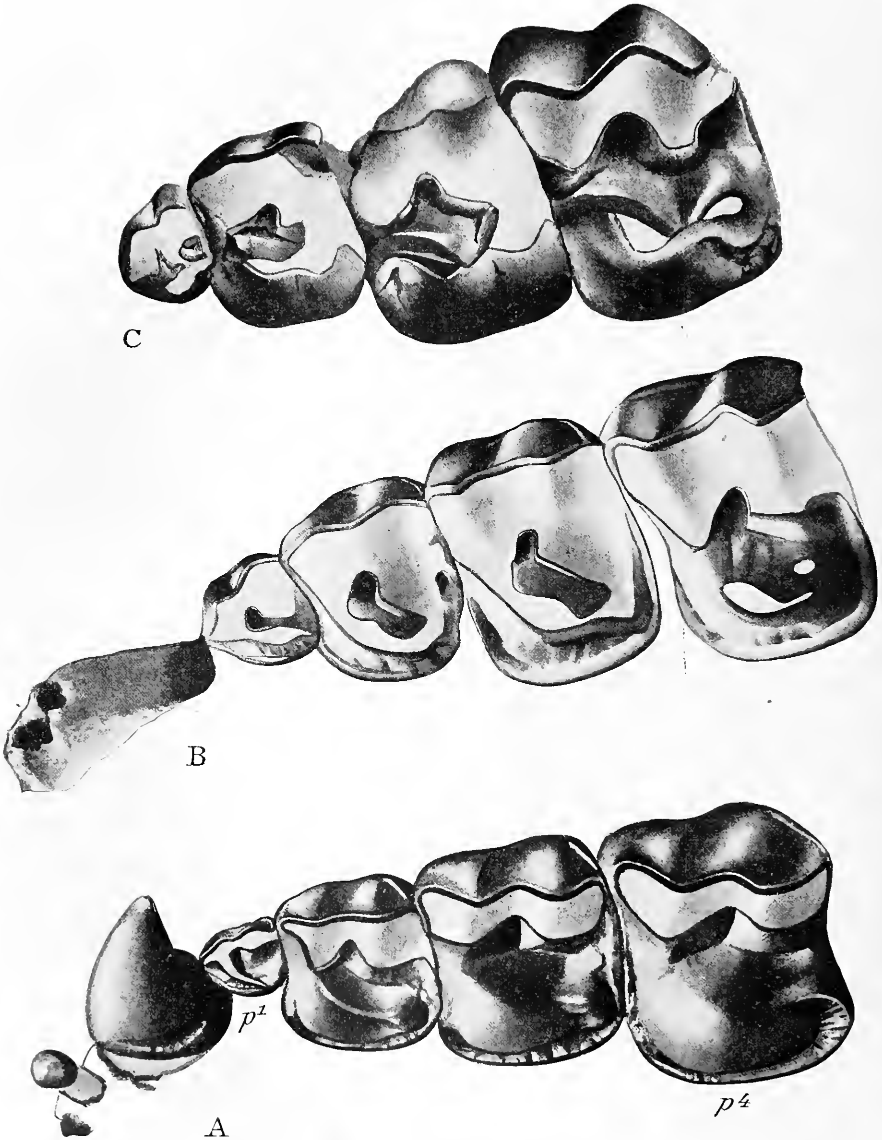
INCISORS AND CANINES OF BRONTOTHERIUM AND TELEODUS

A, *Brontotherium leidyi* (Carnegie Mus. 2093), upper teeth, inferior view. B, *Brontotherium platyceras* (Am. Mus. 1448), upper teeth, inferior view. C, *Brontotherium medium* (Am. Mus. 1051), lower teeth, anterior view. D^1, *Teleodus avus*, type (Yale Mus. 10321), lower teeth, anterior view; D^2, the same, lower incisors, superior view. E, *Brontotherium hatcheri* (Am. Mus. 1068), lower teeth, superior view. F, *Brontotherium leidyi* (Am. Mus. 516), lower teeth, superior view. All natural size



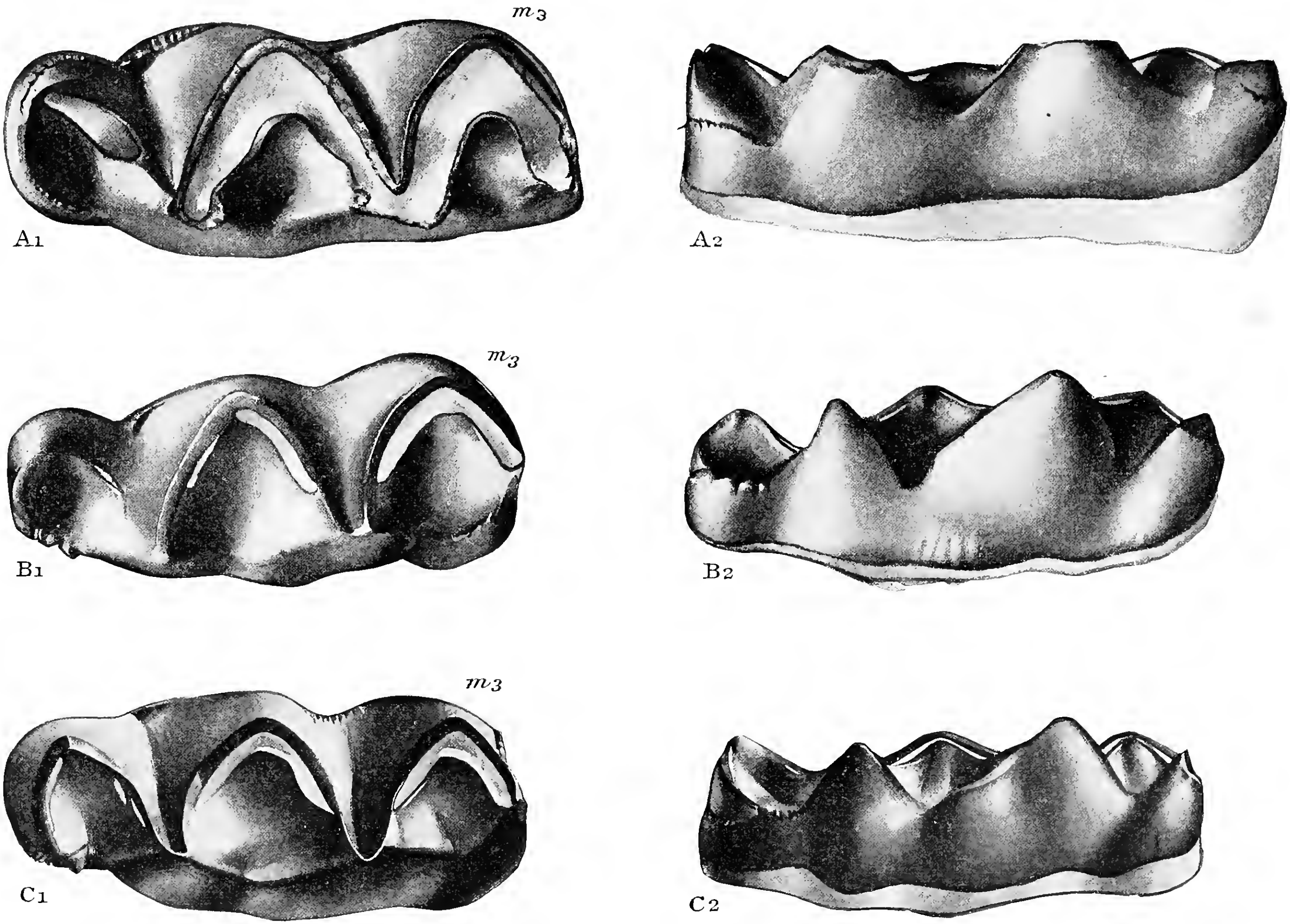
UPPER AND LOWER CANINES OF OLIGOCENE TITANOTHERES

A, *Brontotherium gigas*, supposed female (Am. Mus. 1006), right superior canine, external view. B, *Brontotherium gigas*, male (Am. Mus. 492), right superior canine, external view. C^1, *Brontotherium leidyi* (Carnegie Mus. 93), right superior canine, external view; C^2, the same, left upper canine, internal view. D, *Brontops robustus*, male (Am. Mus. 1083), right superior canine, external view. E^1, *Menodus giganteus*, male (Am. Mus. 505), right superior canine, external view; E^2, the same, left superior canine, internal view. F, *Allops walcotti*, type (Nat. Mus. 4260), right inferior canine, external view. G, *Menodus heloceras* (Carnegie Mus.), right superior canine, external view. H, *Brontotherium medium* (Am. Mus. 1051), right inferior canine, external view. I^1, *Brontotherium leidyi* (Am. Mus. 516), right inferior canine, external view; I^2, the same, left inferior canine, internal view. J^1, *Menodus trigonoceras* (Nat. Mus. 4745), left inferior canine, external view; J^2, the same, right inferior canine, internal view. All natural size



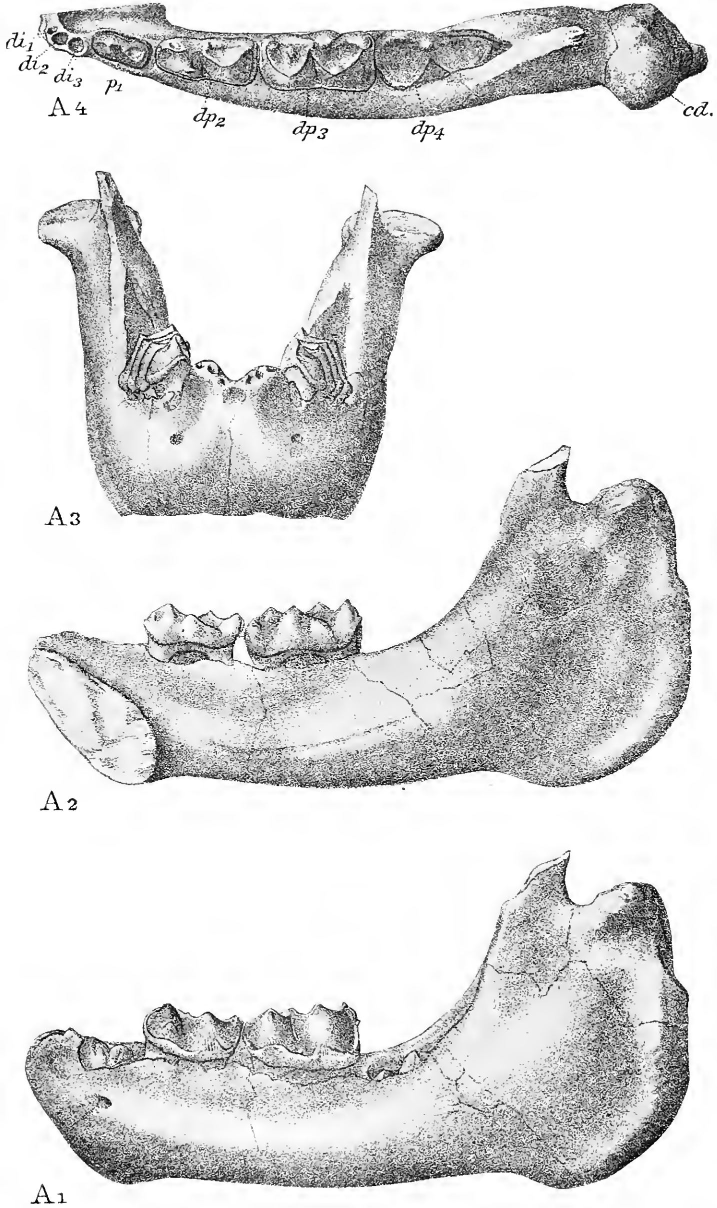
LEFT UPPER PREMOLARS OF OLIGOCENE TITANOTHERES

A, *Brontops brachycephalus*, male (Nat. Mus. 4258). B, *Allops walcotti*, male, type (Nat. Mus. 4260). C, *Brontotherium leidyi*, type (Nat. Mus. 4248). All natural size



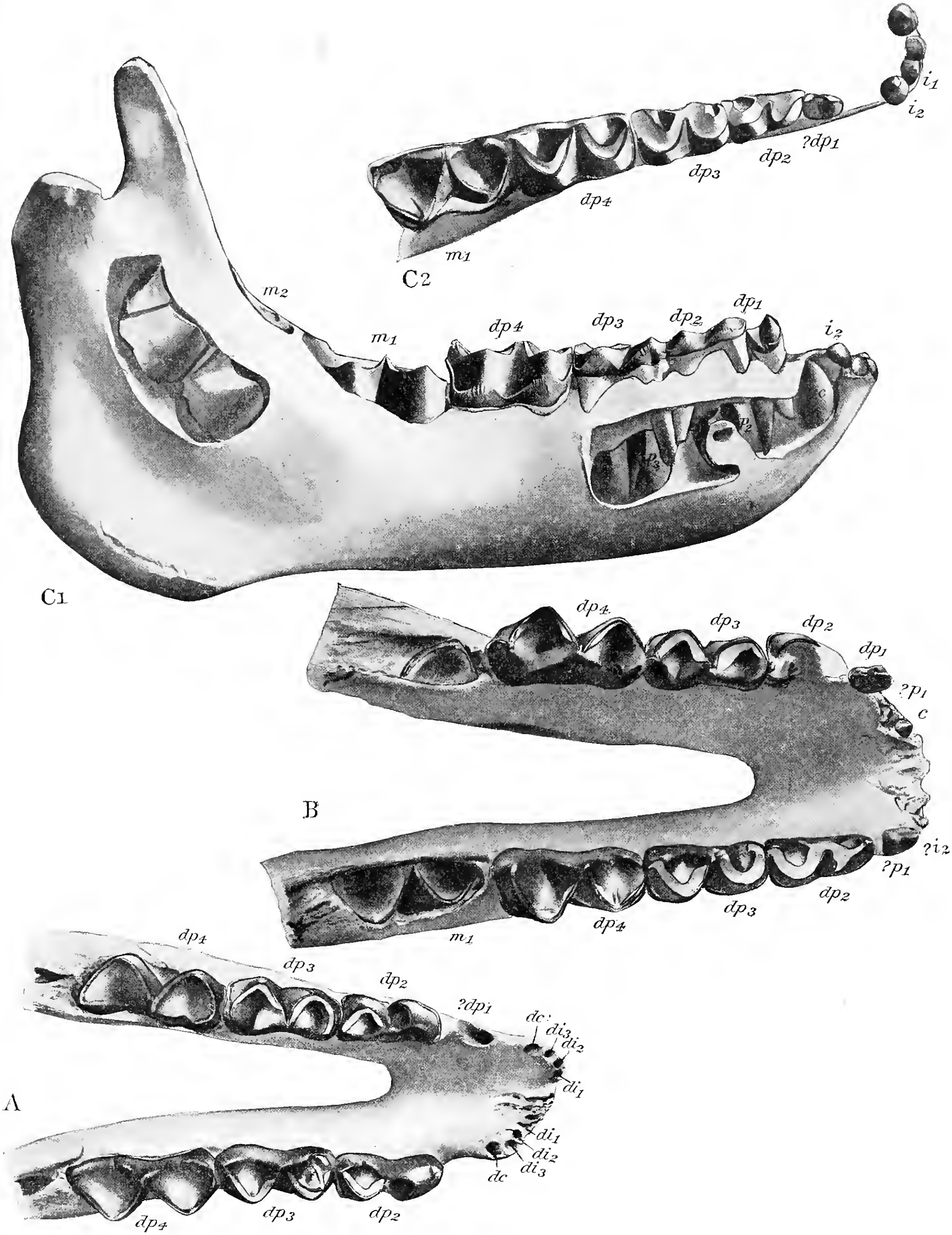
THIRD LEFT LOWER MOLAR IN MENODUS AND BRONTOTHERIUM

A_1, *Menodus giganteus* (*trigonoceras*), female (Am. Mus. 1067), superior view; A_2, the same, internal view. B_1, *Brontotherium leidyi* (Am. Mus. 516), superior view; B_2, the same, internal view. C_1, *Brontotherium leidyi*, paratype (Carnegie Mus. 93), superior view; C_2, the same, internal view. All natural size



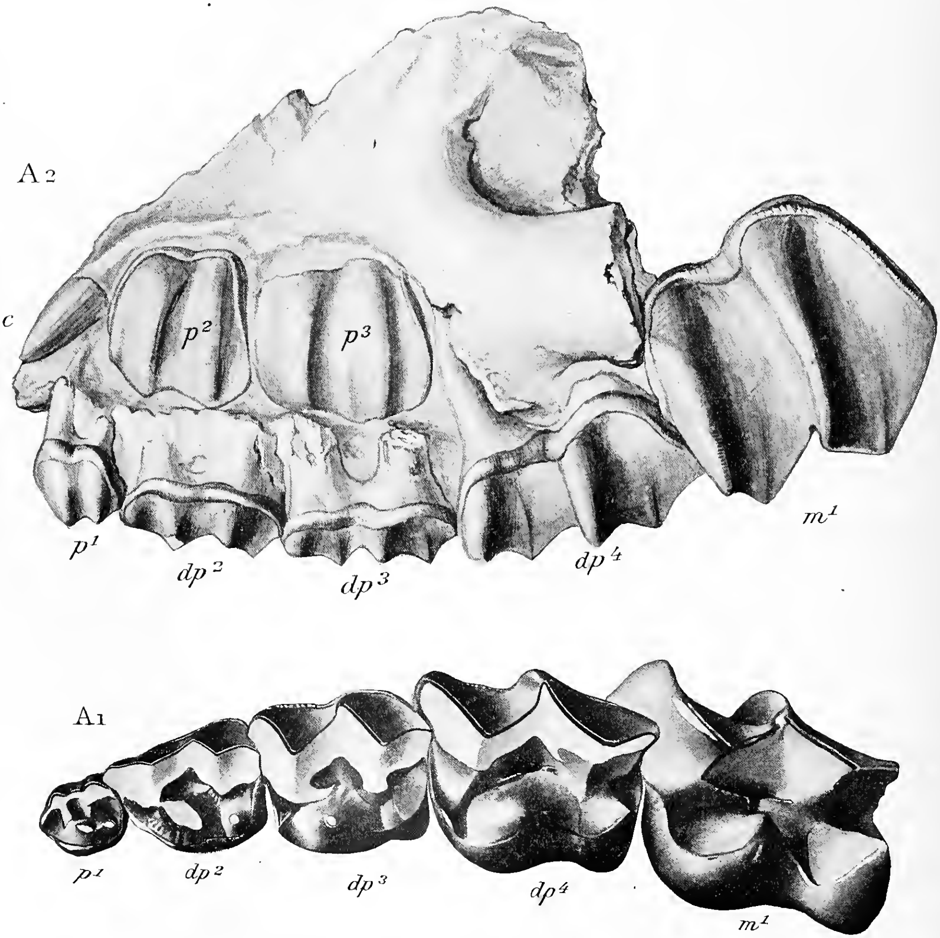
JUVENILE JAW REFERRED BY MARSH TO BRONTOPS

Generic and specific references uncertain. One-half natural size. (See p. 455.) Important because it exhibits the characters of the juvenile skeleton. A_1, External view of the left ramus; A_2, internal view of the right ramus; A_3, anterior view; A_4, superior view of the left ramus. cd, Condyle; *di*, alveolus for first deciduous incisor; di_2, alveolus for second deciduous incisor; di_3, alveolus for third deciduous incisor; p_1, first premolar (coming in with deciduous series and probably belonging with it); dp_2, second deciduous premolar; dp_3, third deciduous premolar; dp_4, fourth deciduous premolar



JUVENILE JAWS AND TEETH OF OLIGOCENE TITANOTHERES

A, *Menodus giganteus* (Am. Mus. 510), superior view. B, *Menodus giganteus* (Am. Mus. 509), superior view. C_1, *Brontops dispar* Carnegie Mus. 124), external view of right ramus; C_2, the same, superior view of dentition. All one-half natural size



SUPERIOR DECIDUOUS AND PERMANENT GRINDING TEETH OF MENODUS GIGANTEUS

A_1, Am. Mus. 497, deciduous premolars and first permanent molars of left side, crown view; A_2, the same, showing permanent teeth embedded in the alveolar region. Both two-thirds natural size

CHAPTER VII

EVOLUTION OF THE SKELETON OF EOCENE AND OLIGOCENE TITANOTHERES

SECTION 1. METHODS BY WHICH THE TITANOTHERE SKELETON HAS BEEN STUDIED

PRINCIPLES OF THE EVOLUTION OF THE LIMBS OF HOOFED ANIMALS

The postcranial skeleton of the titanotheres, although less fully known than the skull, is no less significant in its bearing on our knowledge of the evolution of these animals and of that ancient West which was their habitation or the scene of their migrations. To understand that ancient West we must try to bring its animals and plants back to life. The attempt to restore the titanotheres as living and migrating animals has led to the establishment of four new principles in the evolution of the limbs of the hoofed mammals generally, principles that have been worked out by the author in cooperation with Dr. William K. Gregory, who has published (Gregory, 1912.1, pp. 267–294) a preliminary study which includes many independent observations of his own on the mechanics and adaptations of limb movement. These principles were discovered through comparison of the skeleton and musculature of all the perissodactyls and of the proportions of the upper and lower limb segments in a large number of ungulates, including perissodactyls, artiodactyls, amblypods, and proboscideans. These four principles of limb evolution, which had been only partly or incompletely recognized previously and which are fully described in Chapter IX, are briefly as follows:

1. The relative length and the angulation of the upper and lower segments of the limbs and the planes of the articular facets furnish a means of elucidating the adaptations to speed and to weight in all the hoofed mammals, living and extinct. Thus by determining the relative lengths and proportions of the limb segments among living forms in which the speed, weight, and general limb movements are known, we may estimate the adaptations to similar functions and habits in the titanotheres and other extinct forms.

2. Apart from their ancestral paleotelic adaptations, all ungulates, in their bony and muscular systems, show secondary cenotelic adaptations to similar mechanics of speed and weight, which form closely analogous or convergent groups and are exhibited in the form and the proportions of the limbs and of the shoulder and pelvic girdles.

3. Within each of the nine families of perissodactyls that are more or less closely related to the titanotheres analogous or convergent adaptation produces closely similar limb and shoulder-girdle forms from more or less dissimilar ancestral forms.

4. Between the primitive, light-limbed, subcursorial *Lambdotherium* type and the ponderous *Brontotherium* type, the titanotheres pass through four stages of limb types (figs. 685, 686). From a light body and limb type (*Lambdotherium*), analogous to that of the primitive cursorial horses, they enter a medium limb stage (*Eotitanops*) like that of the tapirs, then pass through something near a primitive rhinoceros stage (*Mesatirhinus*), and ultimately attain the final titanothere stage (*Brontotherium*), which is in some respects similar to that seen in the elephants.

The titanotheres and other hoofed mammals that exhibit these four stages in the development of the limbs are broadly designated as follows:

1. Subcursorial digitigrades, partly perfected in swift limb movements, including *Phenacodus* (condylarth), *Eohippus* (horse), *Lambdotherium* (titanothere), primitive types of ungulates of lower Eocene time, in which limb proportions are inherited from ancestral unguiculates and show evidence of remote ambulatory and even of still more remote arboreal adaptation (Matthew, Gregory). In these animals the radius and tibia are relatively long; the metapodials, typified by Mts III and Mtc III, are relatively short.

2. Mediportal digitigrades, of medium weight and speed, with moderately heavy body and limbs and clumsy motion (digitigrade), such as *Tapirus* (tapir), *Mesatirhinus* (titanothere). Most middle-sized quadrupeds of middle Eocene time have limb proportions intermediate between the cursorial and graviportal extremes. These proportion ratios survive in the existing *Tapirus*, which, however, in its body and limb proportions is more cursorial than the Eocene titanotheres.

3. Subgraviportal digitigrades, partly transformed into or prophetic of the weight-bearing (graviportal) type, such as *Palaeosyops* (titanothere).

4. Graviportal digitigrades, of perfected weight-bearing type, with angulate limbs capable of more or less rapid movement according to the length and the angulation of the limbs, such as *Opsiceros* (black rhinoceros), *Brontotherium* (titanothere). These animals are all digitigrades—that is, the feet rest partly on terminal hoofs, partly on pads beneath the phalanges. They are heavy or bulky forms, such as the rhinoceroses and titanotheres, which retain the digitigrade type of foot, although some (*Menodus*) have straight hind limbs.

Besides the four types of limbs or limb movement that are exemplified in the titanotheres there are three other types, which are not yet known in animals of the titanothere group, as follows:

1. Primitive ambulatory (plantigrade), such as *Pantolambda* (amblypod); also the opposite extreme.

2. Cursorial unguligrade, with swift type of limb and secondarily elongated feet, such as *Neohipparion*, *Equus* (horse), *Gazella* (gazelle), all light, long-footed types, in which the limbs terminate in single hoofs and the pads beneath the phalanges are reduced or wanting.

3. Rectigrade-graviportal, straight-limbed, weight-bearing type, with special pillar-like or vertical weight-bearing disposition of the limbs and short gravigrade feet, such as *Elephas*, *Mastodon* (elephants); also such clumsy, slow-moving forms as *Coryphodon* and *Uintatherium* (amblypods), with gigantic or heavy bodies supported on straight or column-like limbs in which the terminal phalanges and hoofs are reduced and the limb is supported on a heavy pad.

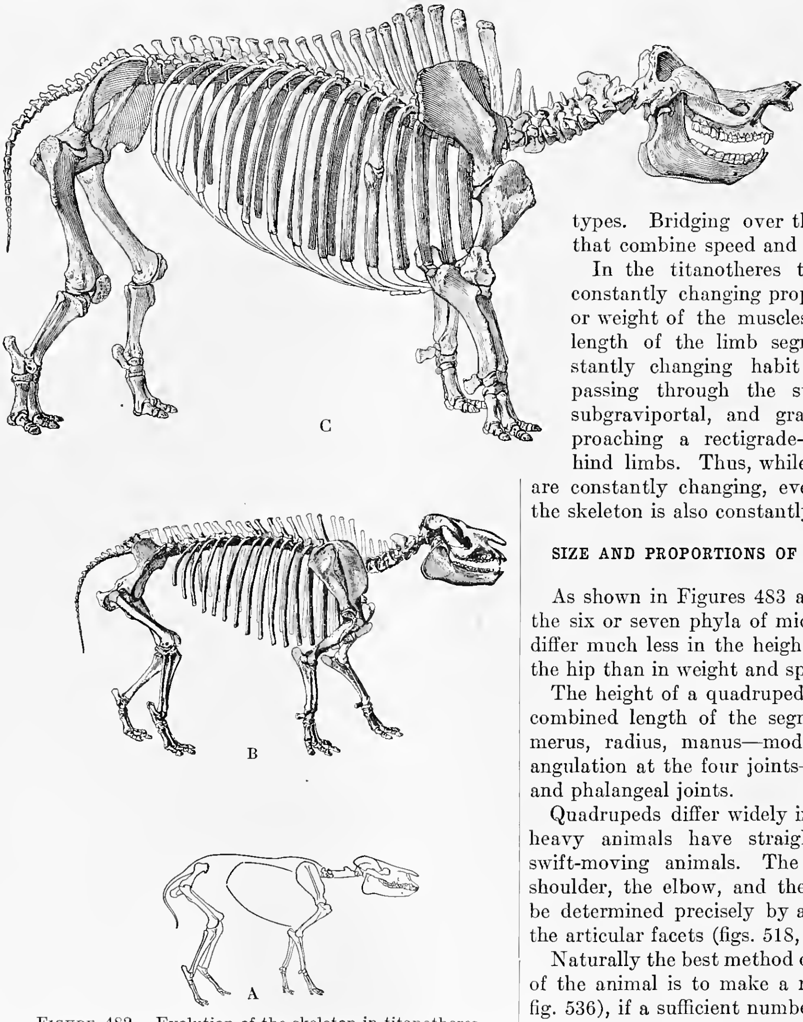


FIGURE 482.—Evolution of the skeleton in titanotheres

A, First stage (subcursorial): *Eotitanops borealis;* lower Eocene. B, Middle stage (mediportal): *Palaeosyops leidyi;* middle Eocene. C, Final stage (graviportal): *Brontops robustus;* lower Oligocene. Scales approximate; A too large. (See fig. 483.)

In general, the stages represented by these types indicate that two main divergent directions were taken in limb adaptation—namely, into cursorial or speed types or into graviportal or weight types. Bridging over these extremes are types that combine speed and weight.

In the titanotheres there is an evolution of constantly changing proportion both in the mass or weight of the muscles and bones and in the length of the limb segments, adapted to constantly changing habit of speed and weight, passing through the subcursorial, mediportal, subgraviportal, and graviportal types and approaching a rectigrade-graviportal type in the hind limbs. Thus, while the bones of the head are constantly changing, every muscle and bone in the skeleton is also constantly changing.

SIZE AND PROPORTIONS OF EOCENE TITANOTHERES

As shown in Figures 483 and 661, the members of the six or seven phyla of middle Eocene titanotheres differ much less in the height of the shoulder and of the hip than in weight and speed.

The height of a quadruped depends upon the total combined length of the segments—the scapula, humerus, radius, manus—modified by the flexure or angulation at the four joints—shoulder, elbow, wrist, and phalangeal joints.

Quadrupeds differ widely in respect to angulation: heavy animals have straighter limbs than light, swift-moving animals. The normal angles at the shoulder, the elbow, and the phalangeal joints may be determined precisely by a study of the planes of the articular facets (figs. 518, 664, 666, 667).

Naturally the best method of ascertaining the height of the animal is to make a restoration (*Palaeosyops*, fig. 536), if a sufficient number of parts are available, laying out the limbs in their proper angulation, as indicated by the planes of the articular facets and measuring the net height directly.

It is seldom that the material is so complete that all the limb segments and articular facets can be measured and determined for the purpose of estimating height, so that we may be forced to make estimates based on the ratios of the length of the parts preserved to those of similar animals of known height.

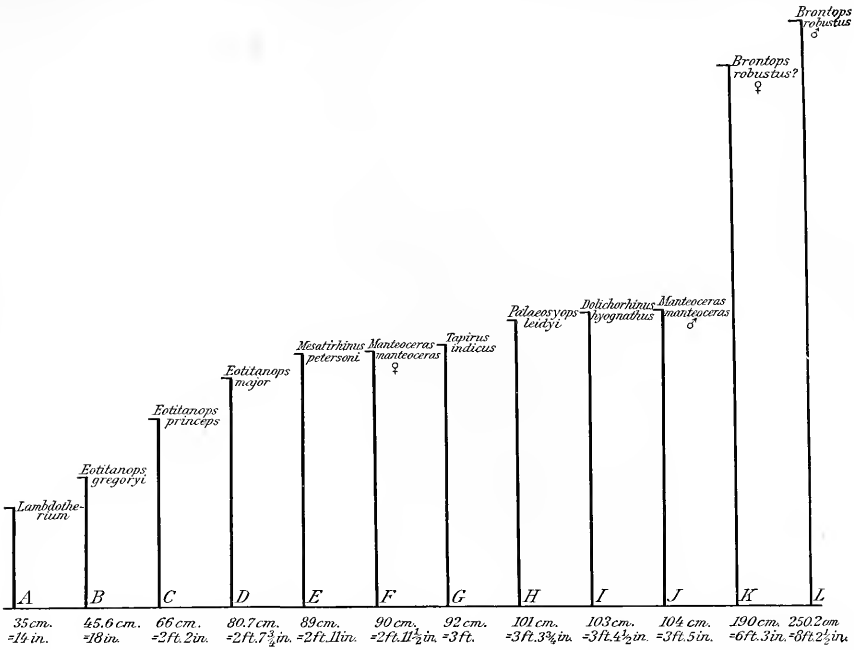


FIGURE 483.—Estimated height at the shoulder (to top of scapula) of Eocene and Oligocene titanotheres (see below), compared with that of the tapir (*Tapirus indicus*)

A, Lambdotherium popoagicum; B, Eotitanops gregoryi; C, Eotitanops princeps; D, Eotitanops major; E, Mesatirhinus petersoni; F, Manteoceras manteoceras (female); *G, Tapirus indicus; H, Palaeosyops leidyi; I, Dolichorhinus hyognothus; J, Manteoceras manteoceras* (male); *K, Brontops robustus?* (female, Am. Mus. 518); *L, Brontops robustus* (type, male). One twentieth natural size.

Estimated heights of Eocene titanotheres

	Length of humerus (centimeters)	Length of femur (centimeters)	Height to top of scapula		Designation in Figure 483
			Centimeters	Inches	
Lower Eocene:					
Lambdotherium popoagicum			[a] 38	15	A
Eotitanops gregoryi			45. 6	18	B
Eotitanops princeps	20. 3	25	[b] 66	26	C
Eotitanops major			80. 7	31. 8	D
Middle Eocene:					
Mesatirhinus petersoni	26+	35	[c] 89	35	E
Manteoceras manteoceras, ♀	[d] 29		[d] 90	35½	F
Tapirus indicus (modern tapir)	25	32	92	36	G
Limnohyops monoconus?	29. 3	35. 5	[e] 92	36	
Palaeosyops leidyi	32. 5	38	101	39¾	H
Manteoceras manteoceras, ♂		39. 3	[f] 104	41	J
Upper Eocene:					
Dolichorhinus hyognathus	31. 5	38. 6	[g] 103	40½	I
Lower Oligocene:					
Brontops robustus	53	78	[h] 190	75	K
Brontops robustus [i]	61. 5	82	250. 2	98½	L

---

[a] Scapula and humerus conjectural.

[b] Humerus known; scapula and radius conjectural. Restored from known relative length of humerus, scapula, and radius in allied forms.

[c] Forearm and manus Princeton Mus. 10013, humerus and scapula supplied from other individuals.

[d] Femur known; other segments unknown. Height computed by assuming same relative length of limb segments as in *Palaeosyops leidyi.*

[e] Manus, forearm, and humerus known, scapula computed.

[f] Femur known, other segments unknown. Height computed by assuming same relative length of limb segment as in *Palaeosyops leidyi.*

[g] Composite restoration (fig. 579).

[h] Measured from mounted skeleton (Am. Mus. 518).

[i] Type skeleton (Yale Mus. 12048).

DIVERGENCE AND CONVERGENCE IN THE SKELETON OF POLYPHYLETIC SERIES

DIVERSE ADAPTIVE TYPES OF LIMB STRUCTURE

Our study of the locomotor skeleton of the titanotheres strongly supports the polyphyletic theory that we derived from the study of the skull and the teeth—namely, that there were two larger branches or groups of Eocene titanotheres, the palaeosyopine and the *Manteoceras-Dolichorhinus*, each of which was divided into two or more smaller branches or subfamilies.

The interpretation of the structure of the feet and limbs would be simple if the feet and limbs of all these six or seven genera were invariably divergent, but the law of convergence again comes into play, and long after one subfamily has diverged from another there remain or arise within each subfamily forms which, through convergent adaptation and inheritance, parallel in foot and limb adaptation forms in the other subfamilies.

To make this double convergence clear we recall the existence in Eocene time of five distinct groups or subfamilies of titanotheres with respect not only to geologic level but to divergence as to speed and to weight, namely:

- Palaeosyopine group:
  - Lower Eocene:
    - Lambdotheriinae (cursorial types).
    - Eotitanopinae (subcursorial types).
  - Middle Eocene:
    - Palaeosyopinae (mediportal and subgraviportal types).
- *Manteoceras-Dolichorhinus* group:
  - Middle and upper Eocene:
    - Manteoceratinae (subgraviportal types).
    - Dolichorhininae (mediportal types).

The Lambdotheriinae (fig. 486) are primitively cursorial, like the early Eocene Equidae and Lophiodontidae.

How far the Eotitanopinae may be directly ancestral to the Palaeosyopinae or Manteoceratinae we do not know.

The known Eotitanopinae (figs. 484, 492) are light-limbed, or subcursorial—that is, the feet are relatively shorter (more mediportal) than those of the tapir and less light in structure than those of the primitive Equidae.

In the various Palaeosyopinae we find a condition somewhat transitional between the tapir and the heavier types, like the rhinoceros. These animals include more heavy-limbed (*Palaeosyops*) and light-limbed (*Limnohyops*) types.

Similarly within the *Manteoceras-Dolichorhinus* group there are two series of forms, mediportal (*Mesatirhinus*) and subgraviportal (*Manteoceras*). Thus we discover mediportal Palaeosyopinae (such as *Limnohyops*) and mediportal Dolichorhininae (such as *Mesatirhinus*), which are somewhat alike in their limb adaptations and can be separated only by careful scrutiny of certain less conspicuous features of ancestral separation, which bring out the subfamily characters. There are also graviportal Palaeosyopinae (such as *Palaeosyops*), which resemble graviportal manteoceratines (such as *Manteoceras*) in some respects but differ in others.

It has taken a vast amount of study of the scattered and often unassociated limb materials to determine the real subfamily relationships in the limbs of these different forms, which are concealed by the veneer of similar adaptation or cenotelic resemblance; but it may now be demonstrated positively that in each subfamily of the middle Eocene titanotheres there were relatively light-limbed and relatively heavy-limbed forms. The differences between these adaptive extremes of relatively rapid-moving and slow-moving forms may be observed and measured in every single bone of the limbs, and especially in the small bones of the carpus and tarsus.

To illustrate how a single bone may be highly distinctive, an outline of the central bone of the carpus, the magnum, as it appears in different forms, is given herewith (fig. 485). On the left is the magnum of the subcursorial *Eotitanops*, relatively high and narrow; on the right that of the subgraviportal *Palaeosyops robustus*, relatively broad and low. In general, high and narrow proportions of the magnum characterize cursorial forms and low and broad proportions characterize graviportal forms. Thus the transformation of this single bone reflects the kind of allometric change which prevailed in all parts of the skeleton.

Or, to take the foot as a whole (fig. 484), the manus of *Mesatirhinus* represents the mediportal extreme among the titanotheres analogous to that of *Tapirus*, while the manus of *Palaeosyops* represents the subgraviportal extreme analogous to that of *Hippopotamus*. Both types of feet occur at the same geologic levels and in the same geographic regions; they belong to contemporaneous titanotheres, one perhaps seeking forest ground like the habitat of *Tapirus*, the other the borders and possibly the waters of rivers and lakes like the habitat of *Hippopotamus*.

There are thus, as shown in Figures 502, 503, 510, 515, 520, wide adaptive radiations among the Eocene titanotheres in modes of locomotion on different kinds of soil.

All these adaptively diverse types of limb structure appear to have been derived from a small and primitive type, which was a subcursorial, light-limbed, slender-footed, and relatively speedy animal, well adapted for escape rather than combat.

The adaptive transformation of the limbs of titanotheres has not yet been traced so continuously as that of the skull or of the teeth; the scattering of parts of limbs has rendered the association and identification of many separate bones exceptionally difficult. We are still in doubt as to the limb structure in certain phyla, especially in *Telmatherium*. Much remains to be discovered through further exploration in the field.

This deficiency of material renders all the more valuable the broader investigation and comparison with other Perissodactyla which will be presented in Chapter X. The new and precise system of comparative measurements of the limbs establishes certain laws of limb adaptation and enables us to estimate fairly closely the speed and weight-bearing powers of the various kinds of titanotheres.

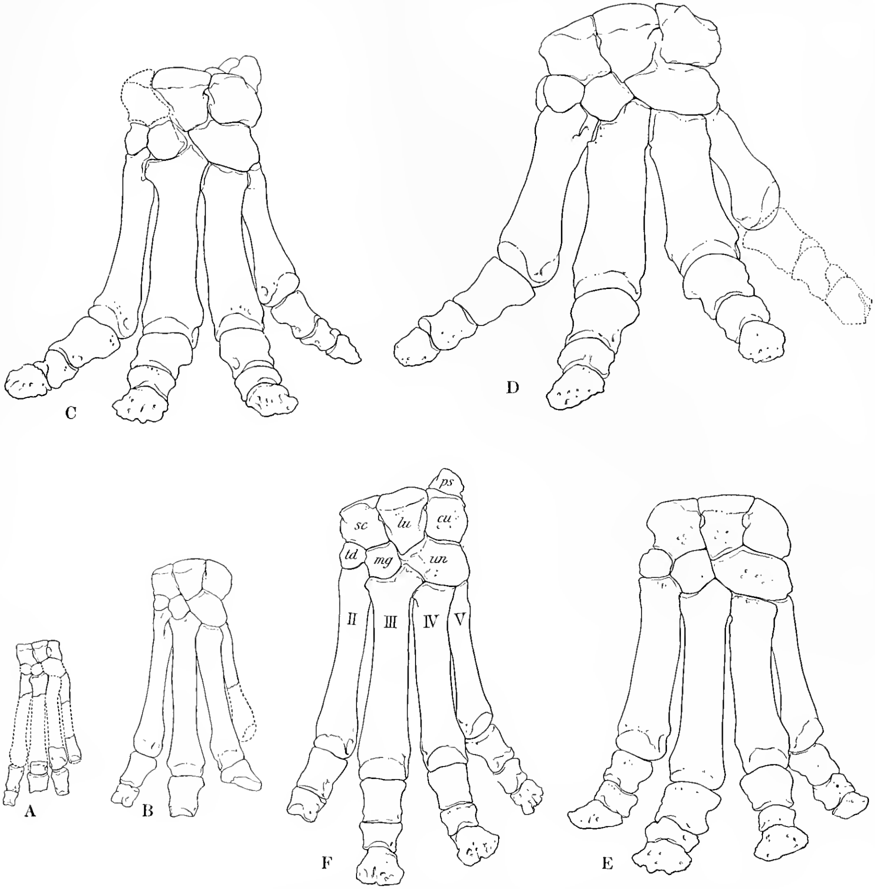


FIGURE 484.—The phyla of Eocene titanotheres, as represented by the manus

A, Lambdotheriinae (*Lambdotherium*); B, Eotitanopinae (*Eotitanops*); C, Palaeosyopinae (*Limnohyops*); D, Palaeosyopinae (*Palaeosyops*); E, Manteoceratinae (*Manteoceras*); F, Dolichorhininae (*Mesatirhinus*). One-third natural size.

1. *Existence of many phyla.*—The chief conclusions drawn from the limb bones of titanotheres, moreover, confirm those drawn from the skull—namely, the existence of six or more distinct phyla in the lower Oligocene. That there were six or more contemporaneous but more or less independent phyla, characterized by differences of limb structure and modes of locomotion, is clearly shown, as well as the fact that these include two main phyla each of which embraces at least three subphyla (genera). Members of these six or more phyla were separated by the weight, shape, and proportions of the body, feet, and limbs, such separation being indicative of a considerable range of size, speed, and migrating ability in search of food. This demonstrates the existence of two early radiations (subfamilies) and of subsequent branch radiations (genera).

FIGURE 485.—Progressive broadening of the magnum in Eocene titanotheres

A, *Eotitanops* (subcursorial); B, *Mesatirhinus* (mediportal); C, *Limnohyops* (mediportal); D, *Palaeosyops* (subgraviportal). One-half natural size.

2. *Adaptive characters superposed on ancestral.*—Similar limb and foot proportions, like similar skull

proportions, were independently developed in unrelated phyla and are often misleading as to real relationships. Thus the subfamilies duplicate each other in adaptation; there arose in both subfamilies short-footed and long-footed forms, as summarized in various tables.

TERMS USED IN DESCRIBING THE SKELETON OF THE TITANOTHERES

The following list includes most of the terms used in this monograph in describing the postcranial skeleton of the titanotheres:

Terms used in describing the postcranial skeleton of the titanotheres

English terms	Latin terms	Abbreviations used on illustrations
Shoulder girdle and fore limb		
Scapula	Scapula	*sc.*
Superior or suprascapular border	Margo suprascapularis	*ss.*
Anterior or prescapular border	Margo prescapularis	*cb.*
Posterior, postscapular, axillary border	Margo axillaris	*gb.*
Spine	Spina scapulae	
Tuberosity of spine	Tuberositas spinae scapulae	*t. sp.*
Supraspinous or prescapular fossa	Fossa prescapularis (supraspinata)	*fos. sup. sp.*
Infraspinous or postscapular fossa	Fossa postscapularis (infraspinata)	*fos. inf. sp.*
Internal subscapular surface	Facies subscapularis	
Neck of scapula	Collum scapulae	
Coracoid process	Processus coracoideus	*pr. cor.*
Coracoid border	Margo coracoideus	
Glenoid cavity	Cavitas glenoidalis	*glen.*
Humerus	Humerus	*h.*
Head	Caput humeri	*cap.*
Greater tuberosity	Tuberculum majus	*t. maj.*
Lesser tuberosity	Tuberculum minus	*t. min.*
Bicipital groove	Sulcus bicipitalis	*s. bic.*
Deltopectoral crest	Crista deltopectoralis	
Deltoid tuberosity	Tuberositas deltoidea	*t. del.*
Tuberosity for the teres major or latissimus dorsi	Tuberositas teres	*t. te.*
Winding (brachialis) surface	Facies spiralis	*brach. ant.*
Ectocondyle	Ectepicondylus	*ectep.*
Extensor (supinator) crest	Crista "supinatoria" (extensoria)	*cr. "sup."*
Entocondyle	Entepicondylus	*entep.*
Distal articular surface	Facies distalis	
"Capitellum" for radius	capitellum	*cptl.*
"Trochlea" for ulna	trochlea humeri	*trch.*
Olecranal, anconeal (posterior) fossa	Fossa olecrani	*fos. ol.*
Supratrochlear (anterior) fossa	Fossa supratrochlearis	
Radius	Radius	*r.*
Head	Caput radii	
Internal process	Processus internus capitis radii	*pr. in.*
External process	Processus externus capitis radii	*pr. ex.*
Radiohumeral or trochlear facet	Facies proximalis (radiohumeralis) radii	*cptl. h.*
Biceps tubercle	Tuberositas bicipitalis radii	*tbclm. rad.*
Extensor groove	Sulcus extensoria	*s. ex.*
Brachialis rugosity	Rugositas brachialis	*br. ant.*
Styloid process	Processus styloideus radii	*pr. sty.*
Radiocarpal facet	Facies distalis (radiocarpalis) radii	
Ulna	Ulna	*u.*
Olecranon	Olecranon	*ol.*
Olecranal fossa	Fossa olecrani	*fos. ol.*
Ulnohumeral trochlea	Incisura semilunaris (facies ulnohumeralis)	*inc. sml.*
External facet of the ulnohumeral trochlea	Facies externa incisurae semilunaris	*fac. ex.*
Coronoid process	Processus coronoideus (anconaeus) ulnae	*pr. anc.*
External process	Processus externus ulnae	*pr. ex. u.*
Lesser sigmoid fossa	Fossa sigmoidea minus	*fos. sig. min.*
Ulnoradial facets	Facies ulnoradialis	
Ulnocarpal facet	Facies distalis (ulnocarpalis)	
Styloid process	Processus styloideus ulnae	*pr. sty. ul.*
Carpals	Carpalia	
Proximal row, scaphoid, lunar, cuneiform, pisiform	Os scaphoideum, os lunare, os cuneiforme, os pisiforme.	*sc., lu., cu., ps.*
Posterior tuberosity of lunar	Tuberositas posterior ossis lunaris	

Terms used in describing the postcranial skeleton of the titanotheres—Continued

English terms	Latin terms	Abbreviations used on illustrations
Shoulder girdle and fore limb—Continued		
Carpals—Continued.	Carpalia—Continued.	
Distal row, trapezium, trapezoid, magnum, unciform.	Os trapezium, os trapezoideum, os magnum, os unciforme.	*tz.*, *td.*, *mg.*, *unc.*
Posterior tuberosity of magnum	Tuberositas posterior ossis magni	
Metacarpals II–V	Metacarpalia II–V	*II*, *III*, *IV*, *V*.
Phalanges, 1st, 2d, 3d, or ungual	Phalanges	
Sesamoids	Ossa sesamoidea	
Sacrum, pelvic girdle, hind limb		
Sacrum	Sacrum	*sac.*
Sacrals 1–4	Vertebrae sacrales 1–4	
Sacro-iliac rugosity	Rugositas iliosacralis	
Pelvis	Pelvis	
Right and left innominate bones	Os innominatum, dextrum et sinistrum	
Ilium	Ilium	*il.*
Superior or supra-iliac border	Margo superior	*cr. il.*
Sacral process	Tuber sacrale	*tu. sac.*
Lateral process	Tuber coxae	*tu. cox.*
Iliosacral rugosity	Rugositas iliosacralis	
Dorsum or dorsal surface (gluteal fossa)	Facies dorsalis	
Ventral surface (iliac fossa)	Facies ventralis	
Neck of ilium	Collum ilii	
Rectus tuberosity	Processus antero-inferior	*pr. ant. inf.*
Pubis	Pubis	*pu.*
Symphysis pubis	Ramus superior	*ram. sup. pb.*
Pubi-ischiadic symphysis	Symphysis pubi-ischiadica	
Pectineal tuberosity, pubic spine	Tuberositas pectinea	
Obturator (thyroid) fenestra	Fenestra thyroidea	
Ischium	Ischium	*is.*
Obturator (thyroid) fenestra	Fenestra thyroidea	*f. thyr.*
Tuberosity	Tuberositas ischii	*tu. is.*
Ischial spine	Spina ischii	*sp. is.*
Femur	Femur	*f.*
Head	Caput femoris	*cap.*
Ligamentum teres pit	Fovea capitis	*lig. ter.*
Digital fossa	Fossa trochanterica (digitalis)	
Great trochanter	Trochanter major	*tr.*^{1}, *t.*′
Second or lesser trochanter	Trochanter minor	*tr.*^{2}, *t.*′′
Third trochanter	Trochanter tertius	*tr.*^{3}, *t.*′′′
Linea aspera	Linea aspera	
Plantaris fossa	Fossa plantaris	
Internal tuberosity	Tuberositas interna	*t. in.*
External tuberosity	Tuberositas externa	*t. ex.*
Entocondyle, inner femorotibial trochlea	Entocondylus	*con. in.*
Ectocondyle, outer femorotibial trochlea	Ectocondylus	*con. ex.*
Patellar trochlea, surface	Trochlea patellaris	*trch.*
Inner keel, outer keel	Carina interna, carina externa	
Patella	Patella	*p.*
Tuberosity for the quadriceps femoris	Tuberositas tibiae	
Tuberosity for the patellar ligament	Tuberositas ligamenti patellae	
Tibia	Tibia	*t.*
Tibiofemoral trochlea	Facies proximalis	
Entocondylar surface	Facies eutocondylaris	
Ectocondylar surface	Facies ectocondylaris	
Spine	Spina	*sp.*
Cnemial crest, tubercle	Crista cnemialis (tuberculum)	*cr. cn.*
Supero-external tuberosity	Tuberositas supero-externa	*t. ex.*
Supero-internal tuberosity	Tuberositas supero-interna	*t. in.*
Popliteus fossa	Fossa poplitealis	
Distal posterior process	Processus distalis posterior	
Tibiocalcaneal trochlea	Facies articularis inferior	
Internal malleolus	Malleolus internus	*mal. int.*

Terms used in describing the postcranial skeleton of the titanotheres—Continued

English terms	Latin terms	Abbreviations used on illustrations
Sacrum, pelvic girdle, hind limb—Continued		
Fibula	Fibula	*fb.*
Head	Caput fibulae	
Fibulotibial facet	Facies articularis superior	
Shaft	Corpus fibulae	
Fibulocalcaneal facet	Facies articularis inferior	
External malleolus	Malleolus externus	*mal. ext.*
Calcaneum	Calcaneum	*cal.*
Tuber calcis	Tuber calcis	*tu. cal.*
Sustentaculum	Sustentaculum tali	
Sustentacular facet	Facies sustentacularis	*sus.*
Ectal facet	Facies ectalis	*ect.*
Inferior facet	Facies inferior	*inf.*
Cuboid facet	Facies cuboidea	*cb.*
Astragalus	Astragalus	*as.*
Astragalotibial trochlea	Trochlea astragali	*cr. ex., cr. in.*
Head	Caput astragali	
Neck	Collum astragali	
Navicular facet	Facies navicularis	(*nav.*)
Cuboidal facet	Facies cuboidalis	(*cb.*)
Tarsals	Tarsalia	
Navicular	Os naviculare	*nv.*
Entocuneiform	Os entocuneiforme	*cn.*^{1}
Mesocuneiform	Os mesocuneiforme	*cn.*^{2}
Ectocuneiform	Os ectocuneiforme	*cn.*^{3}
Cuboid	Os cuboideum	*cb.*
Metatarsals II–IV	Metatarsalia II–IV	*mt. II–IV.*
Phalanges	Phalanges	*ph.*

SECTION 2. THE POSTCRANIAL SKELETON OF LOWER EOCENE TITANOTHERES

SUBFAMILY LAMBDOTHERIINAE

Lambdotherium

Lambdotherium is a small, swift, slender-limbed, relatively abundant animal, less abundant than the contemporary horses but more abundant than the small lophiodonts (*Heptodon*). The largest *Lambdotherium* measures about 14 inches (350 mm.) at the shoulders, as compared with the smallest *Eotitanops* (*E. gregoryi*), which measures about 18¼ inches (456 mm.) at the shoulders. It exceeds in size most of the contemporary species of *Eohippus* and equals the large *Eohippus robustus* of the lower Wasatch.

Lambdotherium popoagicum

The materials of *L. popoagicum* are extremely scanty; in only two specimens (Am. Mus. 4880, 14903) are parts of the skeleton associated with the teeth, and these parts are very fragmentary. (See figs. 486–489.)

In the atlas (fig. 487) the vertebrarterial canal pierces the anterior portion of the base of the transverse process; that is the primitive condition in titanotheres and in Perissodactyla generally.

The restoration of the fore limb (fig. 488) is highly conjectural, because the lengths of the bones are unknown. The proportions are heavier than in *Eohippus*. The ratio of the radius to the humerus is estimated at 90 per cent, the same as in *Eohippus*.

The scapula (fig. 487) presents an elongate neck (tr. 19 mm.) and the lower part of the postspinous fossa is very narrow; the lower part of the prespinous fossa, which is not all preserved, is slightly broader; the spine descends rather low. The distal end of the humerus indicates the presence of a small entocondyle, and its narrow rotula accords with the deep, laterally compressed proximal articular surfaces of the ulna and radius. The length of the radius is estimated at 103 millimeters; the shaft is rather narrow and sharply convex. The ulna is elongate and has a high, deep, laterally compressed olecranon process; the proximal portion of the shaft behind the radius is deep.

The carpus (fig. 489) is correlated with this slender structure, being relatively high and narrow but broader than in *Eohippus;* the scaphoid rests chiefly on the magnum anteriorly, and the high and narrow lunar exhibits a broad supporting unciform facet and an oblique nonsupporting magnum facet. The magnum, wanting in this specimen, was probably small; it is relatively broad in *Eohippus*. The cuneiform is rather high and narrow.

The manus exhibits four digits; the ends of the metapodials show a tendency to functional tridactylism, because the median digit (III) is larger than the adjoining digits. This enlargement of D. III is indicated not only by its diameter but by the enlargement of its proximal phalanx, which is much broader than the proximal phalanges of D. II or D. IV. This indicates a rather pronounced tendency to mesaxonic structure, whereas the middle Eocene titanotheres exhibit either a primary or secondry paraxonic and finally isotetradactyl condition. D. V is somewhat shorter and more slender.

The structure of the astragalus of this specimen (Am. Mus. 4880), as inferred from the distal end of the tibia which is preserved, indicates that the keels of the astragalus were quite sharp.

The tarsus is compared with that of the less cursorial *Eotitanops* and the more cursorial *Eohippus* in Figure 502. An astragalus associated with Am. Mus. 2991 exhibits a high, long neck and a high, narrow sustentacular facet, showing that the astragalocuboidal facet was very narrow (figs. 491, 503).

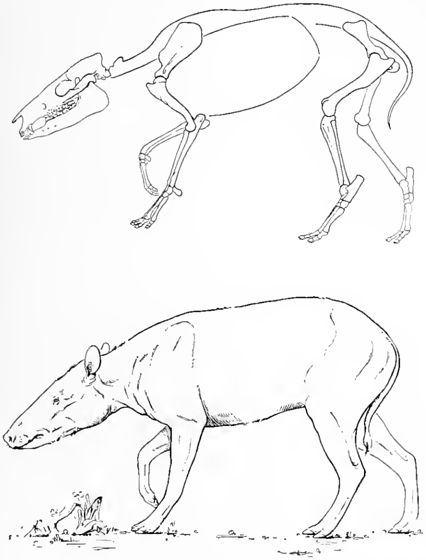


FIGURE 486.—Reconstructed skeleton and restoration of *Lambdotherium popoagicum* Cope

Made by E. S. Christman under the direction of W. K. Gregory. One-tenth natural size. This provisional reconstruction is based on the following American Museum specimens from the Wind River Basin, Wyo.: 14907 (Alkali Creek, Wolton), maxilla, malar, top of cranium; 14903 (Alkali Creek, Buck Spring), squamosal, basicranial region; 14899 (Alkali Creek, Buck Spring), lower jaw; 4880, distal end of scapula, fragments of humerus, radius, ulna, and manus; 14921 (Wolton), astragalus and calcaneum. Remaining parts conjecturally modified from *Eohippus* and other contemporary perissodactyls.

SUBFAMILY EOTITANOPINAE

Eotitanops

Our knowledge of the skeleton of the species of Wind River *Eotitanops* is relatively small; we know that there were gradations of size from smaller and lighter to larger and heavier, subcursorial forms, the general evolution being in the direction of the known middle Eocene titanotheres. The pes especially gives us valuable records of this progressive increase in size and weight.

As compared with the middle Eocene titanotheres of the Bridger formation these lower Eocene forms were small and light limbed and had high, narrow ankle and wrist joints, resembling most nearly the light-footed members of middle Eocene age, such as *Mesatirhinus*. In the skeleton, as in the skull, there are general primitive features that accord with the other lower Eocene perissodactyls, such as the lophiodonts (*Heptodon*) and horses (*Eohippus*). The details of the carpus and tarsus remind us also of these lower Eocene perissodactyls, although *Eotitanops* is decidedly larger and less distinctively cursorial than either *Heptodon* or *Eohippus*. The abbreviation of the fifth or outer digit (Mtc V) of the manus forbids our describing the animal as functionally tetradactyl; taken with the extreme displacement of the lunar on the unciform (a tridactyl specialization) this reduction tends to support the idea of Gregory that these animals, after having entered an evolution toward tridactylism, reversed the process and reentered tetradactylism in middle Eocene time.

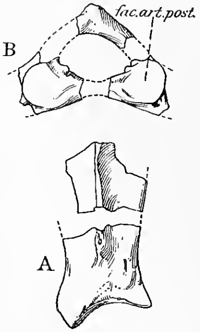


FIGURE 487.—Atlas and scapula of *Lambdotherium popoagicum*

Am. Mus. 4880, Wind River Basin, Wyo., Wind River formation. A, Distal portion of left scapula, outer side view; B, rear view of incomplete atlas. Two-thirds natural size.

Measurements, in millimeters, of teeth and limb bones referred to Eotitanops, compared with Lambdotherium and Tapirus

	Lambdotherium	E. gregoryi	E. borealis
Lower grinding teeth (p_2–m_3)	64	78. 4	98
Median metatarsal, length			85
Median metacarpal, length			
Humerus, length			
Femur, length			

	E. princeps	E. major	Tapirus terrestris
Lower grinding teeth (p_2–m_3)	105		118
Median metatarsal, length		104	114
Median metacarpal, length	87		113
Humerus, length	205		
Femur, length	[a] 250		

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[a] Estimated.

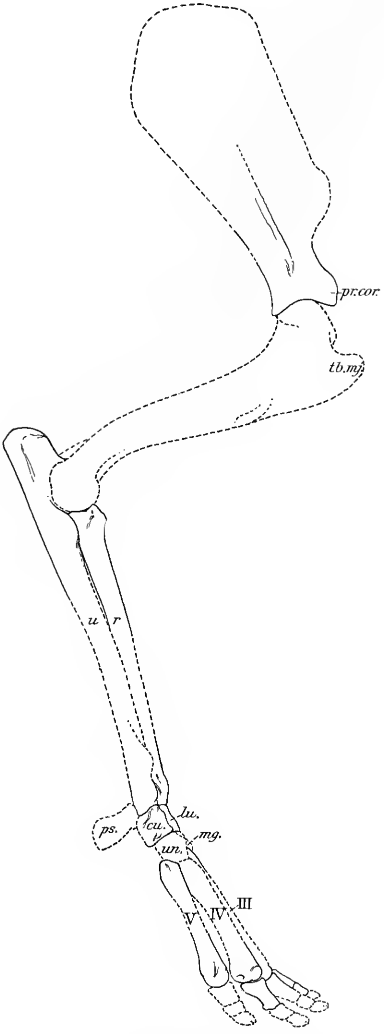

FIGURE 488.—Fore limb of *Lambdotherium popoagicum*

Am. Mus. 4880, Wind River Basin, Wyo., Wind River formation, level B. Incomplete forearm, external view. The length of the elements is conjectural. One-half natural size.

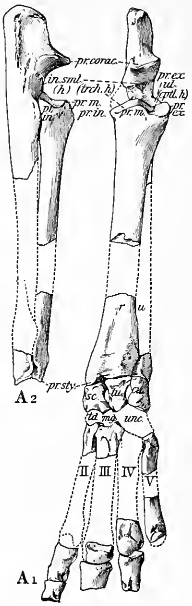

FIGURE 489.—Forearm and manus of *Lambdotherium popoagicum*

Am. Mus. 4880, Wind River Basin, Wyo., Wind River formation, level B. Incomplete left forearm and manus. The length of the radius and of the metacarpals is conjectural. A1, Front view; A2, outer side view of forearm. One-half natural size.

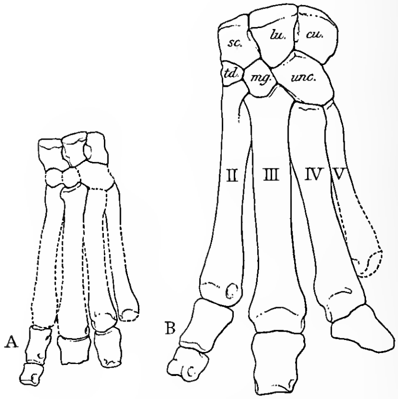

FIGURE 490.—Left manus of *Lambdotherium* and *Eotitanops*

A, *Lambdotherium* (Am. Mus. 4880); B, *Eotitanops* (Am. Mus. 296), showing the ancestral type of titanothere. The length of the metacarpals in *Lambdotherium* is conjectural. One-half natural size.

The association of limb bones with teeth of the same individual is a very rare occurrence. Thus the reference (see table on p. 585) of several of the hind feet is inferred only from the size and degree of slenderness of the limbs.

Eotitanops gregoryi Osborn

There is reason to believe that *Eotitanops gregoryi* was both small and slenderly proportioned; that *E. borealis* and *E. princeps* were still of light construction, corresponding with the delicately constructed skull of *E. borealis*; and that the little-known *E. major* was somewhat more massive in its proportions. The whole range of adaptive radiation of the limbs is subcursorial or less truly cursorial than either *Lambdotherium*, *Heptodon*, or *Eohippus*. Estimates of the heights of these animals, which, it will be recalled, were not successive but partly contemporaneous, are as follows:

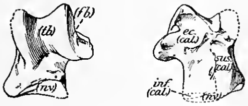

Figure 491.—Astragalus of *Lambdotherium popoagicum*

Am. Mus. 2991, Wind River Basin, Wyo., Wind River formation, level B. Left astragalus, front and rear views. Two-thirds natural size.

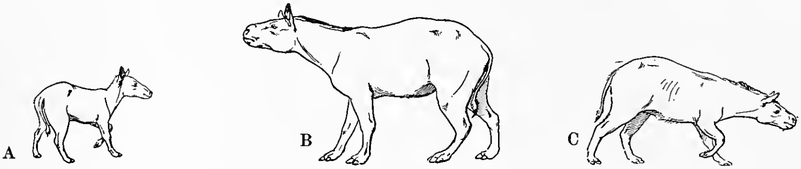

Figure 492.—Restorations of the lower Eocene titanotheres of the Wind River formation

A, *Lambdotherium popoagicum;* B, *Eotitanops princeps;* C, *Eotitanops gregoryi.* One-thirtieth natural size.

Height of Lambdotherium and Eotitanops

Type	Estimated height at shoulder	
	Millimeters	Inches
Smallest and most cursorial (Lambdotherium)	350	14
Second smallest true titanothere known (Eotitanops gregoryi)	450	18
Of intermediate size (E. princeps)	660	26
Of largest size (E. major)	800	32

Eotitanops borealis and E. princeps

The species and the mutations of *E. borealis* and *E. princeps* are so closely related that their skeletal parts may be conveniently described under a single heading.

Atlas of Eotitanops borealis

The atlas of *E. borealis* is preserved in the neotype skeleton (Am. Mus. 14887, fig. 495). In that specimen, which is the earliest known, we observe a broad resemblance to the atlas of the middle Eocene *Mesatirhinus* and of the existing *Tapirus*, both probably representing the primitive perissodactyl type. The characters are (1) centrum relatively elongate, (2) facets for axis in obliquely convergent planes, (3) vertebrarterial canal entering slightly above posterior rim of transverse process and issuing on lower median face of same. Comparison with the atlas of *Mesatirhinus* (fig. 560) indicates that we have here the ancestral titanothere type, which is highly modified in some of the progressive forms.

Cervical and dorsal vertebrae of Eotitanops princeps (type)

The two posterior cervicals (C. 6, C. 7), three scattered dorsals, and one caudal of the type (Am. Mus. 296, fig. 496) show the following characters: (1) Neck relatively short as in *Palaeosyops;* C. 1 to C. 7 estimated at 180 millimeters as compared with 320, the estimated basal length of the skull; (2) cervicals with broad depressed centra, facets oblique (length of centra, C. 6, 25 mm.; C. 7, 26); (3) three scattered dorsals laterally compressed, centra elongate, measuring, ?D. 3, 26 millimeters; ?D. 4, 25; ?D. 10, 29.

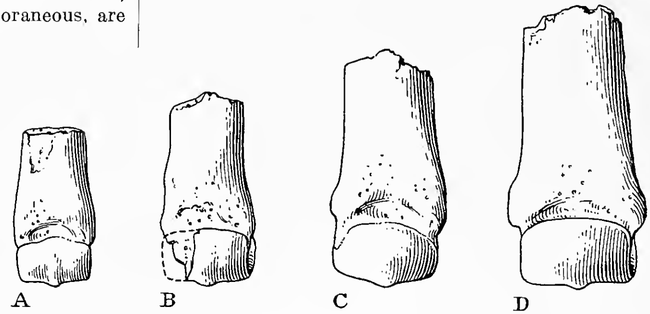

Figure 493.—Metatarsals of *Eotitanops*

Median metatarsals of *E. gregoryi* (A), *E. borealis* (B), *E. princeps* (C), *E. major* (D). Natural size.

Radius and lunar of type of Eotitanops borealis

The radius (Am. Mus. 4892) associated with the type upper molars is incomplete; it exhibits an asymmetrical proximal articular surface, and a prominent internal distal projection (styloid process) of the distal articular surface.

The lunar is a very distinctive element in the lower Eocene titanotheres, especially in the fact that in the front view it rests mainly on the unciform and retains a narrow vertical facet anteriorly for the magnum, although in the back view it rests almost equally upon the magnum and the unciform. This is an adaptation to tridactylism or functional reduction of digits I and V.

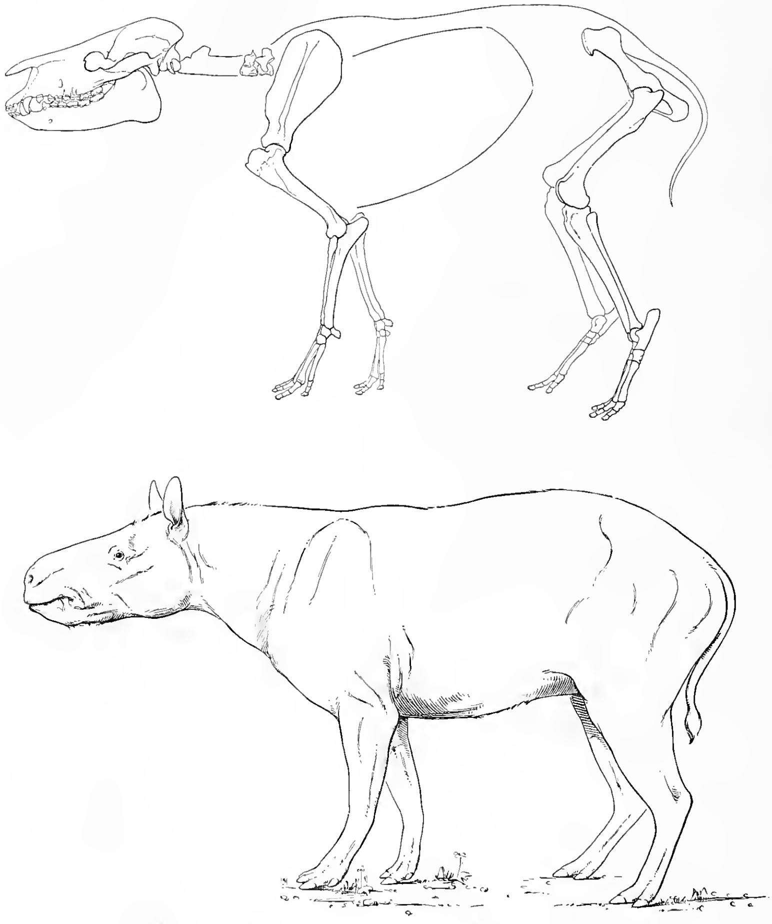

FIGURE 494.—Reconstructed skeleton and restoration of *Eotitanops borealis*

Made by E. S. Christman under direction of W. K. Gregory. About one-tenth natural size. The provisionally reconstructed skeleton is based on the following American Museum specimens from the Wind River Basin, Wyo.: No. 14887 (*E. borealis*, Dry Muddy Creek 12 miles above mouth), skull, pelvis; No. 296 (*E. princeps*), lower jaw, humerus, manus, femur; No. 14888 (*E. borealis*, Alkali Creek, Davis ranch), part of scapula, pes. Remaining parts conjectural.

Fore feet of Eotitanops princeps (type)

This type (Am. Mus. 296), originally described as *E. borealis* and now referred to the mutation *E. princeps*, is the only individual in which portions of the fore and hind limbs, vertebrae, and jaws are known, enabling us to establish the proportions.

The manus is numerically tetradactyl, but a striking feature is the slenderness of the fifth digit (Mtc V). The carpus is narrow and deep—transverse measurement 41 millimeters, vertical 34 (through cuneiform and unciform). The lunar presents anteriorly a superior transverse measurement of 17 millimeters as compared with a total vertical measurement of 22; it presents inferiorly a broad, oblique unciform facet and a narrow, nearly vertical magnum facet, similar to but relatively smaller than that seen in *Mesatirhinus megarhinus;* posteriorly it rests half on the magnum, half on the unciform. As this bone, therefore, practically distributes three-fourths of its front weight to the unciform, it exhibits an extreme displacement which appears to be a character common to the early Eocene Perissodactyla generally. Similarly the scaphoid is narrow (13 mm.) and deep anteroposteriorly (24 mm.) with a vertical measurement of 19 millimeters; it covers the entire superior face of the magnum. The magnum is a very distinctive bone as seen in front, being small, vertically extended (12 mm.) and laterally compressed (9 mm.). The unciform is a vertically deep element measuring 22 by 19 millimeters transversely. The metacarpal displacement is also extreme, Mtc II and Mtc III abutting widely against the magnum and unciform respectively. The metacarpals are distinguished by the small size of Mtc V, in which the shaft measures only 6 millimeters anteroposteriorly by 9 transversely. Mtc II has a length of 79 millimeters and a shaft diameter of 12 transverse by 7 anteroposterior, being, therefore, relatively large. Mtc III is still larger; it measures 85 millimeters vertically and 13 transversely. Mtc IV measures 73 millimeters vertically and 11 transversely. Thus Mtc IV is decidedly smaller than Mtc II. This lack of symmetry in the digits on either side of the third digit is characteristic of the early Eocene titanothere manus; it prepares the way for the secondary paraxonic condition in which Mtc II, III, IV, V become more nearly subequal.

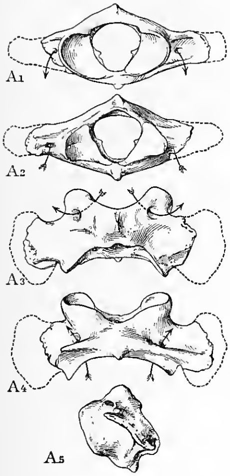

FIGURE 495.—Atlas of *Eotitanops borealis*

Am. Mus. 14887 (neotype atlas associated with skull; cf. fig. 250). A_1, Anterior or condylar surface; A_2, posterior or cervical surface; A_3, dorsal; A_4, ventral; A_5, side view. One-third natural size.

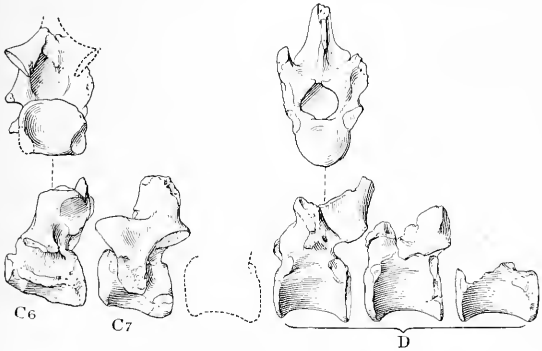

FIGURE 496.—Vertebrae of *Eotitanops princeps*

Cervical (C_6, C_7) and dorsal (D) vertebrae associated with the type lower jaw (Am. Mus. 296). One-half natural size.

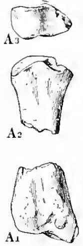

FIGURE 497.—Radius of *Eotitanops borealis*

Am. Mus. 4892, fragments of the right radius associated with the type upper teeth. A_1, Distal part; A_2, proximal part; A_3, proximal view. One-third natural size.

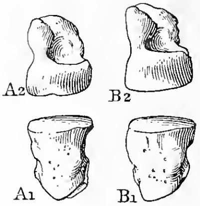

FIGURE 498.—Lunars of *Eotitanops*

Left lunar of *E. borealis* (Am. Mus. 4892, type; A_1, front view, A_2, top view) and *E. princeps* (Am. Mus. 296, type; B_1, front view, B_2, top view).

Humerus and femur

The two limb bones known, the humerus and femur, are distinguished by the lateral compression of the shafts in harmony with the compression of the manus; they indicate that *E. princeps* as compared with the middle Eocene titanotheres was narrow chested and slender limbed, that its proportions most nearly resemble those of *Mesatirhinus* of the middle Eocene, and that the corresponding elements are much more primitive.

The humerus (fig. 500) is relatively elongate, a primitive character; the great tuberosity is less developed than in more recent types. The shaft in the upper third measures 20 millimeters transversely, 35 anteroposteriorly, as

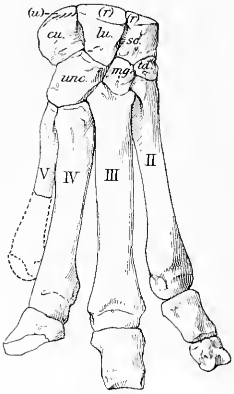

FIGURE 499.—Manus of *Eotitanops princeps*

Am. Mus. 296; Wind River Basin, Wyo.; Wind River formation, level B. Right manus of type. One-half natural size.

compared with the total length, 205; the proximal measurement across the tuberosities is 49, while the measurement of the head to the front of the great tuberosity is 67; the moderately prominent deltoid crest extends 88 millimeters below the head, and the supinator ridge rises 60 millimeters above the interior border of the radial trochlea.

The femur (fig. 500) has only partly assumed the distinctive titanothere family characters; the shaft has not yet flattened; it more closely resembles that of other subcursorial Eocene perissodactyls, such as *Hyrachyus*, rather than the mediportal middle Eocene forms. Among the middle Eocene titanotheres its closest resemblances are to the femur of *Mesatirhinus*. The head is lacking. From the great trochanter to the bottom of the internal condyle the shaft measures 250 millimeters. The bone is further distinguished from that of some of the more recent or middle Eocene titanotheres by the laterally compressed and deeply recurved great trochanter, by the very prominent second trochanter, by the lateral compression or convexity of the shaft anteriorly between the trochanters, a character which it shares with *Mesatirhinus*, by the flattening of the shaft posteriorly between and below the trochanters, by the elevated patellar facet facing anteriorly and inferiorly.

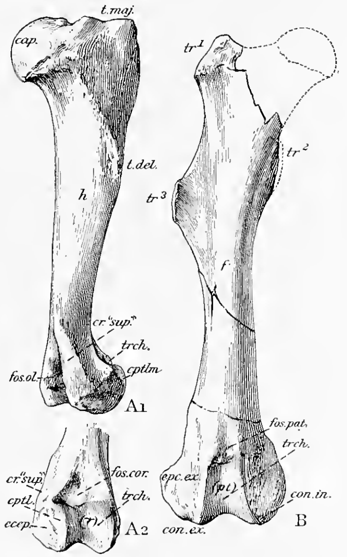

FIGURE 500.—Humerus and femur of *Eotitanops princeps*

Am. Mus. 296, Wind River. Right humerus (A_1, A_2) and femur (B) of type. One-third natural size.

Pelvis of Eotitanops borealis (neotype)

The proportions of the left innominate bone preserved in the neotype of *Eotitanops borealis* (Am. Mus. 14887) indicate a subcursorial type of pelvis, slenderly built, with the following characters: (1) Neck of ilium relatively narrow (tr. 29 mm.); (2) tuber-coxae and external border of ilium partly concave; (3) pubo-ischiadic fenestra elongate or vertically compressed; (4) plane of ilium at angle to that of pubis; (5) proportions of subcursorial rather than of mediportal type.

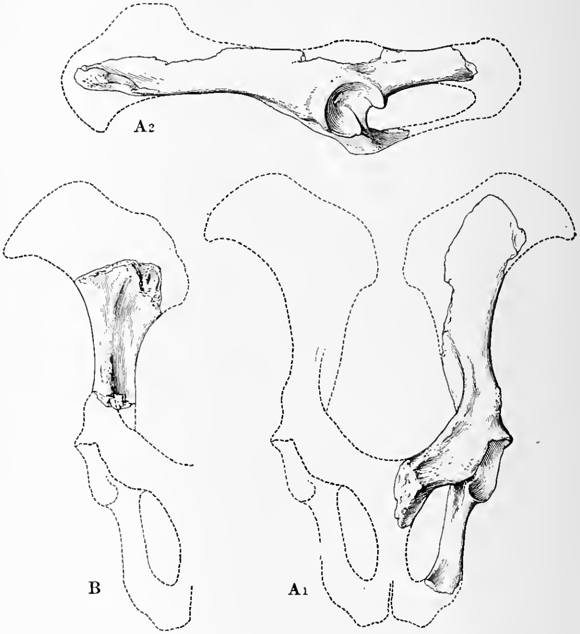

FIGURE 501.—Pelvis of *Eotitanops borealis*

A, Am. Mus. 14887 (neotype), incomplete pelvis associated with skull, ventral (A_1) and outer side (A_2) views; B, Am. Mus. 14888, fragment of left ilium, indicating a somewhat wider ilium than that in the preceding specimen, associated with teeth and other parts, ventral view. One-third natural size.

Pes of Eotitanops

The pes as compared with those of the other lower Eocene Perissodactyla (fig. 502)—namely, *Eohippus* (Equidae) and *Heptodon* (Lophiodontidae)—again exhibits *Eotitanops* as approaching the relatively large and slow-moving perissodactyls of the period, although possessing many characters in common with the contemporary lighter-limbed forms.

In the comparative outlines of Figure 502 it will be observed that *Eotitanops borealis* stands midway between *Eohippus venticolus* and *Hyrachyus agrarius*, as a transition between cursorial and mediportal adaptation. The changing proportions of the astragalus, calcaneum, and ectocuneiform are especially significant. Attention should be called to *Eotitanops* as isotridactyl—that is, the three metapodials are more uniform in size than those of either *Eohippus* or *Hyrachyus*.

Peculiar features of the *Eotitanops* pes are (1) elongate neck of astragalus; (2) a vertically elongate cuboid (inferential); (3) elevated ectocuneiform; (4) Mts III with cuboid facet narrow or wanting; (5) Mts IV with broad ectocuneiform facet; (6) metapodials keeled posteriorly; (7) proximal median phalanges relatively short; (8) inferior astragalocalcaneal facets usually small, entirely separate from sustentacular. The gradations in size of the associated or referred foot bones of *Eotitanops* are well shown in the accompanying series (fig. 503) displaying the distal ends of the metapodials. These gradations correspond broadly with those we have observed in the dental series and with the successive increases in size.

Eotitanops major Osborn

Type.—Am. Mus. 14894, a left median metatarsal (fig. 493, D); also the distal end of the right tibia.

Specific characters.—Of superior size; Mts III 104 millimeters longitudinal, 16 transverse, index 15.

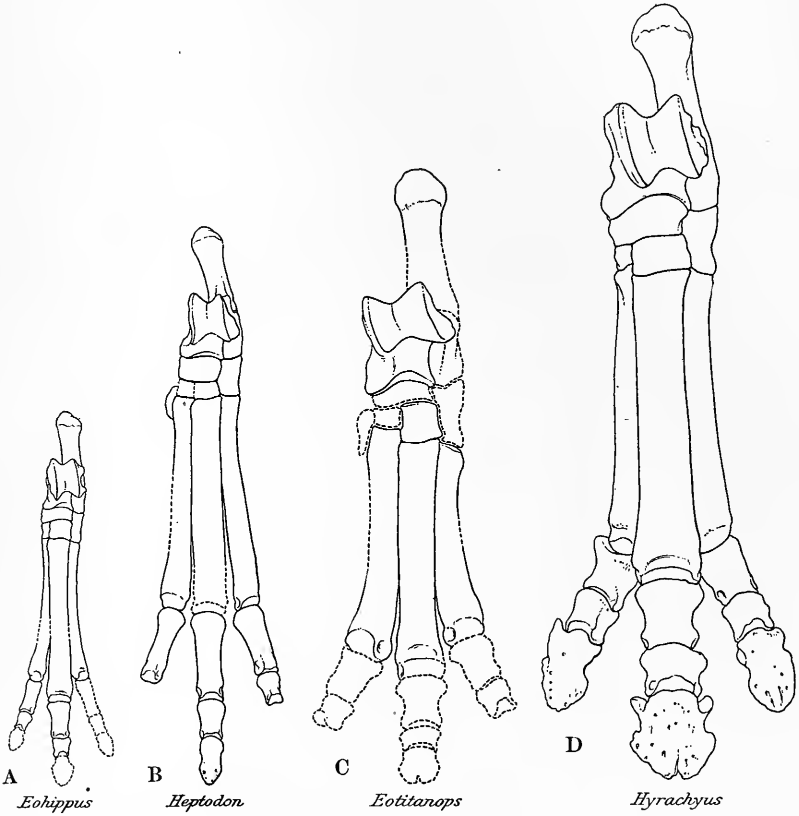

FIGURE 502.—Left pes of cursorial and subcursorial Eocene Perissodactyla

A, *Eohippus venticolus*, a primitive hippoid with narrow, slender foot and enlarged median metatarsal; B, *Heptodon calciculus*, a primitive lophiodont with side toes not reduced; C, *Eotitanops borealis*, a primitive titanothere with broader tarsals and metatarsals D, *Hyrachyus agrarius*, a primitive cursorial rhinoceros. One-half natural size.

This ill-defined species indicates the existence in Wind River time of a relatively large, slender-footed titanothere, which is possibly ancestral to some of the short-footed middle Eocene types.

A comparison of the measurements of *E. major* with those of *E. borealis*, from the Wind River formation (Am. Mus. 14888), indicates an animal of much larger size but of the same foot proportions as shown by the index. There is a small cuboidal facet.

Measurements of Eotitanops major and other species, in millimeters

	E. borealis	E. major	Mesatirhinus petersoni	Tapirus terrestris
Median metatarsal, III, length	86	104	120	114
Width of shaft	13	16	21	21
Index	15	15	17	18
Tibio-astragalar facet, transverse	21	25	------	------
Tibia, distal, transverse	26	33	------	------

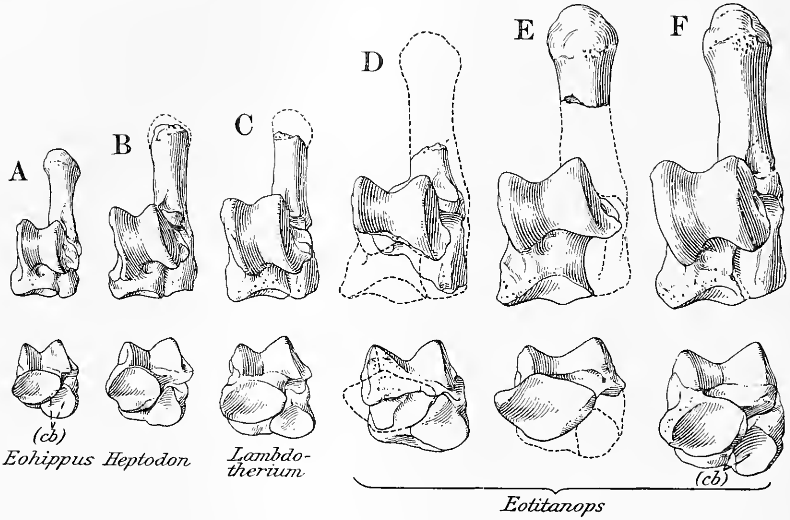

FIGURE 503.—Astragalus and calcaneum of cursorial and submediportal lower Eocene Perissodactyla

Front and distal views. A, *Eohippus* sp., with narrow astragalus (in distal view the astragalus barely touches the cuboid); B, *Heptodon calciculus;* C, *Lambdotherium popoagicum;* D, *Eotitanops gregoryi*; E, *Eotitanops borealis;* F, *Eotitanops* sp. The cuboid facet (cb) on the astragalus is better developed in the later stages, though it is still much narrower than in middle Eocene titanotheres. Two-thirds natural size.

SECTION 3. MIDDLE EOCENE GROUPS AND PHYLA

The titanotheres of middle Eocene time may be grouped as follows:

- *Palaeosyops* (subgraviportal and brachypodal).
- *Limnohyops* (mediportal and mesatipodal).
- *Manteoceras* and *Dolichorhinus* (subgraviportal and brachypodal).
- *Mesatirhinus* (mediportal and mesatipodal).

DOUBLE PARALLELISM IN THE PALAEOSYOPINE AND MANTEOCERAS-DOLICHORHINUS GROUPS

The double parallelism of graviportal and mediportal proportions is so strong that it may again be said that truly ancestral (paleotelic) characters prove to be less conspicuous, obvious, or apparent than adaptive (cenotelic) characters. We must search for real subfamily relationships in inconspicuous parts of the limbs, as in the form of the facets between the bones of the carpus and tarsus, or in the shape of the small bones on the sides of the manus, such as the trapezium and pisiform, and of the pes, such as the entocuneiform. There are also certain proportions in the respective width or depth of the elements of the carpus and tarsus which remain highly distinctive.

Every segment of each limb develops as a unit independently of every other segment. Allometric adaptation of each segment follows the general or uniform laws that are observed in other quadrupeds. These laws bring about the convergence or parallelism.

Allometric change may progress entirely independently of affiliation to remote ancestral stock or syngenesis; descendants of primitive mesatipodal forms may remain mesatipodal or may become either brachypodal or dolichopodal.

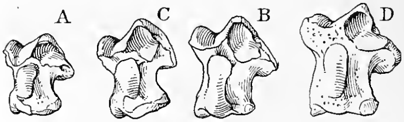

FIGURE 504.—Astragalocalcaneal facets in lower Eocene Perissodactyla

A, *Eohippus* sp.; B, *Heptodon calciculus;* C, *Systemodon primaevus;* D, *Lambdotherium popoagicum.* Two-thirds natural size.

Like brachycephaly and dolichocephaly in the skull, an allometric tendency toward brachypody or dolichopody generally proceeds to an extreme, but not invariably.

FAMILY AND SUBFAMILY CHARACTERS OF SKELETAL PARTS IN MIDDLE EOCENE TITANOTHERES

VERTEBRAE, ATLAS

Palaeosyopinae.—In the atlas of *Limnohyops*, as in *Palaeosyops*, the spinal nerves (see fig. 508, A) issue nearer the median line than in *Telmatherium* (fig. 508, B); the neural arch and the bridge over the vertebral artery are narrow. The axis is rather narrow, with a slender odontoid process. The postero-inferior tuberosity is moderately developed.

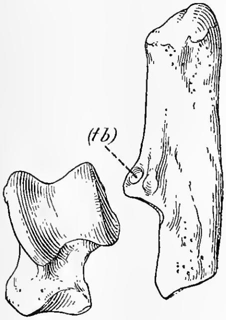

FIGURE 505.—Left astragalus and calcaneum of *Eotitanops* sp.

Am. Mus. 14895, Wind River Basin, Wyo.; Wind River formation, level B. Facet for tibia (*tb*). Two-thirds natural size.

In the atlas of *Palaeosyops* (Am. Mus. 1580, fig. 508, A), as in *Limnohyops*, the spinal nerves issue nearer the median line than in *Telmatherium*. Unlike *Limnohyops* the neural arch is broad and powerful; the inferior vertebrarterial bridge is wide; the pleurapophyses expand broadly in both directions. The postero-inferior tuberosity is moderately strong.

Telmatheriinae.—In the atlas of *Telmatherium ultimum* (Am. Mus. 2060; fig. 508, B) the spinal nerves are well separated, the pleurapophyses expand laterally but do not flare, the inferior vertebrarterial bridge is broad, but the canal itself is contracted, foreshadowing the exclusion of the vertebral artery from the canal, which is a very distinctive character of some of the Oligocene titanotheres. The occipital cotylus is broad with massive borders; the odontoid facet is exceptionally broad and open (thus distinguished from that of *Manteoceras*). The postero-inferior tuberosity is moderately strong.

Manteoceratinae.—The atlas of *Manteoceras* (Am. Mus. 12204, fig. 508, E) has the characters we should expect to find in a broad-skulled member of the Manteoceratinae: the vertebrarterial opening is very large posteriorly; the bridge is narrow (16 mm.) and rounded; the articular facets for the axis form a widely open angle; the postero-inferior tuberosity, which underlies the axis, is stout and prominent, as in the Oligocene titanotheres.

Dolichorhininae.—In *Mesatirhinus* (Am. Mus. 1523, fig. 508, C) the pleurapophyseal wings are not known; the atlas presents an approximation to that of *Dolichorhinus:* (1) the centrum is relatively elongate, (2) the spinous foramina are nearer together, (3) the vertebrarterial canal is covered by a bridge of medium length, (4) the facets for the axis are approximated and obliquely face each other, (5) the cotyli for the occipital condyles are relatively deep, (6) there is a reduced postero-inferior tuberosity.

In *Dolichorhinus* (fig. 508, D, Am. Mus. 1844, 13164 associated with skull), the body is relatively elongate, the occipital cotyli are very broad and deep, the spinous nerve notch is very deep and narrow, the pleurapophyses flare widely, the vertebraterial canal is more open than in *Telmatherium ultimum.* As in *Mesatirhinus* prominent bony processes connect the transverse ligament above the odontoid process.

Summary.—The atlas of *Palaeosyops* and *Limnohyops* conforms to the brachycephalic types of skull, that of *Dolichorhinus* to the dolichocephalic type; those of *Telmatherium* and *Manteoceras* are intermediate between these extremes.

SCAPULA

From the limited materials in our possession (*Palaeosyops*, *Dolichorhinus*, *Metarhinus*) we observe that the scapula of the Eocene titanotheres is subject to wide adaptive range from the more elongate mediportal type of the supposed *Metarhinus* to the broader subgraviportal type of *Palaeosyops.* The scapula is, however, quite distinctive in its family or syngenetic form as compared with that of other Perissodactyla, being characterized as follows: (1) a vertically elongated supraspinous fossa, which is equally broad above and below, giving a relatively straight anterior border; (2) a relatively large infraspinous fossa of subtriangular form, in which the border rapidly contracts toward the neck—on this border is a distinct "angle" which becomes sharply marked in later types; (3) a broad, short neck, or collum scapulae. This is the graviportal prototype from which the scapula of the heavy Oligocene titanotheres is readily derived. On the whole, this middle Eocene scapula is analogous to that of the mediportal *Tapirus*, but it is distinctly tending toward and even modified in the graviportal direction.

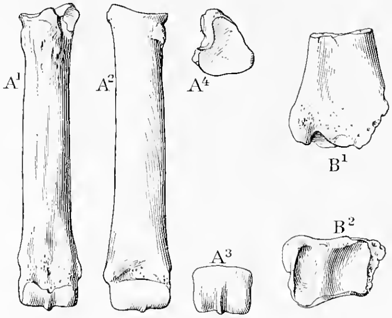

FIGURE 506.—Metatarsal and tibia of *Eotitanops major*

Am. Mus. 14894 (type), Wind River Basin, Wyo.; level B. Median metatarsal: Back (A^1), front (A^2), distal (A^3), and proximal (A^4) views. Distal end of left tibia: Front (B^1) and distal (B^2) views. One-half natural size.

Only three scapulae are known, as follows: (1) Mediportal, *Dolichorhinus longiceps* (figs. 509, 582); (2) subgraviportal, *Palaeosyops* (figs. 509, 545), with height 345 millimeters, breadth 260; (3) supposed *Metarhinus* (figs. 509, 576, Am. Mus. 1873, Uinta B), elongate compared with that of *Palaeosyops*—namely, length 265 millimeters, breadth 165 (estimated). The supposed *Metarhinus* may be taken as the mediportal type; it is less expanded toward the upper border.

FIGURE 507.—Restoration of *Eotitanops borealis*

Modeled by E. S. Christman. About one-twelfth natural size

In *Mesatirhinus* we should expect to find the scapula proportioned somewhat like that in *Tapirus;* unfortunately this scapula is unknown.

HUMERUS

We have observed (fig. 510) that the characters of the humerus of the titanothere family are rapidly intensified by adaptation. Each genus exhibits distinctive ratios of length of the humerus and radius, as shown in the accompanying table.

Measurements of fore limb of certain titanotheres compared with tapirs, in millimeters

	Humerus	Radius	Radio-humeral ratio	Mtc III	Metacarpo-humeral ratio
Tapirus terrestris	205	177	86	106	50
Tapirus indicus	250	228	91	120	48
Eotitanops princeps (borealis), Am. Mus. 296	203			85	41
Limnohyops? monoconus, Am. Mus. 11689	293	228	77	109	37
Palaeosyops leidyi, Am. Mus. 1544	325	235	72	113?	34?
Palaeosyops copei?, Am. Mus. 12205	340?	237	69?	106	30
Dolichorhinus hyognathus, Am. Mus. 13164	[a] 315	[a] 284	81?		
Menodus trigonoceras, Munich Mus	620	520	83	240	38
Brontops robustus, Yale Mus. 12048 (type)	608	504	82	230	37
Brontops sp., Am. Mus. 518	528	478	90	214	40

[a] Estimated.

It will be observed that in *Palaeosyops* and *Dolichorhinus* the humerus is much longer than the radius. These are subgraviportal types, but even in the mediportal *Limnohyops* the humerus is somewhat longer than the radius.

It is, however, a very marked distinction of the titanotheres, already pointed out, that as they become heavier the radius elongates more rapidly than the humerus. Thus the radiohumeral ratio rises from 72 in *Palaeosyops leidyi* to 90 in *Brontotherium gigas.*

The rugose muscular attachments of the humerus rapidly assume progressive graviportal characters, which even in the lower Bridger enable us to distinguish readily the titanothere humerus. These characters are strengthened in the Oligocene titanotheres and were undoubtedly correlated with certain distinctive motions of the fore limbs as follows: (*a*) The great tuberosity of the humerus expands into a broad, elevated plate; the deltoid crest descends into a distinct tuberosity; the supinator crest secondarily increases in size and prominence. Of the above characters the platelike great tuberosity (fig. 510) is the most distinctive. (*b*) Distally the radio-ulnar articulation (rotula and capitellum) is decidedly asymmetric; this asymmetry persists in the titanotheres; its significance is fully explained on page 602. (*c*) The ectocondylar or supinator crest is already quite prominent. (*d*) The entocondyle is less prominent.

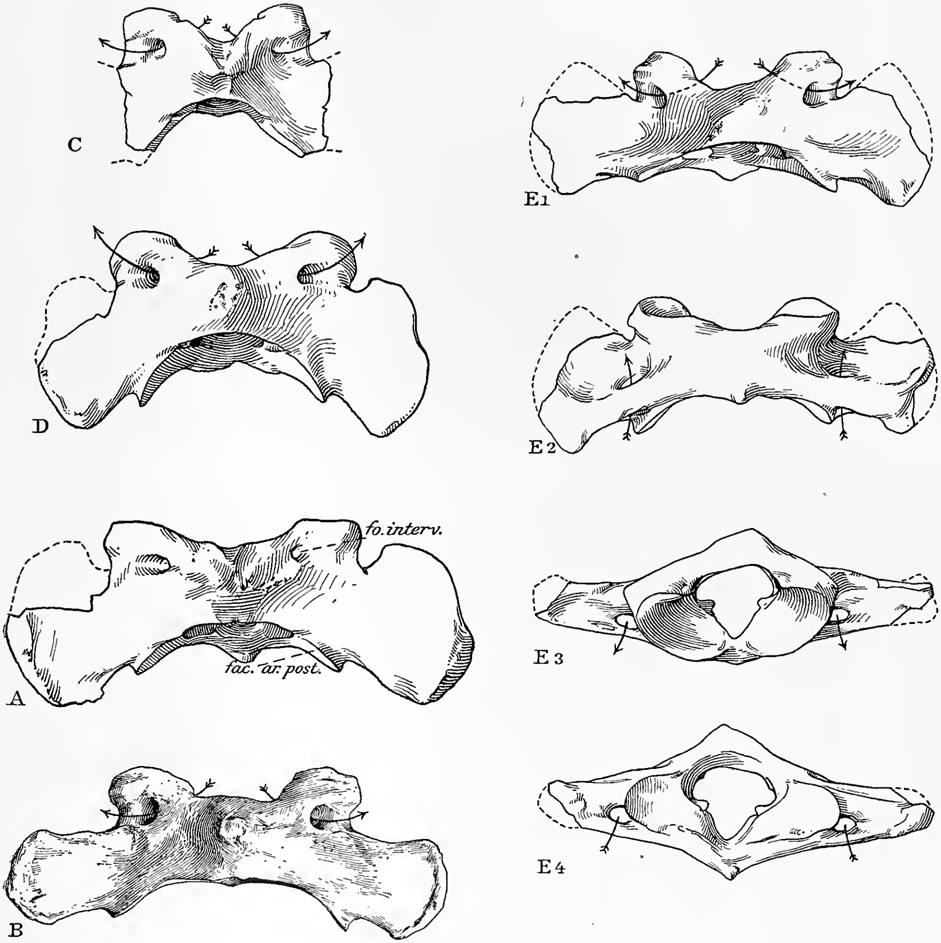

FIGURE 508.—Atlas of Eocene titanotheres

A, *Palaeosyops robustus*, Am. Mus. 1580, upper Bridger; B, *Telmatherium ultimum*, Am. Mus. 2060 (type), Uinta C; C, *Mesatirhinus megarhinus*, Am. Mus. 1523, upper Bridger; D, *Dolichorhinus* sp., Am. Mus. 1844, Uinta C. A–D, Dorsal views. E, *Manteoceras manteoceras*, Am. Mus. 12204, upper Bridger: E_1, Dorsal view; E_2, ventral view; E_3, anterior view; E_4, posterior view. One-third natural size. The arrows indicate the course of the first spinal nerve and vertebral artery.

Primitively (*Eotitanops borealis*) the deltoid tuberosity of the humerus is near the upper part of the shaft; secondarily it is extended downward. Primitively the great tuberosity is a sessile prominence divided by a shallow median notch; secondarily it becomes very prominent and platelike and is divided by a very deep median notch. Primitively the ectocondylar crest, which is small, is distinctly defined, rising somewhat on the shaft (*Eotitanops*); secondarily it rises and widely expands. A distinctive feature of the humerus as compared with that of the Hyracodontidae and Amynodontidae is the prominent rugosity (fig. 500) on the inner side of the shaft for the tendon of the latissimus dorsi muscle.

Figure 672 gives a comparison of the humeroradial articulations of *Tapirus*, *Palaeosyops*, and *Rhinoceros*. We observe that the asymmetry of the trochlea and capitellum persists in graviportal types, whereas the cursorial *Equus* acquires a more symmetrical form.

Although this titanothere elbow joint has points of similarity with that of the tapirs, paleotheres, and other primitive perissodactyls, the form as a whole appears to be somewhat distinctive. Viewed from below, the trochlea is much broader than the capitellum; the trochlea is nearly plane, the capitellum sharply convex. In the Oligocene titanotheres (fig. 510) the capitellar area widens out so that there is less marked asymmetry with the trochlea.

Correlated with this is the asymmetry of the upper end of the radius as seen from the front, the trochlear portion being depressed, the capitellar portion elevated. A series of comparative views of the proximal end of the radius in several genera (fig. 511) brings this point out clearly.

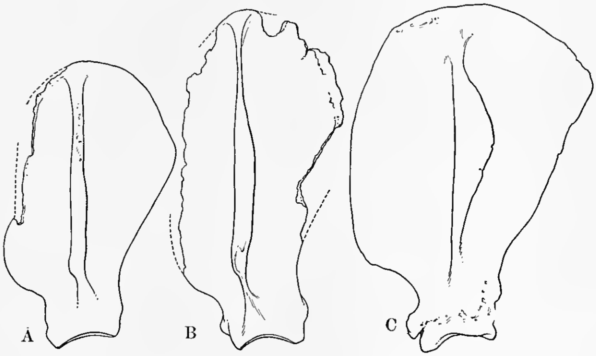

FIGURE 509.—Types of scapula in middle Eocene titanotheres

A, *Metarhinus*, Am. Mus. 1873 (mediportal); B, *Dolichorhinus* sp., Am. Mus. 1833 (mediportal); C, *Palaeosyops robustus*, Am. Mus. 1580 (subgraviportal).

In the primitive ulna (*Lambdotherium*) the olecranon is decidedly erect and truncate at the top; it becomes more depressed and pointed in the progressive weight-bearing forms. In *Limnohyops* and *Mesatirhinus* is seen an intermediate mediportal condition (fig. 511). In *Mesatirhinus* it is rounded and moderately rugose at the extremity; in *Limnohyops* more heavily rugose. In the graviportal forms (*Palaeosyops*, fig. 511) it becomes pointed and heavily rugose at the extremity, prophetic of the condition in the heavy Oligocene titanotheres. In *Dolichorhinus* it is incurved, abbreviated, and depressed. The shaft of the ulna is of the flattened, trihedral form. This olecranon process is cleft by a faint groove superiorly, which becomes very distinct in the Oligocene forms.

MANUS

Evolution of the manus.—The ancestral form of manus and pes is, as shown above, subcursorial. The principles of convergent mediportal and graviportal adaptation, observed in the arches and limbs, also dominate the foot structure; the divergence, in fact, is still more conspicuous. On the principles set forth above (pp. 583–584), vertical elongation of every element of the carpus and tarsus as a rule points to speed, while depression and transverse extension point to weight.

The general trend of the evolution of the manus and pes in the titanotheres is from the relatively high and narrow subcursorial type (*Eotitanops*) through an intermediate or mediportal type (*Mesatirhinus*) into a relatively broad and low graviportal type (*Palaeosyops*).

From the conspicuous adaptive divergences either in the mediportal or the graviportal direction, it is first necessary to select the relatively obscure family or universal characters of the manus and pes. The digital formula is that of all primitive perissodactyls. The manus has four digits (mesaxonic to subparaxonic); the pes has three digits (mesaxonic). One peculiar feature of the titanotheres is that (as in the amynodont rhinoceroses alone among all other perissodactyls) the primitive four digits persist in the manus. The pes in the titanotheres, as in all other perissodactyls, because it is connected with the chief locomotor organ, the hind limb, is more reduced in size and more progressive in form than the manus.

Primitive manus.—The manus of the earliest types known (*Lambdotherium*, *Eotitanops*) is mesaxonic—that is, the third, median digit (D. III) is distinctly the largest, as in *Eohippus*, *Heptodon*, and *Lophiodon*. The retention and expansion of the fifth digit (D. V) to share the weight appears to be partly secondary.

Adaptive manus.—The titanothere family characters may be summed up as follows: (1) Persistent tetradactylism, with considerable adaptive divergence among the genera in the relative length of the four digits, especially of D. V, which is relatively shorter in some forms (*Palaeosyops*, *Limnohyops*) and longer in others (*Mesatirhinus*, *Manteoceras*); (2) in the front view of the metacarpals, Mtc II, while supporting mainly the trapezoid, articulates broadly against the magnum; Mtc III, while mainly supporting the magnum, also articulates broadly against the unciform; (3) the trapezium is likewise present (in Eocene time) and articulates with the side of the trapezoid, also with Mtc III, and often (especially in Manteoceratinae) with the scaphoid; (4) the proximal phalanges are of

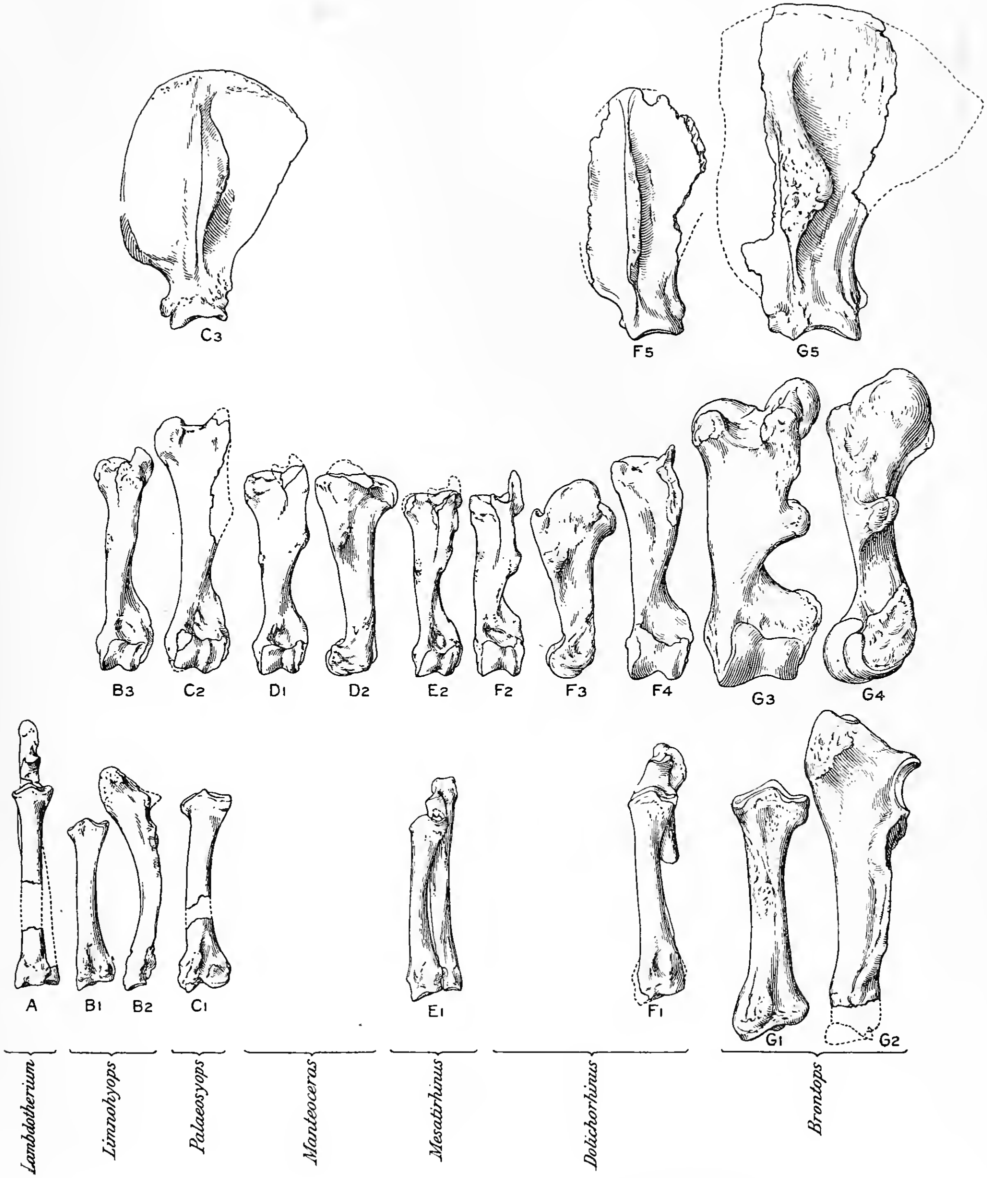

FIGURE 510.—Types of fore limb in Eocene and Oligocene titanotheres

Subcursorial: A, *Lambdotherium;* slightly less than one-third natural size. Mediportal: B_1–B_3, *Limnohyops;* E_1, E_2, *Mesatirhinus;* slightly less than one-eighth natural size. Subgraviportal: C_1–C_3, *Palaeosyops;* D_1, D_2, *Manteoceras;* F_1–F_5, *Dolichorhinus;* slightly less than one-eighth natural size. Graviportal: G_1–G_5, *Brontops;* slightly less than one-twelfth natural size.

relatively broad type (mediportal and graviportal), never elongate (cursorial) as in the primitive horses; (5) the median phalanges are short; (6) the distal phalanges expand at the extremities and exhibit deep median clefts, indicating the attachment of broad horny hoofs like those of the rhinoceroses rather than narrow or appressed hoofs of the equine or hyracodont type. The phalanges differ considerably in length and in breadth in different genera.

Manus of the palaeosyopine group.—The palaeosyopine group includes three genera, *Telmatherium*, *Limnohyops*, *Palaeosyops;* the manus of the last two named is known. Of these *Limnohyops* is more primitive and mediportal in its proportions and articulations and is thus analogous to the primitive and mediportal *Mesatirhinus* of the Dolichorhininae. Figure 512 shows how similar these two forms are, yet a very close examination of the details of structure in the carpals and tarsals proves beyond question that they belong in separate subfamilies and diverged from each other at a remote period.

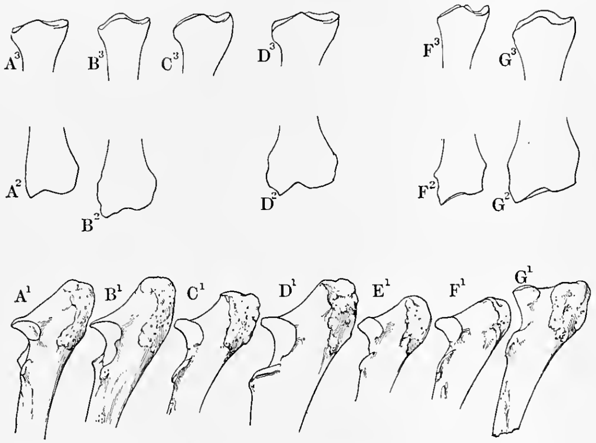

FIGURE 511.—Characteristic details of radius and ulna in middle and upper Eocene titanotheres

Lower row, proximal end of left ulna, outer view. Middle row, distal end of left radius, front view. Upper row, proximal end of left radius, front view. A, *Limnohyops monoconus*?; B, *Limnohyops laticeps;* C, *Palaeosyops* cf. *P. leidyi;* D, *Palaeosyops robustus;* E, F, *Mesatirhinus petersoni;* G, *Dolichorhinus hyognathus.* One-sixth natural size.

The following dry descriptive details are of philosophic interest to the comparative anatomist because they demonstrate the assertion made above that we can discover a distinct syngenetic (common origin) character in each element of the carpus when closely examined and compared. They prove that the relatively light-limbed and more rapidly moving *Limnohyops* retains more of the ancestral form and proportion (thus analogous to *Mesatirhinus*) while the short-footed *Palaeosyops* diverges most widely in the graviportal direction (thus analogous to *Manteoceras*).

Limnohyops characters.—Of mediportal proportions; mesatipodal; carpus more elevated and compressed than in the subgraviportal *Palaeosyops*; metacarpals and digits relatively longer than in *Palaeosyops* but relatively broader than in *Mesatirhinus;* digit V rather short; scaphoid and cuneiform relatively high; lunar high, resting mainly on unciform, obliquely on magnum; magnum high, laterally compressed; second phalanges abbreviated; terminal phalanges cleft and spreading distally as in *Mesatirhinus.*

There are two subtypes of *Palaeosyops* manus. (See figs. 537, 549.)

Palaeosyops characters (Am. Mus. 12205).—Of graviportal proportions; brachypodal; carpus broad but less depressed than in *Palaeosyops ?robustus;* digits more abbreviated and spreading than in *Palaeosyops leidyi*; trapezium large, with no scaphoid articulation apparent; magnum relatively high, rather broad, with but five distinct faceted angles; the lunar facet in front view is continuous with the unciform; terminal phalanges irregular, rounded distally.

Manus of the Manteoceras-Dolichorhinus group.—In this subfamily *Mesatirhinus* is the primitive and mediportal type analogous to *Tapirus* and *Limnohyops*, while *Manteoceras* is the modified subgraviportal type analogous to *Palaeosyops*, although less extreme. Close comparison of the carpals of *Mesatirhinus* and *Dolichorhinus* demonstrates the manteoceratine affinity and divergence from the palaeosyopine type.

Mesatirhinus.—A mediportal carpus or relatively high, narrow fore foot, all the elements being vertically elongated but less so than in *Tapirus terrestris.* Mesatipodal; total breadth of carpus of a typical specimen (*M. megarhinus*) 65 millimeters, total depth 43; scaphoid less deep anteroposteriorly than in *Palaeosyops*, appearing relatively high and narrow; lunar very high, with oblique magnum facet, thus in front view bearing principally on unciform; trapezium narrow, with scaphoid, trapezoid, and Mtc II facets; trapezoid relatively large; magnum high, relatively narrow, and subquadrate, with high facets, hook of magnum more symmetrical, broadly spatulate, with deep median groove; unciform with its longest diameter oblique instead of horizontal, as in *Palaeosyops*; Mtc V elongate, manus consequently more tetradactyl; metacarpals decidedly slender but less so than in *Tapirus terrestris*; distal phalanges elongate, cleft, and broadly expanded distally.

Dolichorhinus.—The manus of *Dolichorhinus* represents a sub-brachypodal specialization of the *Mesatirhinus* type, paralleling that of *Manteoceras.* (See p. 606.)

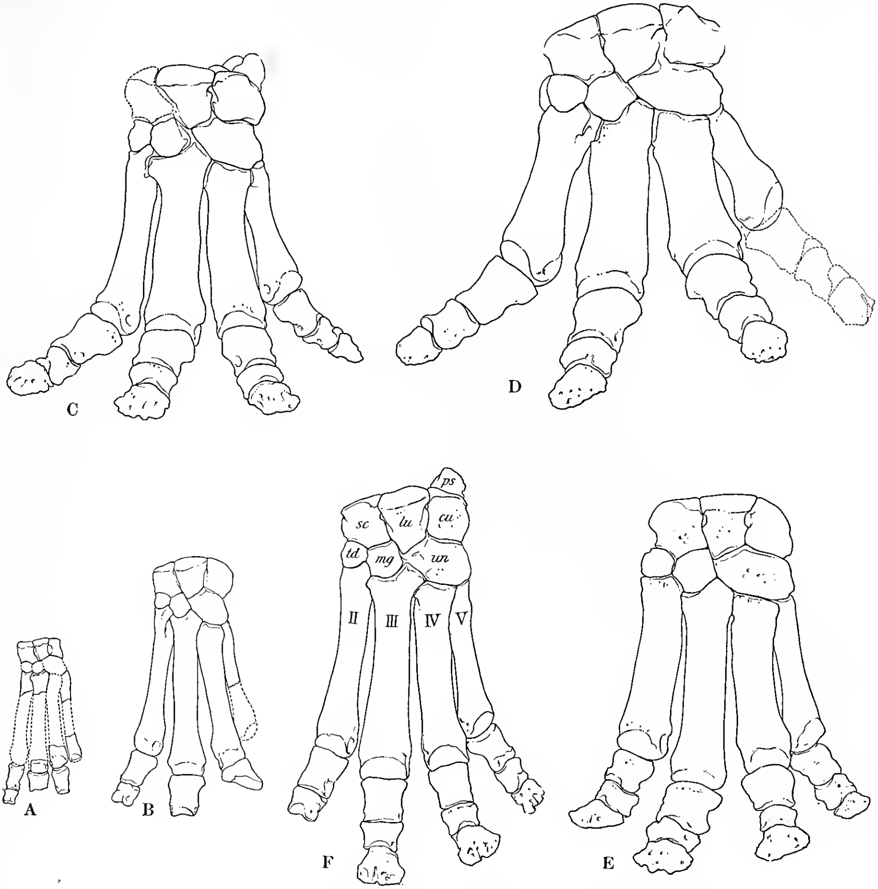

FIGURE 512.—Manus of lower and middle Eocene titanotheres

A, *Lambdotherium popoagicum;* B, *Eotitanops princeps;* C, *Limnohyops monoconus;* D, *Palaeosyops leidyi;* E, *Manteoceras manteoceras;* F, *Mesatirhinus petersoni.* One-third natural size.

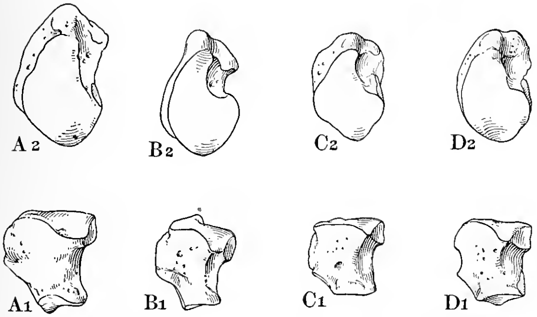

FIGURE 513.—Comparison of the right scaphoid in middle Eocene titanotheres

Lower row, front view; upper row, top view. A, *Palaeosyops leidyi;* B, *Limnohyops monoconus;* C, *Mesatirhinus petersoni;* D, *Manteoceras manteoceras.* One-half natural size.

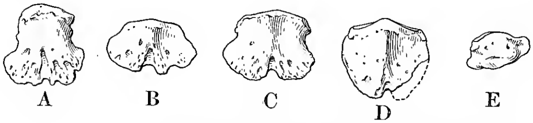

FIGURE 514.—Terminal phalanges of the manus in middle Eocene titanotheres and amynodonts

Generic differences in the terminal (ungual) phalanges of the third digit. A, *Mesatirhinus petersoni?;* B, *Manteoceras manteoceras;* C, *Limnohyops monoconus?;* D, *Palaeosyops* sp.; E, *Amynodon* sp. One-half natural size.

Manteoceras.—A graviportal, or short, broad foot; digits and metacarpals, however, not spreading apart distally as in *Palaeosyops.* Brachypodal; detailed proportions and facets of carpals resembling those of *Mesatirhinus* rather than those of the Palaeosyopinae; lunar high, resting chiefly on unciform with a very oblique magnum facet; magnum relatively high and narrow, with five facets in front view, acuminate above, with lunar unciform facet continuous, forming a broad, flat face, subquadrate as seen from in front, hook of magnum more symmetrical, broadly spatulate; second phalanges abbreviate; terminal phalanges distinctly abbreviate, expanded distally, with a pronounced median groove. From the above description it appears that *Manteoceras* resembles *Mesatirhinus* in the proportion of the carpals. It differs widely in the abbreviation of the metacarpals and especially of the terminal phalanges.

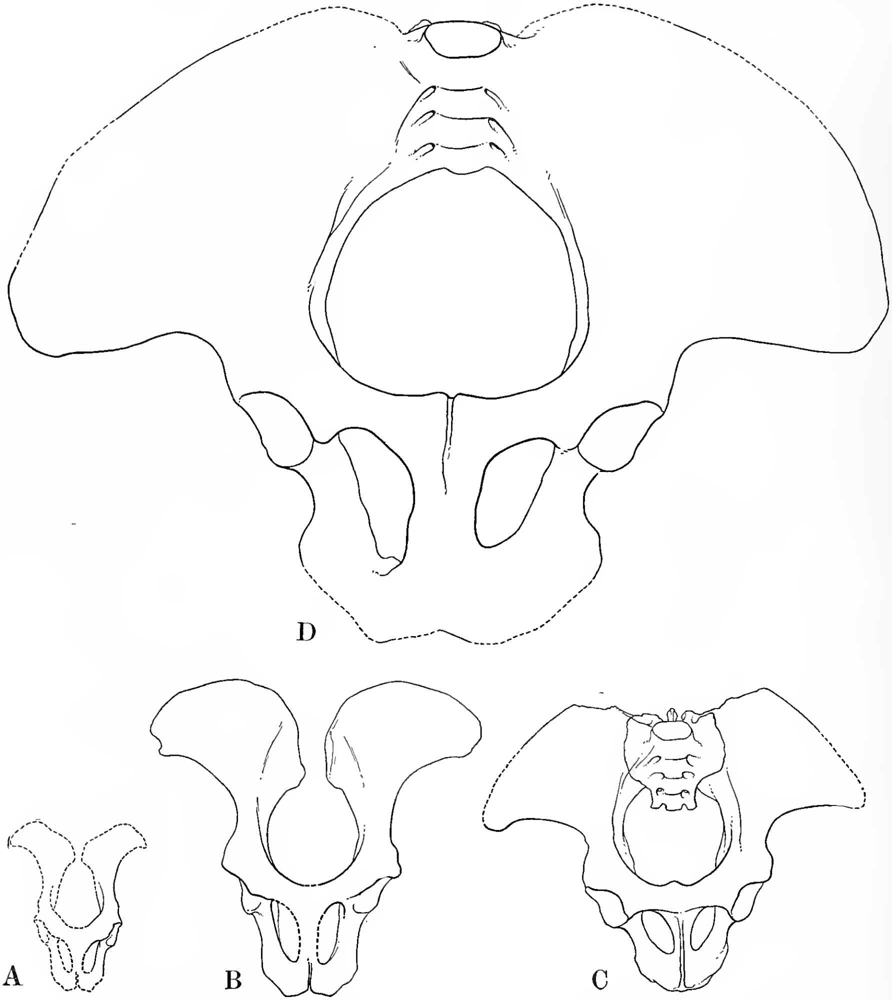

FIGURE 515.—Progressive graviportal adaptation in the pelvis of Eocene and Oligocene titanotheres

A, *Eotitanops borealis* (subcursorial); B, *Palaeosyops major* (mediportal); C, *Manteoceras* sp. (subgraviportal); D, *Brontotherium* sp. (graviportal). One-eighth natural size.

Summary of contrasting characters of the carpus and manus in middle Eocene titanotheres

Palaeosyopine group.	Manteoceras-Dolichorhinus group
Typical genera, Palaeosyops (subgraviportal), Limnohyops (mediportal)	Typical genera, Mesatirhinus (mediportal), Manteoceras, Dolichorhinus (subgraviportal)
1. Carpus broad, composed of relatively broad, low, and deep (anteroposteriorly) elements, correlated with broader spreading digits and spreading or rounded hoofs.	1. Carpus composed of relatively high elements, less deep anteroposteriorly, hoofs truncate and spreading distally.
2. Scaphoid broad, deep anteroposteriorly, outer lateral face prolonged backward, radial facet rounded.	2. Scaphoid relatively high, more shallow anteroposteriorly, radial facet flat.
	2a. Lunar high and laterally compressed, resting chiefly on unciform.
3. Cuneiform (Palaeosyops) broad, chief diameter horizontal.	3. Cuneiform relatively high and laterally compressed.
4. Trapezium large, articulating with trapezoid, with Mtc II, but not generally with the scaphoid.	4. Trapezium large and deep vertically, articulating with trapezoid, with Mtc II, also with scaphoid (Mesatirhinus).
5. Trapezoid relatively large, subquadrate in form in front view.	5. Trapezoid relatively small.
6. Magnum large, with five to six facets, hook of magnum strongly asymmetrical, pointed.	6. Magnum high, relatively narrow, subquadrate, with five facets, hook of magnum more symmetrical.
7. Unciform more horizontal.	7. Unciform more oblique.
8. Metacarpals more mesaxonic—that is, Mtc III relatively elongate; Mtc V abbreviate.	8. Metacarpals more paraxonic—that is, Mtc V well developed and podium more tetradactyl.
9. Metacarpals with deep proximal facets for the carpals at the extremities.	9. Metacarpals with proximal facets for carpals truncated rather than deep, with distal facets less globose.
10. End phalanges rounded or spreading at the extremities.	10. End phalanges broadly expanded distally.

PELVIS

The pelvis of the middle and later Eocene titanotheres has passed beyond the mediportal *Tapirus* stage and is in a stage between the subgraviportal and graviportal, conforming with the principles of the evolution of the pelvis set forth in Chapter IX (pp. 743–745). Although associated and complete pelves are rare, the material available throws a great deal of light on the characteristic form and development of this important organ.

The chief materials and the geologic horizons at which they were collected are as follows:

Eotitanops borealis, Am. Mus. 14887 (fig. 501): Wind River A or B.
Limnohyops laticeps, Yale Mus. 11000 (fig. 532): Bridger C or D.
Limnohyops? sp., Am. Mus. 2348[1] (fig. 538): Washakie A.
Palaeosyops ?robustus, Princeton Mus. 10232 (fig. 539): Bridger C or D.
Palaeosyops ?major, Am. Mus. 13116 (fig. 533): Bridger B.
?Manteoceras manteoceras, Am. Mus. 2358 (fig. 555): Washakie B.
Dolichorhinus hyognathus, Am. Mus. 1843 (figs. 579, 580): Uinta B.
?Dolichorhinus ?hyognathus, Am. Mus. 1860: Uinta B.

Of the above the pelvis of *Eotitanops* (fig. 501) shows a mingling of subcursorial and prophetic mediportal characters. The complete associated pelvis of the type of *Limnohyops laticeps* in the Yale collection belongs to a juvenile individual, which may partly explain the fact that it is in a more primitive stage of development than any other middle Eocene titanothere pelvis known; the superior border of the iliac crest is partly thin and concave, representing the crista iliaca between the rugose borders of the tuber sacrale and tuber coxae.

A similar pelvis in a somewhat more advanced stage (fig. 538) is that from Washakie A (Am. Mus. 2348), which has been mounted with the skeleton of *Palaeosyops leidyi* in the American Museum. This represents a slightly more advanced stage, which nevertheless retains the thin, slightly concave crista iliaca between the rugose areas of the tuber coxae and tuber sacrale.

A pelvis certainly belonging to *Palaeosyops*, from Bridger B (Am. Mus. 13116, fig. 533), is distinguished by the elongate os innominatum and by the uniformly convex superior crest of the ilium.

Of this type also is the pelvis (fig. 539) in the Princeton Museum (No. 10232), attributable to *P. leidyi* or *P. robustus*, distinguished by a much broader ilium, with a uniformly convex superior border.

Referable to *Manteoceras* is the finely preserved pelvis (Am. Mus. 2358) from Washakie A or B, characterized by very great iliac breadth (fig. 555) and the broad expansion of the supra-iliac border. This is an advanced subgraviportal type, prophetic of the form of the pelvis in the Oligocene titanotheres.

The pelvis associated with *Dolichorhinus hyognathus* from Uinta B (Am. Mus. 1843) is again elongate (fig. 580), with a uniformly convex superior border of the ilium.

The comparative measurements of these pelves are shown in the accompanying table.

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[1] Specimen mounted with skeleton of *P. leidyi* in American Museum.

Measurements of pelves of Eocene titanotheres compared with tapirs, in millimeters

	Tapirus indicus	?Palaeosyops, Princeton Mus. 10232	Palaeosyops major, Am. Mus. 13116	Limnohyops laticeps, Yale Mus. 11000 (type)	Limnohyops, Am. Mus. 2348	?Manteoceras, Am. Mus. 2358	Dolichorhinus, Am. Mus. 1843	Dolichorhinus, Am. Mus. 1860	?Diplacodon elatus	?Protitanotherium
Total length of os innominatum	408	415	444	--------	440	430	--------	470	610	--------
Total length of ilium	258	270	285	--------	290	285	--------	300	--------	335
Total length of ischium	169	190	168	--------	175	140	--------	175	--------	--------
Total width of pelvis across ilia	430	--------	--------	406	500	530	--------	--------	--------	[a]665
Total width of ilium (superior border)	230	265	235	203	280	290	253	--------	--------	340
Anteroposterior pubo-ischiadic symphysis	100	--------	--------	--------	175	185	--------	--------	--------	--------
Total breadth across ischiadic tuberosities	--------	--------	--------	--------	--------	143	--------	--------	--------	--------
Breadth of peduncle of ilium	40	60	53	--------	73	70	--------	--------	--------	65

[a] Estimated.

A comparison of these figures and measurements demonstrates that the main features of the progressive evolution of the titanothere pelvis in graviportal adaptation are the following:

1. Relative expansion of the iliac crest.
2. Reduction of the thin crista iliaca and expansion of the rugose superior borders of the ilium.
3. Relative abbreviation of the os innominatum.
4. Uniform rugose convexity of the superior crest of the ilium.

The above are all progressive graviportal characters. It is demonstrated that even as far back as middle Eocene time the early weight-bearing or subgraviportal type of ilium was well established among the titanotheres, and that from the evidence afforded by the ilium alone these animals were heavier bodied and slower moving of limb than the modern tapirs. Our analysis (see below) of the graviportal adaptation in the ilium makes entirely clear the general functional or adaptive stages through which the pelvis of these Eocene titanotheres is passing. We observe that the relatively elongate ilium of *Limnohyops* is in the first stage, that *Palaeosyops* with its shorter ilium and heavier body has passed beyond this, and that *Manteoceras* possesses the fully developed graviportal type of ilium.

The principal family characters of the pelvis appear to be as follows: (1) The metapophyses of the posterior lumbar vertebrae articulate with the anterior border of the ilium, as in *Equus;* (2) in *Limnohyops* the first and second and half of the third sacral vertebrae expand to articulate with the ilium, whereas in *Tapirus* only one and half of another unite with the ilium; similarly in *Manteoceras* three sacrals enter into the iliac union; (3) the ilium is much longer than the ischium; (4) the superior border of the ilium is slightly indented (*Limnohyops*) or uniformly convex (*Palaeosyops*, *Manteoceras*); (5) the peduncle of the ilium is broad and short, its dorsal border presenting a sharp ridge; (6) the ischia are not separated or cleft posteriorly as in the Amynodontidae, Rhinocerotidae, and other Perissodactyla; (7) the suprasacral area (tuber sacrale) progressively expands; (8) the rugose borders (tuber sacrale and tuber coxae) expand and unite to obliterate the thin intermediate crista iliaca.

ILIUM

The ilium of Eocene titanotheres exhibits a considerable range of generic characters, as follows:

ILIUM OF THE PALAEOSYOPINE GROUP

Limnohyops.—Ilia moderately expanded, with indented superior border.

Palaeosyops.—Os innominatum elongate, iliac crest uniformly convex, expanding into a broad border in Bridger C or D stages.

ILIUM OF THE MANTEOCERAS-DOLICHORHINUS GROUP

Mesatirhinus.—The fragmentary specimen Am. Mus. 1571 exhibits a slender peduncle of the ischium. The ilium is unknown.

Manteoceras.—The pelvis provisionally associated with this genus exhibits a very broad, uniformly convex superior border of the ilium; os innominatum relatively broadening and abbreviated.

Dolichorhinus.—Superior borders of ilium moderately expanded or narrower than in the supposed *Manteoceras;* os innominatum moderately elongate.

The detailed description of these various types of pelves is given in the succeeding section of this memoir.

FEMUR

Materials.—A very large number of femora are preserved, many of which have the tibiae associated. On these it is possible to establish the femorotibial type of the titanotheres, which from the beginning to the end of their evolution is very distinctive. The femur of even the ancestral *Eotitanops* (fig. 500) displays some of the characteristic titanothere features, although it retains the flexed knee, distal patella, and many of the proportions and characters of its primitive subcursorial ancestors.

The femora of the middle Eocene palaeosyopines (*Palaeosyops*, *Limnohyops*) and manteoceratines (*Mesatirhinus*, *Manteoceras*) are seen from Figure 516 to display many special titanothere characters in common.

The chief characters of the femur of the titanotheres are the following, the comparisons shown being made chiefly with the femur of the contemporary Amynodontidae, which are animals of the same size.

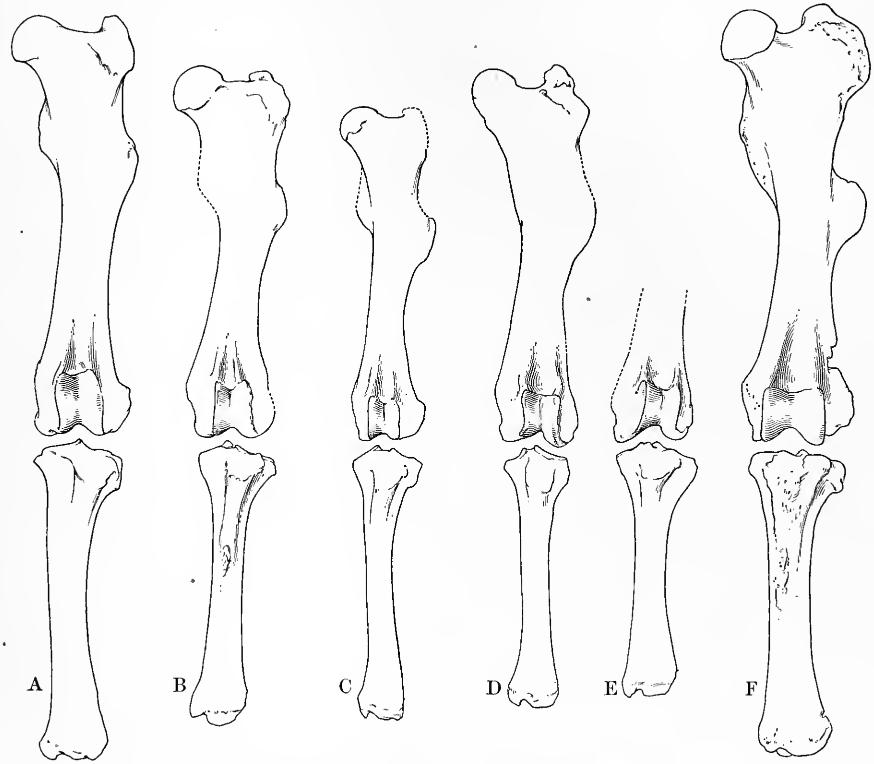

FIGURE 516.—Femora and tibiae of middle Eocene titanotheres

A, *Palaeosyops major*; B, *Limnohyops monoconus*; C, *Mesatirhinus petersoni*; D and E, *Manteoceras manteoceras*; F, *Telmatherium ultimum*. One-sixth natural size.

1. The femur is longer than the tibia. This difference is seen in the early mediportal types and increases with the graviportal adaptation.

2. The head of the femur is primitively more spherical but becomes progressively flatter or less spherical.

3. The shaft is rather straight and flat and has a slight forward curvature inferiorly. The great trochanter, *t′*, is not very high, being but slightly raised above the level of the head and relatively smaller and less prominent than in *Amynodon*. Its inner posterior side is recurved, surrounding a deep, sharply characteristic pit. The second trochanter, *t″*, is relatively less prominent than in primitive rhinoceroses; the third trochanter, *t‴*, is placed high on the shaft, as in all the Equidae and in the primitive Rhinocerotidae (*Hyrachyus*); in Eocene titanotheres it never extends down to the middle of the shaft as in the progressive Rhinocerotidae; the third trochanter is less extensive than in *Hyracodon* or *Amynodon*.

4. The second and third trochanters are more nearly opposite each other, as in the primitive Equidae. This is a peculiar and rather characteristic feature.

5. The external patellar ridge is smaller and less produced superiorly; the distal condylar surfaces for the tibia are somewhat flatter; the internal one is larger.

A most characteristic feature is the patellar trochlea. In the Palaeosyopinae the knee is straighter; in the Manteoceratinae it is more flexed. In the palaeosyopine subgraviportal types (*Palaeosyops*, *Limnohyops*) the patellar trochlea (fig. 518) is more vertical and thus presents much more anteriorly than in the early rhinoceroses (*Amynodon*). This indicates that the femur was carried vertically at an early period. In the manteoceratines the patellar trochlea is more distal and oblique; thus in the more light-limbed *Mesatirhinus* the patellar facet presents more obliquely downward and forward, and the femur was carried more obliquely, as in the rhinoceroses (*Hyrachyus* and *Amynodon*). Even in *Manteoceras* it was more downward than in *Palaeosyops*. Distally the internal and external tibial condyles are nearly subequal. In the amynodonts the external condyle is much more prominent, and the corresponding external tibial facet is produced backward.

Femorotibial ratios.—In all the titanotheres the tibia is much shorter than the femur. This disparity is progressive (tibiofemoral ratio, 77 to 54) in the course of graviportal adaptation.

Length of bones of hind limbs of titanotheres and of tapir, in millimeters

	Femur	Tibia	Tibiofemoral ratio	Mts III	Metatarso-femoral ratio
Tapirus indicus	320	258	80	120	37
Eotitanops princeps, Am. Mus. 296 (type)	[a] 250			86?	34?
Palaeosyops major, Am. Mus. 1316	433	332	77	137	31
Palaeosyops leidyi, Am. Mus. 1544 (type)	370	290	78	110	30
Limnohyops sp., Am. Mus. 11689	[a] 355	285	79	111	31
Manteoceras manteoceras, Am. Mus. 1587	390?	272	69		
Mesatirhinus "petersoni," Am. Mus. 11659	358	285	79	118	33
Dolichorhinus hyognathus, Am. Mus. 13164	386			[a] 119	30
Menodus trigonoceras, Munich Mus	770	430	55	[a] 220	28
Brontops robustus, Yale Mus. 12048 (type)	812	448	55	[a] 212	26
Brontotherium gigas, Am. Mus. 519	780	427	54	200	20

[a] Estimated.

Contrasts with Amynodontidae.—The amynodonts are contemporary semiaquatic rhinoceroses. In *Amynodon* the great trochanter is more elevated; the patellar facet is subhorizontal at the distal extremity of the shaft.

TIBIA

The tibia (fig. 516) is invariably shorter than the femur, the ratios in the various genera being as in the above table. So far as the relative abbreviation of the tibia is indicative of speed and weight, *Manteoceras* is relatively the slowest and *Mesatirhinus* relatively the swiftest of the middle Eocene titanotheres.

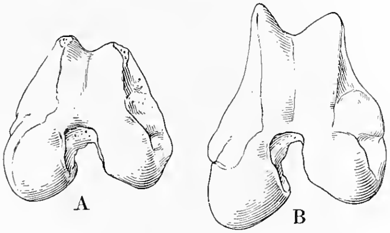

FIGURE 517.—Distal end of the femur in a middle Eocene titanothere and an upper Eocene amynodont

A, *Manteoceras manteoceras;* B, *Amynodon sp.* One-third natural size.

Among the special titanothere characters are the following: (1) External tuberosity of cnemial crest more prominent than internal tuberosity; (2) cnemial crest concave superiorly and deeply excavated on the external side; (3) shaft deeply trihedral in midsection and broadly flattened inferiorly. Characters 2 and 3 persist in the Oligocene titanotheres.

As compared with the large contemporary Rhinocerotoidea (amynodonts and hyracodonts) of middle Eocene time, some of which attained the same size as titanotheres, we observe the following distinctions: (1) In *Palaeosyops* the cnemial crest runs more obliquely inward, crossing the shaft; (2) the crest is broader at the summit and does not extend so far down the shaft as in *Hyrachyus* and *Hyracodon;* (3) the tibia of *Palaeosyops* and *Manteoceras* in proximal and distal views is shallow anteroposteriorly.

As compared with the tibia of *Amynodon*, the titanothere tibia is more robust and lacks the posterior prolongation of the femoral condyle.

FIBULA

The fibula was slender (but relatively less so than in *Amynodon*), subcylindrical, broadly expanded above for the articulation of the posterior inferior surfaces of the external head of the tibia, and closely appressed with the tibia below by a broad articulation, articulating broadly also with the astragalus and exhibiting a postero-inferior facet for the calcaneum during the extreme extension of the foot.

PES

In the pes, as in the manus, we observe certain syngenetic family characters which are peculiar to all titanotheres but which in various genera are more or less concealed by adaptations to speed or to weight.

This law of the dominance of teleogenetic (adaptive) over syngenetic (ancestral) character is in force in every single element of the pes as in the manus.

For example, the articulations between the astragalus and calcaneum exhibit both a mediportal type resembling that of tapirs, of light-limbed rhinoceroses, and of paleotheres and a graviportal type resembling that of other graviportal perissodactyls. We are therefore again compelled to examine minor and less conspicuous characters in order to discover the real syngenetic family resemblance to be found in each element.[36]

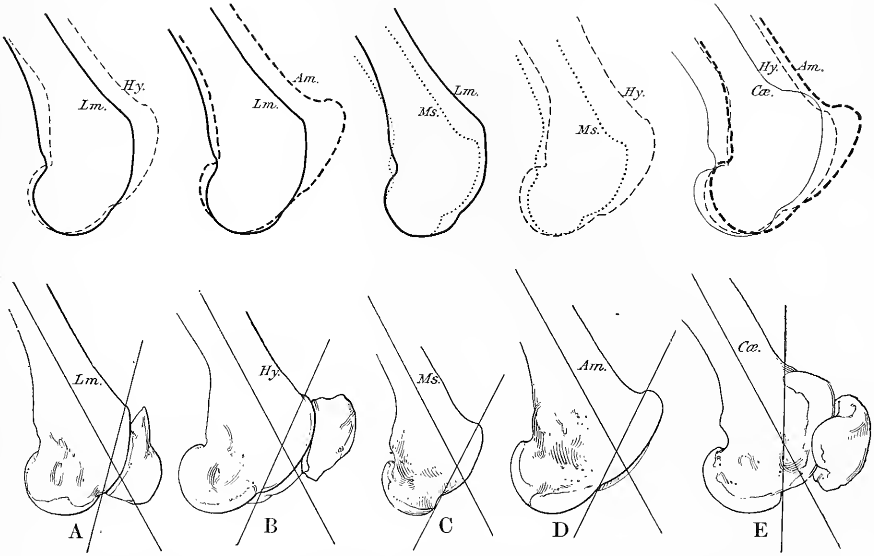

FIGURE 518.—Angulation of the knee joint: relation of patellar facet to long axis of femur

A, C, D, and E, one-fourth natural size; B, one-half natural size. *Lm, Limnohyops; Hy, Hyrachyus; Ms, Mesatirhinus; Am, Amynodon; Cae, Caenopus.*

Among family characters of the pes of the titanotheres are the following:

1. The small fibulocalcaneal facet, as in the Equidae, the fibula barely passing upon the calcaneum in the extreme extension of the foot. A median pit on the astragalus checks the flexion of the tibia by receiving its posterior process.
2. The entocuneiform is very large, articulating on the inner side of the mesocuneiform, of Mts II, and of the navicular, and freely projecting backward from the pes like a pisiform.
3. The mesocuneiform is invariably a very small bone as in primitive mammals.
4. The ectocuneiform is a large element.
5. Mts II and III typically abut on the outer proximal facets against the ectocuneiform and the cuboid, respectively. In one specimen of *Palaeosyops* Mts IV abuts against the ectocuneiform, but this is unusual. Similarly Mts III occasionally does not abut against the cuboid.

In the two middle Eocene groups, namely, the Palaeosyopinae and the *Manteoceras-Dolichorhinus* group, it is possible by very careful study to discover distinctive generic characters by which we may separate every bone of the manus and of the pes, although through convergence and inheritance the bones are often brought to resemble each other closely. The chief subfamily distinctions in typical genera are stated on the following page.

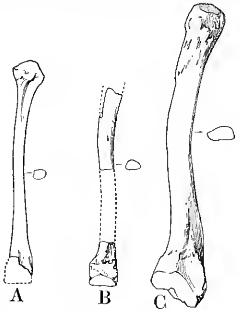

FIGURE 519.—Inner side view of left fibula

A, *Palaeosyops* sp.; B, *Limnohyops monoconus?;* C, *Brontotherium leidyi.* One-sixth natural size.

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[36] The significance of the astragalocalcaneal facets as family characters in Perissodactyla was first pointed out by Osborn in the article "Evolution of the ungulate foot" (Scott and Osborn, 1890.1, pp. 531-569).

Contrast in features of the pes in the middle Eocene groups

I. Palaeosyopine group: Palaeosyops, Limnohyops	II. Manteoceras-Dolichorhinus group: Manteoceras, Mesatirhinus, Dolichorhinus
1. Tarsus broad, composed of anteroposteriorly deep elements, correlated with more or less spreading digits.	1. Tarsus more shallow anteroposteriorly; more elevated in all its elements. Digits less spreading distally.
2. Calcaneum with somewhat rounded or oval shaft of tuber calcis moderately expanded at the summit.	2. Calcaneum with laterally compressed and distally truncate tuber calcis.
3. Cuboid relatively broad.	3. Cuboid high, relatively narrow.
4. Proximal facets on the metatarsals deeply extended anteroposteriorly.	4. Metatarsals with proximal facets relatively shallow. Distal facets more flattened.

PES OF THE PALAEOSYOPINE GROUP

Limnohyops (figs. 520, 530).—The adaptive characters of the pes of this animal, like those of the manus, are primitive, mediportal, and mesatipodal. Digits broader than in *Mesatirhinus* and stouter and heavier than in *Tapirus*—that is, of less swift type. Astragalus with elongate neck and vertically elongate sustentacular facet, unlike the rounded facet of *Palaeosyops*. Calcaneum with tuber deep and expanding at summit. Cuboid deep (shallow in *Palaeosyops*). Entocuneiform very large. Mesocuneiform very small. Ectocuneiform very large, quadrilateral (not vertically extended) as in *Mesatirhinus*. Metatarsals of medium length; Mts III abutting against cuboid, Mts II abutting against ectocuneiform. Terminal phalanges cleft and expanding distally somewhat as in *Mesatirhinus* but more robust.

Palaeosyops.—The most robust and graviportal pes (figs. 520, 540) known among Eocene titanotheres. Digits stout and widely spreading; prominent muscular rugosities indicating powerful flexor and extensor attachments; astragalus readily distinguished by its abbreviated neck, broad, shallow tibial trochlea, and especially by the large and oval sustentacular facet for the calcaneum, as well as by the broad cuboid facet; calcaneum with obliquely placed tuber calcis and expanded summit. Cuboid in two specimens very short, thus Mts IV articulating with ectocuneiform; the broad, abbreviated cuboid apparently a constant character. Other elements of tarsus relatively broad and low, deep anteroposteriorly; Metatarsals broad and stout, broadening at the lower extremities; ectocuneiform large and triangular; mesocuneiform very small, with rounded edges; entocuneiform large, of irregular shape. Terminal phalanges obtusely rounded, very distinctive.

In the passage from *Limnohyops* to *Palaeosyops* we again note the transition from a rather heavy mediportal type, of the proportions of the tapir, to a much heavier (subgraviportal) type with broad, spreading feet adapted to supporting the animal in swampy ground; the reduction of the terminal phalanges points to reduced hoofs, a possible amphibious adaptation.

PES OF THE MANTEOCERAS-DOLICHORHINUS GROUP

As in the manus, we may distinguish the pes by the relatively high and narrow proportions of the podial elements. The mediportal *Mesatirhinus* presents a wide contrast with the subgraviportal *Manteoceras*.

Mesatirhinus.—This mediportal pes (figs. 520, 569, 572) is readily distinguished by its relatively high and narrow proportions. The angles and facets are all sharply defined and sculptured. The bones of the second row of tarsals and proximal facets of metatarsals deep anteroposteriorly. Astragalus with elongate neck, narrow, vertically produced sustentacular facet for calcaneum; a narrow cuboidal facet. Calcaneum very distinctive, with its deep, laterally compressed tuber and truncate distal extremity. Navicular relatively deep and narrow. Cuboid, also high, narrow and compressed in median line. Mesocuneiform and ectocuneiform distinguished by their elevated and sharply quadrate form.

Manteoceras (fig. 557).—Astragalus only known. Tarsus apparently of the same type as in *Mesatirhinus* but relatively broader, judging from the astragalus. Astragalus with a sharply defined tibial trochlea, subelongate neck, vertically elongate, straight-sided sustentacular facet for the calcaneum, of same type as in *Mesatirhinus* but relatively broader; a broad cuboidal facet (unlike *Mesatirhinus*).

Dolichorhinus (Pl. XXXI).—Mesatipodal—that is, metapodials relatively abbreviated, as in *Manteoceras*. A full description appears upon a subsequent page.

Comparing these three forms with respect to the elongation of the metapodials, *Mesatirhinus* is mesatipodal, *Dolichorhinus* is still mesatipodal but transitional, while *Manteoceras* approaches the brachypodal condition. Another type of more elongated manteoceratine foot (Am. Mus. 2352) has been discovered and is described in full below. It is omitted here because its generic association is somewhat doubtful.

SYSTEMATIC DESCRIPTIONS OF MIDDLE EOCENE TITANOTHERES

SUBFAMILY PALAEOSYOPINAE

Mediportal and progressively graviportal titanotheres of the lower and upper Bridger deposits and the lower deposits of the Washakie Basin. Feet mesatipodal to brachypodal. Ungual phalanges truncate to rounded. Astragalus progressively widening.

Limnohyops

The skeleton of *Limnohyops*, so far as known, is readily distinguished in all its parts from that of *Palaeosyops* by its mediportal type—that is, by its lighter construction. Yet the body was heavier and

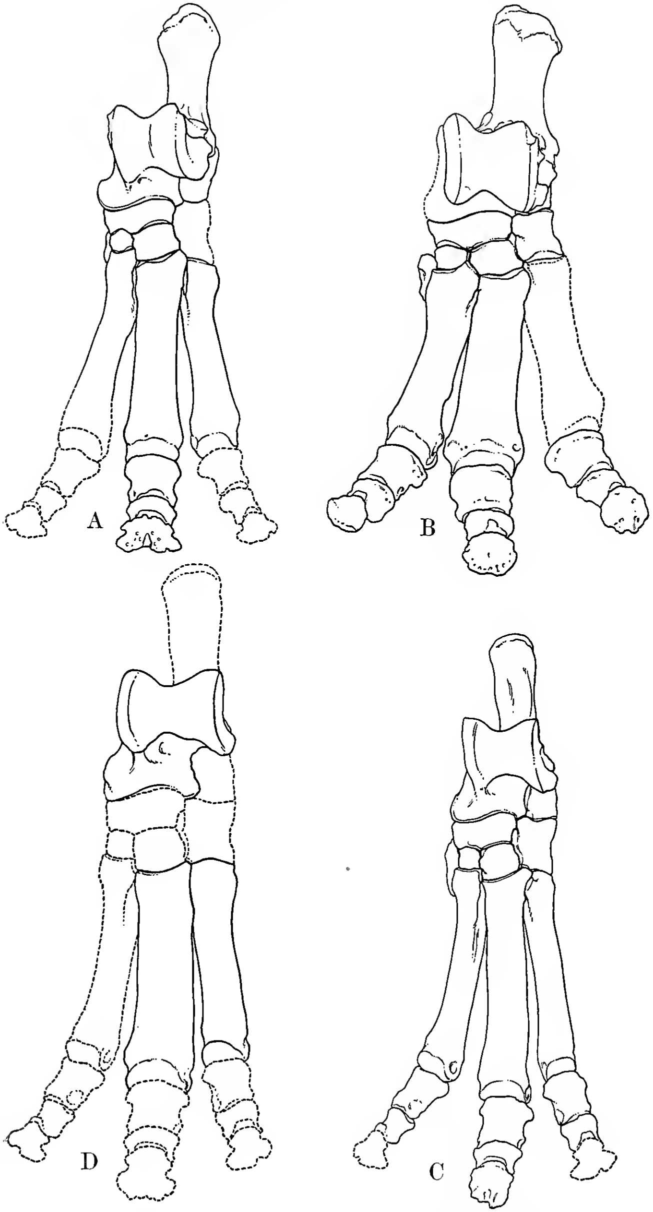

FIGURE 520.—Comparison of pes in four species of middle Eocene titanotheres

A, *Limnohyops monoconus;* B, *Palaeosyops leidyi;* C, *Mesatirhinus petersoni;* D, *Mesatirhinus?* (See p. 643.) One-third natural size. The pes of *Telmatherium* is unknown except in the upper Eocene *T. ultimum*. that of *Manteoceras* is known only from the astragalus.

the motions were slower than in either the American or Asiatic species of *Tapirus*. *Palaeosyops* entered a graviportal line of evolution, but *Limnohyops* was more conservative. Its feet become mesatipodal rather than brachypodal, and the limbs throughout are narrower and more slender than those of *Palaeosyops*. The hand and foot were relatively elongate—that is, they were appressed rather than spreading. The ungual phalanges are truncate, expanding distally, rather than rounded and obtuse, as in *Palaeosyops*. These animals present many adaptive resemblances to *Mesatirhinus* in the manteoceratine subfamily, yet so far as known the parts are somewhat heavier and more robust throughout.

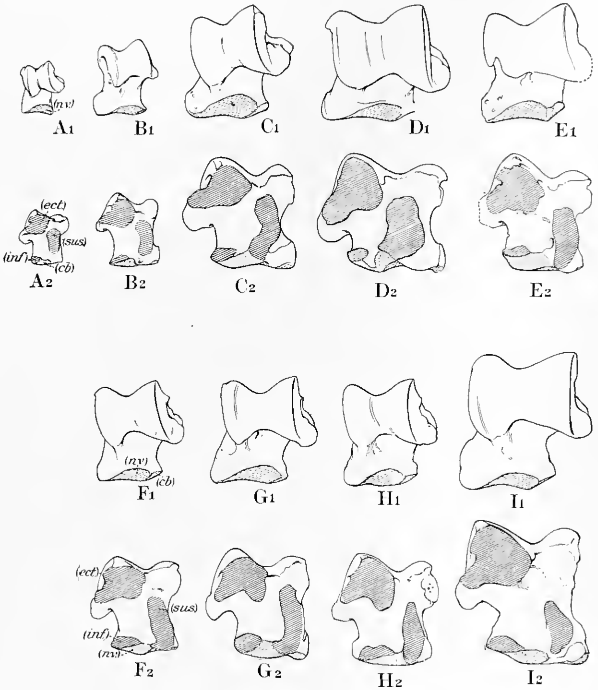

FIGURE 521.—Astragali of Eocene titanotheres

A, *Lambdotherium popoagicum;* B, *Eotitanops borealis;* C, *Limnohyops monoconus;* D, *Palaeosyops robustus;* E, *Manteoceras manteoceras;* F and G, *Mesatirhinus petersoni;* H, *Metarhinus* cf. *M. earlei;* I, *Dolichorhinus hyognathus.* A_1, B_1, etc., front view; A_2, B_2, etc., back view. Astragalo-calcaneal facets: ectal (*ect*), sustentacular (*sus*), and inferior (*inf*); astragalonavicular facet (*nv*); astragalocuboidal facet (*cb*). One-third natural size.

The materials of *Limnohyops* are as follows:

Limnohyops laticeps, Yale Mus. 11000 (type skull and parts of skeleton, Pl. LVII, figs. 261 B, 264, 531, 532); Bridger D (?).

Limnohyops? monoconus, Am. Mus. 11689 (vertebrae, fore and hind limbs, figs. 525 A, 530); Bridger B 2.

Limnohyops? monoconus, Am. Mus. 11699 (manus, radius, and ulna, figs. 525 B, 527); Bridger B 2.

Limnohyops? monoconus, Am. Mus. 11690 (complete hind limb, fig. 529); Bridger B 1.

Measurements of limb bones of Limnohyops laticeps and L. monoconus, in millimeters

	L. laticeps, Yale Mus. 11000 (type)	L. ?monoconus		
		Am. Mus. 11689, Bridger B 2	Am. Mus. 11699, Bridger B 2	Am. Mus. 11690, Bridger B 1
Humerus, length	------	295	------	------
Radius, length	230	230	230	------
Radius, breadth, proximal	53	58	56	------
Radius, breadth, distal	60	55	55	------
Ulna, length	307	312	308	------
Carpus, width	------	[a] 75	------	------
Mtc II, height	------	99	99	------
Mtc III, height	------	109	103	------
Mtc III, distal width (maximum)	[a] 33	33	34	------
Mtc IV, height	------	98	97	------
Mte V, height	------	------	79	------
Femur, length	------	[a] 357	------	387
Tibia, length	------	285	------	297

[a] Estimated.

Two skulls of *Limnohyops* have been found in Bridger B, namely, *L. priscus* and *L. monoconus*, the latter an animal of considerable size. Parts of three skeletons in the American Museum collection (Nos. 11689, 11699, 11690) belong, possibly, to *L. monoconus*. The generic reference to *Limnohyops* is well assured; the specific reference is doubtful. The ground for the generic reference of the skeletal specimens to *Limnohyops* is their agreement in many details with the corresponding bones of the type skeleton of *L. laticeps*, namely, (1) the distal end of Mtc III of the type agrees with Mtc III of Am. Mus. 11699; (2) the radius of Am. Mus. 11689 agrees in length and in details of character with the radius of the type; (3) the ulna of Am. Mus. 11689 agrees closely with that of the type of *L. laticeps*, especially in the rugose area of the olecranon.

Limnohyops monoconus?

Incomplete skeleton from Bridger B 2, Grizzly Buttes, Bridger Basin, Wyo., Am. Mus. 11689

The material includes the atlas, a cervical, several anterior dorsal vertebrae, the humerus, radii, ulnae, incomplete manus and pes, femur, tibia (figs. 510,

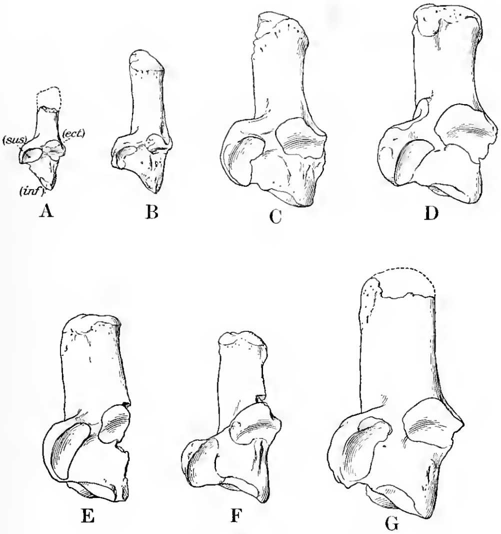

FIGURE 522.—Calcanea of Eocene titanotheres

A, *Lambdotherium popogogicum;* B, *Eotitanops borealis;* C, *Limnohyops monoconus?*; D, *Palaeosyops robustus;* E, *Mesatirhinus petersoni?*; F, *Metarhinus* cf. *M. earlei;* G, *?Mesatirhinus* sp. (Washakie). Astragalocalcaneal facets: ectal (*ect*), sustentacular (*sus*), and inferior (*inf*). One-third natural size.

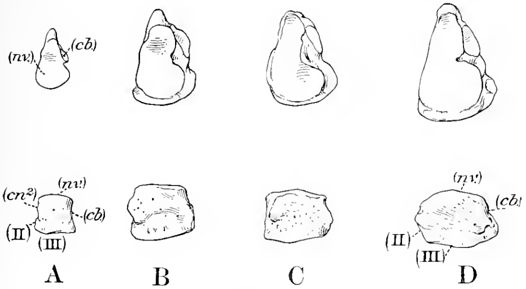

FIGURE 523.—Left ectocuneiform tarsi of lower and middle Eocene titanotheres

A, *Eotitanops borealis;* B, *Mesatirhinus petersoni;* C, *Limnohyops monoconus;* D, *Palaeosyops robustus.* Facets for second metatarsal (II), third metatarsal (III), navicular (*nv*), cuboid (*cb*) and mesocuneiform (cn^2). One-half natural size.

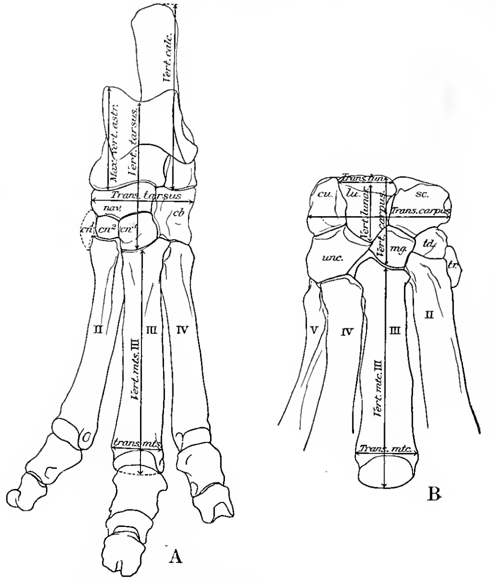

FIGURE 524.—Principal measurements of the carpus and tarsus

A, Tarsus, transverse and vertical; astragalus, vertical (interior and median); calcaneum, vertical; metatarsal III, vertical and transverse, maximum width near distal end. B, Carpus, transverse and vertical; lunar, transverse and vertical; metacarpal III, height and maximum width near distal end.

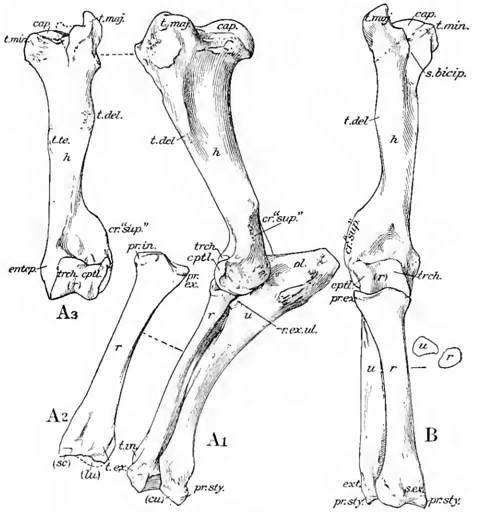

FIGURE 525.—Humerus, radius, and ulna of *Limnohyops monoconus?*

Am. Mus. 11689. A_1 Left humerus, radius, and ulna, outer side view; A_2, left radius, and A_3, left humerus, both front view; B, right humerus, radius, and ulna, the last two partly restored from Am. Mus. 11699, front view. One-sixth natural size. (Compare fig. 527.)

511, 513, 514, 520–522, 685). Measurements of the limb bones are given above.

Adaptive distinctions from Palaeosyops.—This material enables us to further distinguish *Limnohyops* from *Palaeosyops*. Manus and pes mesatipodal rather than brachypodal; all limb bones more slender; humerus relatively shorter; ulna more curved, with distinctive olecranon process; manus narrow; lunar more acutely wedge-shaped distally. Magnum not so wide; metacarpals more slender, femur with more slender, curved shaft. Astragalus more slender, with narrow sustentacular and cuboidal facets; calcaneum with narrow sustentaculum; metatarsals narrow, Mts V more curved, metatarsals not expanding distally; ungual phalanges truncate and square distally.

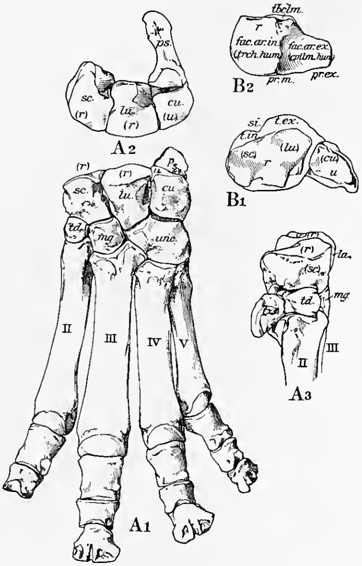

FIGURE 526.—Left manus, radius, and ulna of *Mesatirhinus petersoni* (doubtfully referred)

Princeton Mus. 10013, upper Bridger, placed here for comparison with the manus of *Limnohyops* (fig. 527). A1, Front view of manus; A2, top view of carpus; A3, inner side view of carpus; B1, distal view of radius and ulna; B2, proximal view of radius. One-third natural size.

Palaeosyopine syngenetic characters.—Among the more obscurely but syngenetically important characters tending to ally this animal to *Palaeosyops* are an astragalus having in common the following peculiarities: A pit for a ligament on the internal or tibial face just below the trochlear keel, a rather sharp extension of the superior edge of the navicular facet, a prominent protuberance near the distal end of the tibial face, an inward projection of a sinus or fossa tending to separate the sustentacular facet from the well-developed facet for the tibial sesamoid. Other resemblances with the Palaeosyopinae are seen in the subglobose shape of the distal facets of the metapodials, in the marked anteroposterior depth of the scaphoradial and other carpal facets, in the depth of the proximal metapodial facets, and in the femur with patellar facet facing anteriorly.

Distinctions from the Manteoceras-Dolichorhinus group.—*Limnohyops* is separated from *Mesatirhinus* by the following characters: Limb bones of more graviportal type; humerus longer, radius stouter, more curved; ulna more curved and with larger olecranon; manus somewhat broader and shorter throughout; femur flatter, femur and tibia a little stouter but of about the same relative length; astragalus broader, sustentacular facet farther in toward the middle of the bone; sustentacular facet broader, not so straight sided, forming a much more open angle with the navicular facet, inferior astragalocalcaneal facet smaller; a pit on the internal or tibial face of the astragalus just below the trochlear keel; metatarsals a little shorter and broader. Notwithstanding these differences there are many general adaptive resemblances to *Mesatirhinus*, especially in the femur, tibia, and metatarsals. The differences, however, appear to indicate generic separation.

Limnohyops is analogous to *Manteoceras*, especially in the general characters and proportions of the humerus, tibia, astragalus, and pes—so much so, in fact, that it was formerly referred provisionally to that genus, from which, however, it is distinguished, so far as known, by the following characters: Scaphoid deeper anteroposteriorly, trapezoid facet more

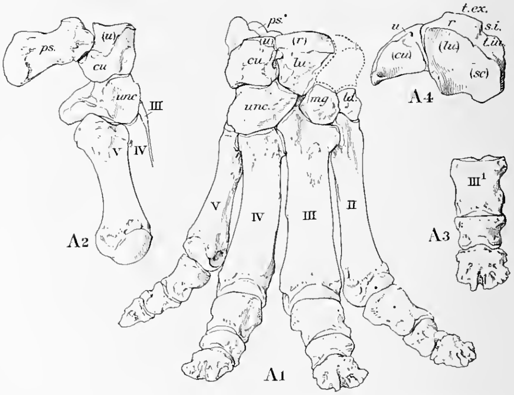

FIGURE 527.—Manus, radius, and ulna of *Limnohyops monoconus* (doubtfully referred)

Am. Mus. 11699, Bridger B 2. A1, Right manus, front view; A2, right carpus, outside view; A3, phalanges of median digit; A4, distal view of radius and ulna. One-third natural size. (Compare fig. 525.)

oblique, magnum facet narrower, lunar facet narrower; distal or phalangal facets of metacarpals and metatarsals more globose, less flattened, proximal facets of same widely truncate posteriorly; tibia relatively longer with narrower proximal end; astragalus with narrower cuboid facet, navicular facet not so deep anteroposteriorly, inner keel of astragalotibial trochlea sharper, prominence on the distal part of the inner or tibial surface not ending in a budlike tuberosity, sustentacular facet less straight-sided.

Forearm and manus from Bridger B 2, Grizzly Buttes west, Bridger Basin, Wyo.; Am. Mus. 11699. Limnohyops ref.

Figure 527. (For measurements see above)

This well-preserved specimen resembles in general appearance the preceding one (Am. Mus. 11689) but differs in the following particulars: The radius is a little more slender; the olecranon of the ulna is deeper; the manus is smaller but agrees in so many close details with the other manus (Am. Mus. 11689) that there can scarcely be any doubt that the two belong to the same genus—namely, *Limnohyops.*

The manus accordingly offers some further points of contrast with that of *Manteoceras*—namely, in the magnum the front face is not so sharply polygonal, the posterosuperior head or eminence is much narrower and extends obliquely backward and downward, whereas that of *Manteoceras* is subtruncate posteriorly and sharply ridged superiorly; the posterior hook of the magnum is much more slender and ends postero-inferiorly in a bluntly oval pitted surface; the facet for the third digit, Mtc III, is deeper anteroposteriorly and narrower posteriorly, that of *Manteoceras* being subrectangular in general outline; the unciform is narrower transversely and deeper vertically, its supero-external or cuneiform facet is less extensive transversely and narrower externally, it is less concave in front view, its supero-internal or lunar facet is less wide, especially posteriorly, all the ridges between adjacent facets are less angulate; the postero-external protuberance of the unciform is much more pointed posteriorly; the cuneiform carpi are much narrower transversely than in *Manteoceras* and reveal many striking detailed differences. Some, or even most, of the foregoing characters of the manus in question may be primitive characters which have been lost in *Manteoceras* in adaptation to the progressive broadening of the manus; but if the manus in question belonged to a direct ancestor of *Manteoceras manteoceras* of the succeeding horizon we should expect it to foreshadow that form a little more definitely, and the very well-marked differences indicate again that it belongs to some other genus.

Analogy to Mesatirhinus.—As compared with *Mesatirhinus* (fig. 526) this manus exhibits a rather striking general resemblance; but the carpals are broader, the scaphomagnum articulation is more oblique, the metacarpals are broader, and the ungual phalanges are larger and not so sharply flaring and truncate distally.

Conclusions.—This manus, although it is more slender than that of *Palaeosyops,* shares with it certain palaeosyopine characters in which it contrasts with *Mesatirhinus* and *Manteoceras,* such as the greater anteroposterior depth of the scaphoid, the angular antero-internal border of the cuneiform, the pointed rather than spatulate hook of the magnum, the broader carpals, metacarpals, and phalanges.

Hind limb from Bridger B 1, lower Cottonwood Creek, Bridger Basin, Wyo.; Am. Mus. 11690. Limnohyops ref.

Figures 516, 518, 519, 523, 686. (For measurements see above)

The material includes only the rather well preserved left hind limb, namely, the femur, patella, tibia, fibula, and pes.

As compared with the hind limb of Am. Mus. 11689, described above, the present specimen differs in its larger size and somewhat stouter proportions, especially of the femur; the metatarsals are noticeably longer and have straighter sides; in the astragalus the sustentacular facet extends a little further dorsad, the ectal facet is less deeply concave, the distal calcaneal facet is larger, and corresponding differences occur in the calcaneum. These differences are accompanied by so many detailed resemblances (in contrast with other genera) that it appears probable that the hind limb in question belongs in the same genus (*Limnohyops*) with Am. Mus. 11689, 11699, above described, though possibly to a different species of that genus.

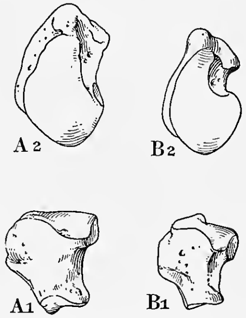

FIGURE 528.—Right scaphoid of *Palaeosyops* sp. (A) and *Limnohyops monoconus* (B)
Front (A_1, B_1) and upper (A_2, B_2) surfaces. One-half natural size.

As compared with other Palaeosyopinae the present specimen offers many resemblances and a few rather decisive differences: the femur, though smaller than that of *P. major,* does not differ greatly in its proportions and offers no clear-cut distinctions; the pes is noticeably higher and more slender; the astragalus is narrower with a narrower neck, more straight-sided sustentacular facet, narrower cuboid facet and sharper internal keel on the trochlea.

Distinctions from Manteoceras-Dolichorhinus group.—From *Mesatirhinus* the specimen differs in its larger size, more robust femur, tibia, and pes, distally diverging vertical sides of Mts III. The astragalus is wider, its ectal facet shallower and not produced downward at the lower internal corner, the sustentacular facet was probably broader, not so straight-sided, and it formed a more open angle with the cuboid facet; the calcanea show corresponding differences. But these differences are accompanied by many general resemblances that indicate the annectent or primitive character of the pes in question.

Comparison with *Manteoceras* is made difficult by the scantiness of the material referable to that genus. The femur is of nearly the same length as in the young male *Manteoceras* (Am. Mus. 1587), but the third trochanter seems smaller; the tibia is absolutely and relatively longer, its proximal end is narrower, its distal end is broader; the patellar facet is decidedly longer and more anterior than in *Manteoceras*. The astragalus, as compared with that of the young *Manteoceras* (Am. Mus. 1587), offers the following differences: The internal trochlear ridge is angulate rather than broadly convex; the ectal facet is shallower, less produced on its lower internal border; the sustentacular facet is much longer; the cuboid facet is decidedly smaller; the navicular facet not so deep anteroposteriorly. As compared with the astragalus of the old female *Manteoceras?* (Am. Mus. 12204) most of the above-described differences also hold good, save that the size in Am. Mus. 11690 is considerably greater and the navicular facet seems proportionately deeper rather than shallower.

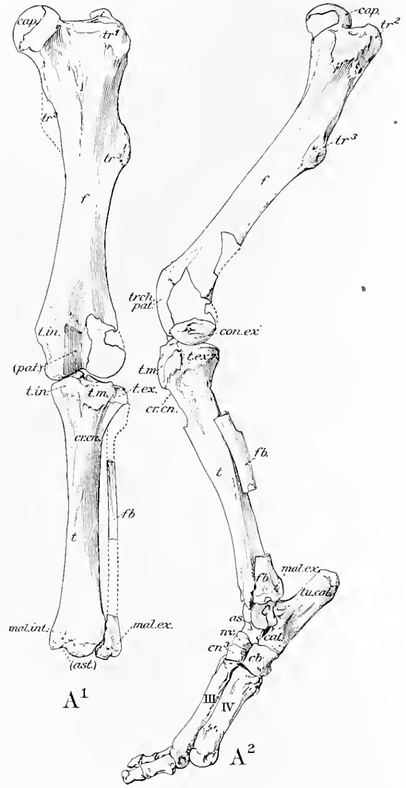

FIGURE 529.—Left hind limb of *Limnohyops monoconus* (doubtfully referred)

Am. Mus. 11690; Bridger B 1. A¹, Front view; A², outer side view. One-sixth natural size.

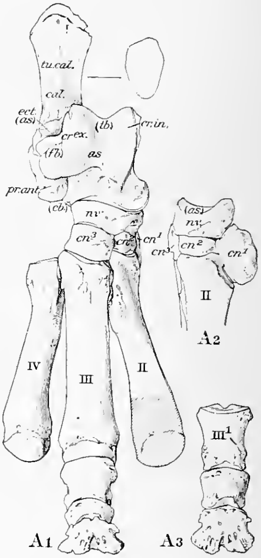

FIGURE 530.—Right pes of *Limnohyops monoconus?*

Am. Mus. 11689; Bridger B 2. A₁, Front view; A₂, outer side view of tarsus; A₃ phalanges of median digit. One-third natural size.

Conclusion.—In brief, the hind limb under consideration appears to belong neither with *Palaeosyops*, *Mesatirhinus*, nor *Manteoceras*. On the other hand, it appears not to differ generically from Am. Mus. 11689, described above, and together with that specimen it may represent a Bridger B member of the *Limnohyops* phylum.

Limnohyops laticeps

Many parts of the skeleton of *L. laticeps* are fortunately preserved with the type skull in the Yale Museum (No. 11000). The geologic level is probably Bridger C or D, at Henrys Fork Hill, Bridger Basin, Wyo.

Cervicals.—The axis and four other cervicals (C. 3, C. 5, C. 6, C. 7) are preserved; the fourth cervical is missing. The epiphyses are mostly detached, indicating a juvenile condition. The axis (C. 2) and third vertebra (C. 3) especially have large inferior keels or hypapophyses. The third to sixth cervicals exhibit broadly depressed inferior lamellae. The seventh (C. 7) is imperforate exhibiting narrow, rodlike transverse processes without inferior lamellae.

Dorsals.—The median dorsals exhibit centra angulate but not keeled inferiorly. In one of the posterior dorsals the centrum is slightly keeled and the spine is elevated (112 mm.) above the base of the centrum.

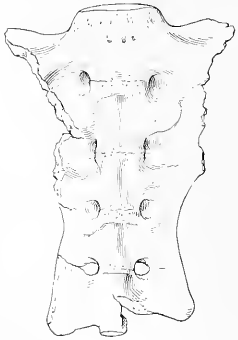

FIGURE 531.—Ventral surface of sacrum of *Limnohyops laticeps*

Yale Mus. 11000 (type); Bridger C or D. One-third natural size.

Lumbars.—The lumbars preserved are apparently the second and the fourth (L. 2, L. 4); the first, third and fifth lumbars are missing. They exhibit increasingly broad centra and moderately broad transverse processes. The zygapophyses are vertically placed, and unlike those of *Palaeosyops* are slightly if at all revolute.

Sacrals.—The most distinctive character of the sacrals is that the sacrum includes five vertebrae, the fifth (S. 1) being due to the coalescence of an anterior caudal. They measure 171 millimeters anteroposteriorly. The first and second sacrals and the anterior portion of a third sacral enter into union with the ilium.

Pelvis.—The innominate bones are preserved almost entire (fig. 532). The left os innominatum measures 406 millimeters anteroposteriorly. The crest of the ilium measures 203 millimeters transversely; the superior border is thin and indented in the median portion or crista iliaca. The rugose tuber sacrale is narrower (80 mm.) than the rugose tuber coxae (140 mm.). The elongate proportions of the innominate bones are partly due to the juvenile nature of this individual.

Fore limb of type.—The proximal and distal portions of the right humerus are preserved. The head and greater tuberosity measure 122 millimeters (anteroposterior); the head measures 65 (transverse); there is a wide and deep bicipital groove; the proportions are somewhat altered by crushing; the distal end of the humerus measures 68 (transverse); the total width of the distal articular surface is 55.

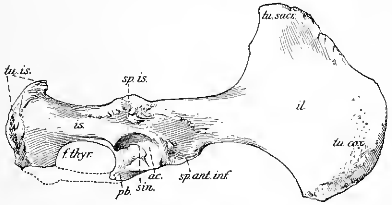

FIGURE 532.—Right os innominatum of *Limnohyops laticeps*

Yale Mus. 11000 (type); Bridger C or D. One-sixth natural size.

The radius and ulna are complete. The radius is distinguished posteriorly by a characteristic median groove; it is 230 millimeters long; its humeral facets measure 53 millimeters transversely and 27 anteroposteriorly.

The ulna is 307 millimeters in length; its distinctive character (see fig. 511) is the downward extension on the outer side of the olecranon of the rugose crest for the triceps muscle.

Palaeosyops

The Eocene titanothere skeleton is best known in members of the genus *Palaeosyops*, which was the largest and the most heavily built titanothere of that time, adapted to slow locomotion on soft ground along water borders and in marshes and swamps. We have the nearly complete skeleton of *P. leidyi* from the upper Bridger and parts of the more progressive *P. robustus* and of the ancestral *P. major*. A titanothere family likeness is seen throughout the axial and appendicular parts, but generic and subfamily differences, closely shared with *Limnohyops*, are apparent throughout.

Up to the end of the lower Bridger deposition we may safely select the largest and most massive titanothere bones as belonging to *Palaeosyops*. The graviportal tendency is especially manifest in the hind limb, with its elongate femur and abbreviate tibia and slight angulation at the knee joint. The broad and spreading foot bones of both manus and pes are especially distinctive. The manus is functionally tridactyl rather than tetradactyl, owing to the reduced condition of the fifth digit, which is set apart from the other digits in a manner peculiar to this genus. The

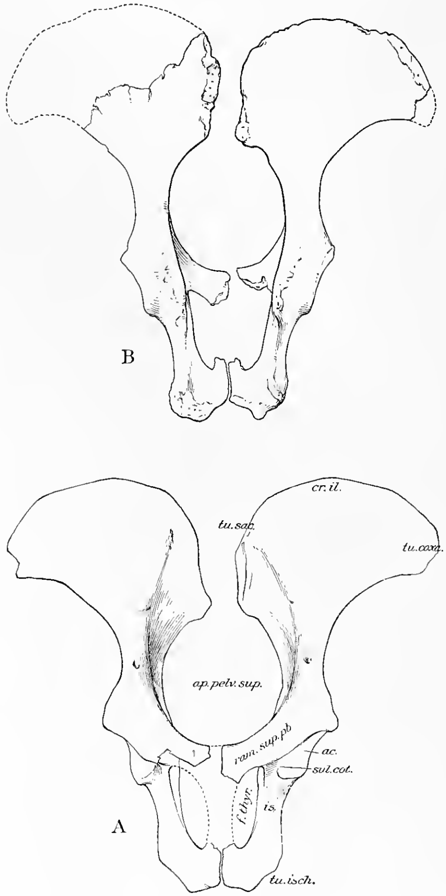

FIGURE 533.—Pelvis of *Palaeosyops major*

Am. Mus. 13116; Bridger B 3. A, Ventral aspect; B, dorso-superior aspect. One-sixth natural size.

terminal phalanges are obtusely rounded and not deeply cleft distally, indicating the presence of imperfect hoofs. Additional evidence of water-loving or semiaquatic habits is found in the weak spines of the dorsal and lumbar vertebrae, which are analogous to those in *Coryphodon* and *Metamynodon.* The dentition points to habits of feeding on the succulent plants which are characteristic of the borders of streams. The skeleton as a whole shows far more aquatic adaptations than that of the tapirs.

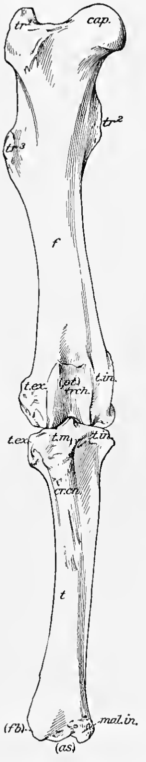

FIGURE 534.—Right femur and tibia of *Palaeosyops major*

Am. Mus. 13116; Bridger B 3. One-sixth natural size.

Palaeosyops major

Palaeosyops major is represented by some well-preserved limb bones and a pelvis associated with the large skull (Am. Mus. 13116) from Bridger B 3. The large size of these bones, coming as they do from so low a level, is very noticeable. They even exceed in total length those of *P. leidyi* (Am. Mus. 1544), but the long bones are more slender. The most characteristic feature of the pelvis (fig. 533) is the narrowness and apparently uniform convexity of the superior or anterior border of the ilium as compared with its expansion in subsequent stages of the development of the titanotheres. This narrowness is a primitive character, corresponding with the low geologic level (Bridger B 3) at which this specimen was found. Other chief generic characters exhibited in this skeleton are the following: Radius (fig. 510) strongly arched forward and having a deep groove for the extensor carpi radialis muscle; ulna (fig. 511) without the incurved olecranon of *Mesatirhinus*; femur with a straight, flattened shaft, and a patellar groove presenting anteriorly; tibia with an outcurved cnemial crest. The short-necked astragalus and the stout calcaneum are likewise of *Palaeosyops* type.

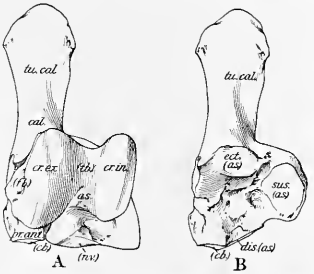

FIGURE 535.—Astragalus and calcaneum of *Palaeosyops major*

Am. Mus. 13116; Bridger B 3. A, Left astragalus and calcaneum; B, left calcaneum with astragalus removed. One-third natural size.

The detailed measurements of this important skeleton as compared with the composite *P. leidyi* (fig. 536) are as follows:

Measurements of skeletal parts of Palaeosyops major and P. leidyi, in millimeters

	P. major, Am. Mus. 13116 (Bridger B 3)	P. leidyi, Am. Mus. 1544 (Bridger C, D)
Femur, length	435	370
Femur, distal breadth	100	93
Femur, breadth across head and great trochanter	127	[a] 132
Tibia, length (middle)	335	290
Radius, length	280–290	235
Ulna, length	378	315
Astragalus, vertical inner face	61	57
Astragalus, proximal width	53	49
Calcaneum, vertical length	119	97
Calcaneum, greatest width	63	62
Mts II, length	126	102
Mts III, length	136	110
Mts III, distal width, transverse	43	42
Pelvis, total length of os innominatum	448	[b] 468
Pelvis, width of crest of ilium	[a] 220	[b] 265

[a] Estimated. [b] Am. Mus. 2348.

Palaeosyops leidyi

Type locality and geologic horizon.—Bridger Basin, Wyo.; Bridger formation, level Bridger C and D.

Skeletal characters.—The first description and preliminary restoration of the skeleton of this species (under the name "*Palaeosyops paludosus*") was published by Earle in his memoir of 1892 (1892.1, p. 314). In this restoration the forefoot of *Mesatirhinus* was erroneously associated. (See fig. 86, p. 151.)

The mounted skeleton of *Palaeosyops leidyi* in the American Museum of Natural History (No. 1544) is a composite one, reconstructed from a number of specimens belonging to different individuals of at least two species (*P. leidyi, P. robustus*) and two geologic levels, collected by the American Museum expedition of 1893 under Dr. J. L. Wortman. The well-preserved skull and lower jaws, the cervical and first two dorsal vertebrae, and the fore limbs down to the manus are from one individual, an old male, No. 1544, the type of *P. leidyi.* The scapulae, ribs, dorsals 4–11, 14–17, caudals 8–10, and four sternals were supplied from No. 1580. The right carpus, belonging to the principal specimen (No. 1544), warrants the completion of the rest of the feet from other specimens, chiefly No. 1550. The left hind limb was made up from Nos. 1582 and 1562; certain of the dorsals and lumbars were supplied from Nos. 1593, 5177, 5158. The foregoing specimens, after careful study, were found to agree very closely in size and other characters, and are probably all referable either to *P. leidyi* or to the closely allied *P. robustus.* But the sacrum and pelvis, No. 2348, from the Washakie Basin, are of somewhat doubtful reference to this genus and may belong to the genus *Limnohyops.* Certain remaining parts (such as caudals 1, 2, 11–18, the right femur, the tibia and fibula, the right cuboid and cuneiforms, most of the unguals, and parts of many ribs and vertebrae) were restored in plaster. (See fig. 536.)

The formula for the vertebral column probably but not certainly is cervicals 7, dorsolumbars 21?, sacrals 4. A careful study indicates that there were 17 dorsals and at least 3 lumbars. The presacral region is rather short, the neck decidedly so, the back moderately so. In adaptation the short neck, high anterior dorsal spines, rather slender mid-dorsal spines, elevated but not very broad lumbar spines, and long ribs indicate a very deep-chested animal of about the same proportions as *Tapirus indicus*, but considerably larger (perhaps one-fifth) and slower in its movements, with decidedly less development of the extensor muscles of the back, as indicated by narrower dorsal spines throughout.

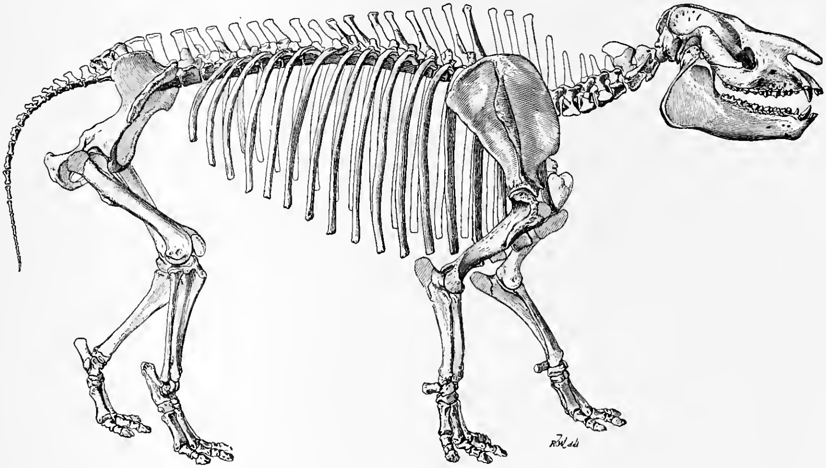

FIGURE 536.—Composite mounted skeleton of *Palaeosyops leidyi*

Including skull, neck, and parts of the fore limb of the type of *P. leidyi* (Am. Mus. 1544) and material from other individuals referred either to *P. leidyi* or to the closely related *P. robustus*. Upper Bridger C and D. One-fifteenth natural size.

The atlas and axis belonging with skull No. 1544 exhibit the following characters: Atlas with large vertebrarterial canal traversing inferior portion only of transverse process (47 mm. broad), which is indented but not perforated to the front as in *Limnohyops laticeps;* first cervical nerve issuing from anterior portion of the neural arch; broadly rugose keel on lower posterior portion of the centrum; transverse measurement of anterior cotyli 102 millimeters, vertical measurement 40, transverse atlas (estimated) 223. Axis also with broadly rugose inferior keel, neural spine moderately extended anteroposteriorly, abutting anteriorly against upper portion of neural arch of atlas. Cervicals 3–6 with neural spines and pleurapophyses (cervical ribs) partly restored; pre- and postzygapophyses placed in decidedly oblique planes facing inward and outward respectively. C. 7 with narrow lamina of neural arch, thin, elevated neural spine restored at the summit. Transverse measurement of neural spine near the base 11 millimeters, anteroposterior measurement 23.

All the upper portions of the neural spines of the anterior dorsals are restored except that of D. 4, which is complete. The base of the spine of D. 1 is laterally compressed and much more extended anteroposteriorly than that of C. 7. Measurements, 29 millimeters anteroposterior, 21 transverse (at base). In D. 2, D. 3 the spines are very stout and transversely extended at the base. In the succeeding dorsals the neural spines become gradually less expanded at the base as they recede in height; but the basal transverse width (35 mm.), the deep posterior concavity, and the moderately limited anteroposterior diameter (24 mm.) are decidedly the characteristic features of all the dorsal spines as far back as D. 12 inclusive; in D. 13 the neural spine begins to be more laterally compressed or flattened and of somewhat greater anteroposterior extent. In D. 4 and D. 10 we have a typical spine complete to the tip. These proportions of the neural spines somewhat resemble those of *Amynodon* and are quite distinct from those in the Oligocene titanotheres *Megacerops* and *Menodus*, as well as from those observed in the horse, tapir, and rhinoceros, in all of which the neural spines are more extended anteroposteriorly than transversely. The anterior dorsal spines are also higher and less elongate anteroposteriorly than in *Dolichorhinus*.

The planes of the zygapophyses are significant as follows: Decidedly oblique planes of the prezygapophyses and postzygapophyses characterize D. 1 and D. 2, both vertebrae belonging with the skull (No. 1544) of *P. leidyi*; this is a point of generic distinction between the Oligocene titanotheres. In D. 3 the planes of the pre- and postzygapophyses suddenly become more horizontal; this horizontal position also characterizes D. 4–D. 11. In D. 14–D. 17 and in all the lumbars the postzygapophyses become cylindrical or partially revolute and are firmly embraced by the deeply concave prezygapophyses as first observed by Earle.

The relations of the vertebrae to the capitula and tubercula of the ribs are clearly shown in the vertebrae belonging with the skull No. 1544, and partly in those belonging to the other individual, No. 1580. All the ribs articulate by prominent and more or less separate anterior and posterior capitular facets with the posterior and anterior vertebral faces respectively. Ribs 1–13 exhibit projecting tubercula; in ribs 14–17 the tubercula become more sessile and reduced. The concave to flat parapophysial facets for the tubercula are decidedly prominent in the anterior dorsals but become less prominent and distinct or pediculate in the posterior ones, the tubercular facet of the ribs being widely separated from the capitular facets. The parapophysial processes for the articulation with the tubercular of the ribs are very stout and downwardly extended, more or less triquetrous, in vertical section, the anterior face being rounded and widely extended outward; in the anterior dorsals the transverse measurement across the parapophyses is 117 millimeters in D. 1, 114 in D. 4, and 99 in D. 8. These processes gradually subside (to 60 mm. tr. in D. 17) in the posterior dorsals.

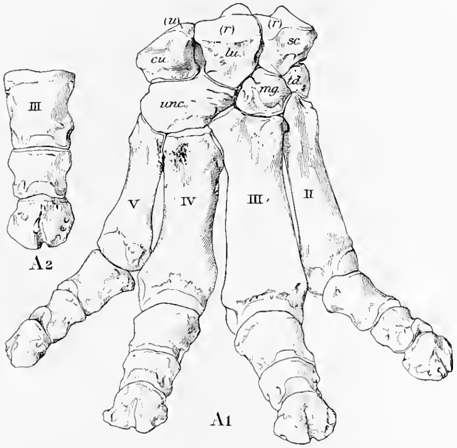

FIGURE 537.—Manus of *Palaeosyops leidyi*

Composite fore foot from Am. Mus. 1544 and 1550 (mounted with 1544). Bridger C or D. A1, Front view; A2, phalanges of the third digit. One-third natural size.

The series of ribs associated with the scapulae (Am. Mus. 1580) indicate a deep and powerful chest; the anterior ribs are broad and flattened externally, the seventh rib assumes a more rounded or trihedral section, which also characterizes the eighth, ninth, and tenth; the eleventh to the seventeenth are smaller, with a flattened oval section; the strength of the chest is attested by the presence of prominent tubercular facets on the posterior ribs. The middle ribs vertically measure 502 millimeters, not allowing for curvature; the last ribs measure 260; the depth of the first rib is approximately 260.

Four sternals (No. 1580) are completely preserved and a portion of the most anterior, there being five preserved in all, though the exact number is not known. The xiphisternum (st. 5) is very shallow, expanding anteriorly and posteriorly, with a linear measurement of 84 millimeters and a transverse measurement posteriorly of 51. The three midsternals are laterally compressed, with the following measurements: St. 4, 42 millimeters (anteroposterior) by 22 (transverse); st. 3, 45 by 28; st. 2, 50 by 22. The presternum (st. 1) is also laterally compressed; the anterior portion is not preserved. The midsternebrae have the same form in Oligocene titanotheres.

The centra of C. 2–4 exhibit broadly rugose posterior keels, which die out in C. 5. The centra of C. 5–D. 2 are slightly convex inferiorly. From this point backward the centra become somewhat laterally compressed, especially toward the lumbars, and are not keeled inferiorly; D. 5 measures 37 millimeters, D. 7, 39; D. 9–D. 15, about 42; D. 17, 48; L. 1, 40; L. 2, 45.

The lumbar vertebrae are estimated in the restoration as three in number, but there may have been four lumbars and but sixteen dorsals. The transverse processes are estimated at 174 millimeters; they are of only moderate breadth.

The sacrals are not preserved. They are present, however, in a specimen referred to *Palaeosyops* sp. (see below).

The three anterior caudals are restored, the neural arch disappears with the supposed ninth, the centra of the fourth, fifth, sixth, ninth, tenth, eleventh (estimated) are preserved (Am. Mus. 1544).

Comparison with the vertebral column of *Brontops* so far as known serves to emphasize the inference based upon the study of the skull that there are few resemblances except in family characters and many differences, and that *Palaeosyops* is not in the line of ancestry of this Oligocene genus.

The structure of the scapula in this species is known from that of another individual, Am. Mus. 1580, associated with this mount. The general proportions of the scapula are breadth 260 millimeters, height 345, and, like the proportions of the limbs, denote a slow-moving animal; the total areas of the prescapular and postscapular fossae are approximately equal; the prescapular fossa (origin of supraspinatus muscle) is subrectangular and exhibits a marked downward extension of the anterior border, an especial characteristic of all titanotheres, to a point within 115 millimeters of the glenoid border; at this point the fossa measures 104 millimeters in front of the spine; the postscapular fossa (origin of infraspinatus, teres major, teres minor muscles), on the other hand, is triangular, the broadest point, 131 millimeters, being near the superior border; the posterior border rises thus in a nearly straight line from the glenoid to the superior border and then sweeps around in a uniformly convex curve to the point above the anterior notch. This scapula conformation is remotely paralleled by that of *Tapirus indicus*, which, however, differs in the greater depth of the supracoracoid notch; it also resembles that of certain early rhinoceroses (*Caenopus occidentalis*), which, however, lacks the anteroposterior breadth; it is also somewhat similar in type to that of *Rhinoceros sondaicus*, differing again in the greater breadth and the absence of retroversion of the spine. These comparisons are naturally valuable not as indicative of relationship but as pointing to analogous development of the shoulder muscles and gaits of these animals; they are distinctively noncursorial. The breadth above the glenoid, including the coracoid process, is 87 millimeters, the width of the neck is 80. The spine rises gently from above the neck with a retroverted border reaching its widest point 210 millimeters above the glenoid and 144 millimeters below the superior border; at this point the spine rises 50 millimeters above the postscapular fossa.

The humerus of *P. leidyi* found with the skull (No. 1544) is intermediate in its robust proportions, which are between those of *Tapirus indicus* and those of *Rhinoceros* (*Dicerorhinus*) *sumatrensis*. In general the muscular processes are about as strongly developed as in *Tapirus indicus*. The proportions of the bones of the fore limb are accurately determined from bones of both sides found with the skull. The upper arm (humerus) (310 mm.) is considerably longer than the forearm (ulnoradius) (235 mm.), as it usually is in slow-moving animals. The proportions of the humerus are similar to those in *Tapirus indicus*, the approximate breadth across the great tuberosity being 103 millimeters and the total distal breadth 92; the lesser tuberosity (insertion of subscapularis) and the greater (insertion of supraspinatus and infraspinatus) are moderately prominent; the greater tuberosity rises into a platelike crest very characteristic of the titanotheres; it sends in an internal hook; the bicipital groove is thus broad and shallow; the highest point of the deltoid crest (insertion of pectoralis major and deltoid) is 119 millimeters below the head, it is slightly retroverted; below this point it subsides gradually into the shaft; the supinator ridge is sharply defined, but not hooked, its summit being 109 millimeters above the trochlea; the entepicondyle or internal eminence is relatively low and obtuse; distally the radial trochlea of the humerus is divided unequally into a smaller, less convex internal portion and a larger, more decidedly convex external portion (the tuberculum). Earle (1892.7, p. 357) has directed attention to the fact that this conformation of the trochleae differs somewhat from that of other Perissodactyla; it is correlated with the more elevated and plane internal humeral facet and the more depressed and concave external humeral facet of the radius.

The elevation of the inner side of the front face of the radius is characteristic of titanotheres but is seen also to a considerable extent in *Amynodon*. The width of the humeral trochlea is 63 millimeters. There are broad and deep anconal and supratrochlear fossae but no perforation; the upper end of the radius measures 63 to 67 millimeters transversely.

The shaft of the radius arches well away from the ulna and expands distally to a width of 62 to 67 millimeters. There is a distinct extensor groove in the anterior distal face.

The ulna has a stout olecranon and straight trihedral shaft well separated from that of the radius, with a broadly transverse section, of which one face presents directly forward and is hollow or grooved above and flattened below.

The right carpus belongs to the same individual as the skull (Am. Mus. 1544). The specific character of the carpus is its great breadth (91 mm.) as compared with its maximum depth (54 mm.) measured from the lunar to the bottom of the unciform. Similar broad and low proportions characterize each element. The lunar is especially distinctive, measuring 36 millimeters transversely, 31 vertically, with an exceptionally broad facet for the magnum (fig. 537); a small trapezium was present but is not preserved in this specimen. In this, as in all other titanotheres, there were large facets on the inner side of the magnum and unciform for Mtc II and Mtc III, respectively.

The metapodials (Am. Mus. 1544, 1550) are relatively broad and distally expanded; the lengths or vertical diameters are, Mtc II, 107 millimeters; Mtc III, 112; Mtc IV, 97; Mtc V, 75. Mtc III has a vertical diameter of 112 millimeters and a transverse diameter distally of 46; the shaft of each has a relatively broad and shallow flattened section, this being a characteristic family feature. The metapodial displacement is very marked, Mtc II and Mtc III abutting widely against the magnum and unciform, respectively. The proximal portion of the shaft of Mtc II presents a small facet to which the trapezium was attached. The three phalanges of D. III measure 39, 26, and 23 millimeters in length, respectively. The distal phalanges are broadly rugose (tr. 35 mm.) with a deep medial cleft; the upturned distal facets of the second phalanges indicate that when the foot was drawn backward the unguals were more sharply extended on the second phalanges. Even with this reservation the fore foot was broad and spreading distally, the transverse measurement across the inner and outer toes resting on the ground being 240 millimeters. *Palaeosyops* thus presents a very wide contrast to the relatively narrow fore foot of *Mesatirhinus*. The contemporary species of rhinoceros (*Amynodon*) is also distinguished by the height and lateral compression of all the elements of the carpus and metacarpus and by the greatly reduced terminal phalanges.

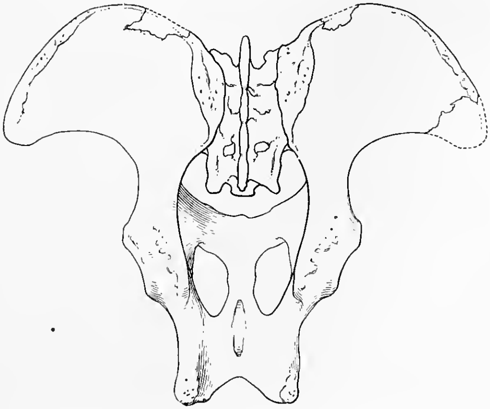

FIGURE 538.—Pelvis of *Limnohyops* (doubtfully referred)

Am. Mus. 2348, superior view. Washakie ?A. One-sixth natural size.

The pelvis and sacrum in this mounted specimen (Am. Mus. 2348) are from the Washakie Basin, Wyo. As noted above it may belong to *Limnohyops*, because the supra-iliac border does not exhibit the uniformly convex arch seen in *Palaeosyops*. The sacrum, however, differs from that of the type of *Limnohyops* in being composed of four vertebrae, the last two of which are clearly caudosacrals. The sacral plates extend deeply down the inner sides of the ilia, the total oblique measurement from the summit of the sacral spines to the bottom of these plates being not less than 170 millimeters. The greatest width of the plate anteriorly is 136 millimeters as compared with the total length of the four sacrals, 159 millimeters; the spines are moderately broad, thin, and coalesced at the summits. The fourth or posterior sacral extends the plate well beyond the posterior superior crest of the ilium.

In general the pelvis (Am. Mus. 2348) is decidedly elongate as compared with that of the Oligocene titanotheres. The total length (465 mm.) is only 23 millimeters less than the total breadth (488 mm.). The superior crest of the ilium, actually measuring 265 millimeters transversely, has a uniformly concave transverse surface with a moderately thickened superior border slightly sigmoid—that is, convex in its outer half and straight or slightly concave in its inner half—as it rises to its convex junction with the sacrum. The distinctive feature of this pelvis is the slightly concave "crista iliaca" between the broadly rugose tuber coxae and tuber sacrale. The conformation of this border is analogous to that of *Rhinoceros sondaicus* and of other quadrupeds the ilia of which are transitional between the purely cursorial type of ilium seen in *Equus* and the weight-carrying type with a uniformly convex superior border seen in *Uintatherium*, *Elephas*, and *Menodus*. The neck of the ilium measures 67 millimeters transversely. The median border of the posterior pelvic opening is marked by an elongate sharp ridge constituting the spine of the ischium (origin of gemellus superior, coccygeus, and levator ani muscles) opposite the acetabulum, behind which is the well-defined lesser ischiadic notch. Behind this the ischiadic border is rounded until it passes into the prominent ischiadic tuberosity. The vertical depth of the ischium at this point is 117 millimeters. The pubo-ischiadic symphysis measures 174 millimeters anteroposteriorly. The obturator foramina are elongate, oval, measuring 87 millimeters (anteroposterior) by 49 millimeters (transverse), separated by 19 millimeters, the narrowest point of the symphysis.

The hind limb has a total length from the head of the femur to the tip of the median phalanx of D. III of 940 millimeters as compared with 810, the total length of the fore limb, and 500, the expansion of the ilia. These figures give an idea of the chief proportions of the animal.

The femur (Am. Mus. 1582) measures 370 millimeters as compared with 290 of the tibia, this excessive length of the upper limb being correlated with relatively slow movements. The chief characters of the femur are as follows: The long, straight shaft flattened superiorly on the posterior surface; great trochanter moderately elevated; breadth across head and great trochanter 132 millimeters (estimated); apex of third trochanter 143 millimeters below head; apex of second trochanter 132 millimeters below head;

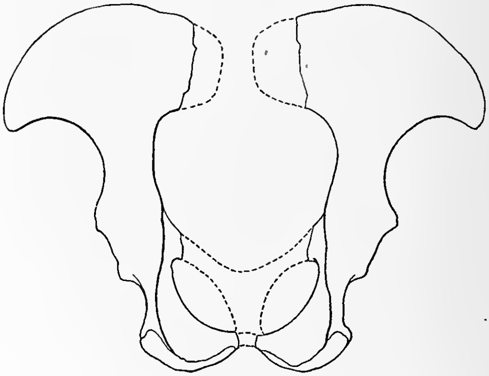

FIGURE 539.—Pelvis of *Palaeosyops* cf. *P. leidyi*

Princeton Mus. 10232, superior view. After Earle. One-sixth natural size.

both trochanters somewhat elevated and nearly opposite each other (an important point of distinction from the rhinoceroses); shaft narrowing, with a rounded anterior and flattened posterior surface below trochanters; transverse measurements, distally 93 millimeters, across condyles 83; the internal and external condyles are equally elevated but the internal condyle is somewhat smaller; patellar facet moderately elongate, vertically placed—that is, looking forward and very slightly downward; vertical measurement 63 millimeters, transverse 40. This is the titanothere type of femur, which, although varying in proportion in the longer-limbed forms, is readily distinguishable from that of *Amynodon* and of other contemporary Perissodactyla.

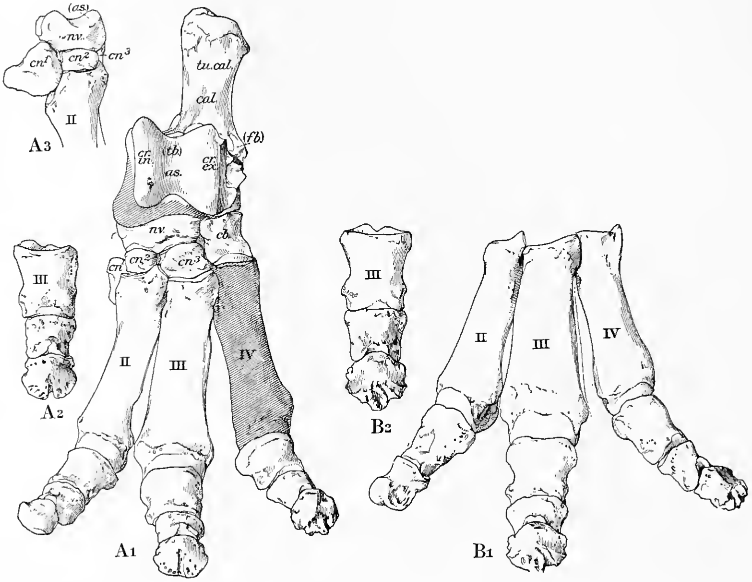

FIGURE 540.—Left pes of *Palaeosyops leidyi*

Am. Mus. 1589: A_1, Front view of pes with the phalanges foreshortened; A_2, upper view of phalanges of the median digit; A_3, inner side view of tarsus. Am. Mu 11682: B_1, Front view of pes; B_2, upper view of phalanges of the median digit. One-third natural size.

The tibia (Am. Mus. 1562) is distinguished by a moderate development of the cnemial crest; posteriorly the popliteal space is bounded by a high internal and a low external border; the posterior surface of the midshaft is gently convex, the inner surface flattened; anteriorly the cnemial crest subsides into the angulate anterior face of the shaft.

The fibula is restored from other specimens. It has a very elevated postero-external facet on the tibia, and inferiorly it articulated not only with the astragalus but also in extreme extension of the pes it barely touched the calcaneum. In the contemporary aquatic rhinoceros *Amynodon* the tibia is relatively shorter, the superior head of the fibula is more inferior in position, and distally the fibula barely, if at all, touched the calcaneum.

The pes is known principally from the associated feet of Am. Mus. 1550 and metapodials and tarsus of Am. Mus. 1582, all finely preserved. It is distinguished generically by the relatively short neck of the astragalus, by the broad and relatively shallow cuboid, navicular, and cuneiforms, and by the moderate elongation of the metatarsals.

The total height of the calcaneum is 107 millimeters as compared with 63, the maximum width; the tuber calcis is suboval in section, the long diameter being obliquely placed; in the extreme extension of the tibia in some individuals this bone passes over posteriorly onto the calcaneum; the fibula also has a calcaneal facet.

The astragalus exhibits characters of family value in the arrangement of the ectal, sustentacular, and inferior facets as shown in Figure 541. The cuboidal facet has a broadly oval external border. The astragalar trochlea measures 50 millimeters transversely, while the depth of this bone on the internal side is 58; the trochlear groove is of moderate depth; on the outer side the trochlear surface thins out posteriorly, becoming confluent with the actual astragalo-calcaneal facet, allowing for the passage of the tibia upon the calcaneum above mentioned; distally the neck of the astragalus measures 48 millimeters transversely and 11 vertically.

On its anterior face the cuboid measures 30 millimeters transversely and 23 vertically. The navicular measures 44 transversely and 14 in its deepest part vertically. The entire breadth of the second row of the tarsi is 65, as compared with 55 in *Rhadinorhinus diploconus*. The entocuneiform is well developed on the postero-internal side of the tarsus, the mesocuneiform is small, while the ectocuneiform is large, with an internal facet for Mts II and an external facet for

Mts IV, a very distinctive feature of this pes, which enables us to distinguish it from that of *Amynodon.*

The metatarsals, like the metacarpals, are moderately long, have flattened shafts, and are widely expanded distally. The vertical measurements are, Mts II, 103 millimeters; Mts III, 110; Mts IV, 103; Mts III, distal breadth, 43. Mts II shows a posterolateral facet to which a vestige of Mts I was probably attached. As regards displacement Mts IV and III are "serial," articulating solely with the cuboid and ectocuneiform respectively; Mts II, on the contrary, is "displaced," with a prominent internal process and abutment against the ectocuneiform.

The spread of the phalanges distally as mounted is 181 millimeters. The proximal phalanges are much the largest and longest in D. III; the first phalanx has a length of 39 millimeters; the second, which exhibits a sharply upturned distal facet, has a length of 25; the third is restored, but the distal phalanx of D. IV, measuring 33 millimeters in length and 35 in breadth, is spreading and distally cleft.

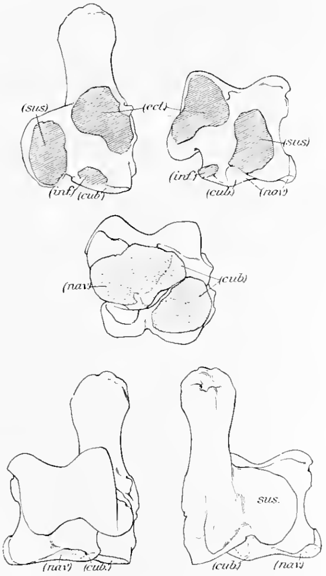

FIGURE 541.—Relations of the ectal, sustentacular, and inferior facets of the astragalus and calcaneum in *Palaeosyops*

One-third natural size.

Measurements of the composite mounted skeleton of Palaeosyops leidyi (Am. Mus. 1544)

	Millimeters
Skeleton:	
Total length, pmx to tail drop	2, 007
Total length, pmx to ischial tuberosity	1, 980
Total height, top of third dorsal spine	1, 090
Total height to top of scapula	1, 010
Total length along vertical column	2, 083
Skull:	
Total length, incisors to occipital condyle	415
Total breadth, transverse zygomata	310
Vertebral column, length:	
27 presacral vertebrae	1, 230
7 cervicals	320
Midcervical centrum	34
17 dorsals	820
Fourth dorsal centrum	38
Fourth dorsal, height of spine	163
3 lumbars	148
Second lumbar centrum	47
4 sacrals	159
19 caudals (partly restored)	615
Ribs:	
Fifth rib, outer curve	545
Eighth rib, outer curve	620
Scapula:	
Length	345
Greatest width	220
Pelvis:	
Os innominatum, total length	465
Width across ilia	488
Fore limb, total length	810
Humerus, total length	325
Radius, total length	235
Ulna, total length	315
Carpus, top of lunar to bottom of magnum	50
Carpus, width	96
Manus, length, lunar to tip of D. III	250
Digit III, length of metacarpal	113
Digit III, breadth of metacarpal	45
Hind limb, total length	940
Femur, total length	370
Tibia, total length	290
Pes, total length, os calcis to tip of D. III	340
Tarsus, height, calcaneum to ectocondyle	76
Astragalus, height, inner face	58
Astragalus, breadth, distal end	48
Calcaneum, total length	100
Calcaneum, total width	63
Mts III, length	110

Palaeosyops robustus

The characters of the postcranial skeleton of *P. robustus,* so far as known, seem to differ but little from those of *P. leidyi.* In the composite skeleton of *P. leidyi* (Am. Mus. 1544) many of the vertebrae, ribs, and parts of the feet and limbs seem to agree in size with the remaining parts associated with the *P. leidyi* type skull and yet are themselves associated with skulls and teeth referred to *P. robustus.*

The seven vertebrae (fig. 544) associated with a skull of *P. robustus* (Am. Mus. 1580) and used in restoring the vertebrae of the skeleton *P. leidyi* agree with those of *Manteoceras* but are nevertheless remarkable in this respect—that the flange on the pleurapophysis of C. 6 was much weaker than that in the rhinoceroses, tapirs, horses, and most placental mammals. The pleurapophysial flange on C. 5 was expanded; it is incompletely preserved, but it does not appear to differ greatly from that of *Manteoceras* or of *Dolichorhinus.* In C. 4–C. 7 the prezygapophyses and postzygaophyses face, respectively, obliquely inward and outward, whereas in D. 1 and in the succeeding dorsals they face respectively upward and downward. This oblique inward and outward facing of the prezygapophysial and postzygapophysial facets, respectively, is seen not only in *Manteoceras*, *Dolichorhinus*, and the Oligocene forms but in ungulates generally and is associated with the vertical movement of the neck.

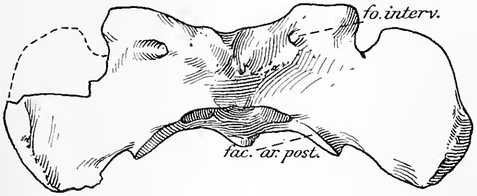

FIGURE 542.—Atlas of *Palaeosyops robustus*

Am. Mus. 1580 Bridger formation, Bridger Basin, Wyo. Top view. One-third natural size.

In C. 5–C. 7 the posterior face of the centrum approaches a transverse oval form, the front face is wider at the top and narrow at the bottom. Comparison with *Manteoceras* is shown in Figure 552.

The neural spines of the cervicals and dorsals are narrow anteroposteriorly and deeply excavated posteriorly. They increase rapidly in height, from 55 millimeters in C. 4, 70 in C. 5, and 135 in C. 7 to 201 in D. 1. The centrum of C. 5 (posterior face) measures 43 millimeters vertically, 55 transversely; that of C. 6 begins to assume the narrower and deeper form characteristic of the dorsals. The lamellae of C. 4 and C. 5 are broadly expanded downward, while those of C. 6 and C. 7 exhibit a transverse rodlike expansion, those of C. 6 measuring 134 millimeters transversely. These parts are not very well preserved in the *P. leidyi* skeleton. The disposition of the lamellae and of the spines is different in details from that in the skeleton of *Dolichorhinus*.

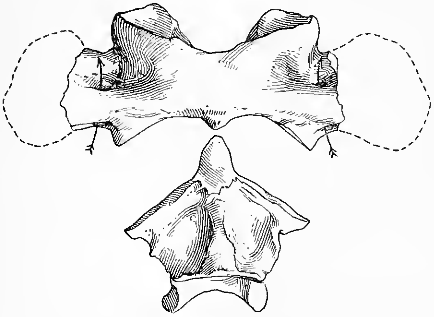

FIGURE 543.—Atlas and axis of *Palaeosyops leidyi?*

Am. Mus. 12201. Bridger C 4. Inferior surface. One-third natural size.

The scapula of *P. robustus* is represented by a referred specimen (Am. Mus. 1580). It is decidedly wider in proportion to its height than the scapula of *Dolichorhinus*. The humerus associated with the skull (Am. Mus. 1580, fig. 546) exhibits a length of 345 millimeters (estimated). It is thus slightly longer and much more massive than the humerus of *Palaeosyops?* sp. (Am. Mus. 12205), from Bridger D, and it is much longer than the humerus of *Manteoceras* from Bridger D (Am. Mus. 12204), which measures 260 millimeters. The distal breadth across the radio-ulnar trochlea is 60 millimeters. The radius (fig. 546) is extremely broad (71 mm.) both proximally and distally, a marked progressive character of the Palaeosyopinae. The ulna also sharply expands distally; the olecranon rises to a pointed rugose knob. The associated carpus agrees closely with that of *P. leidyi* but is of somewhat larger dimensions. Mts IV measures 115 millimeters; Mts III expands to 49 distally. Other characters of the *Palaeosyops robustus* manus are as follows: The most massive type, exhibiting graviportal and perhaps aquatic adaptation; brachypodal; carpus very broad (94 mm.) in upper Bridger specimens, deep anteroposteriorly (40 mm.), measuring vertically from summit of lunar to bottom of magnum 50 millimeters; metacarpals robust, shafts widely spreading distally; scaphoid very deep anteroposteriorly and laterally (thus differing from

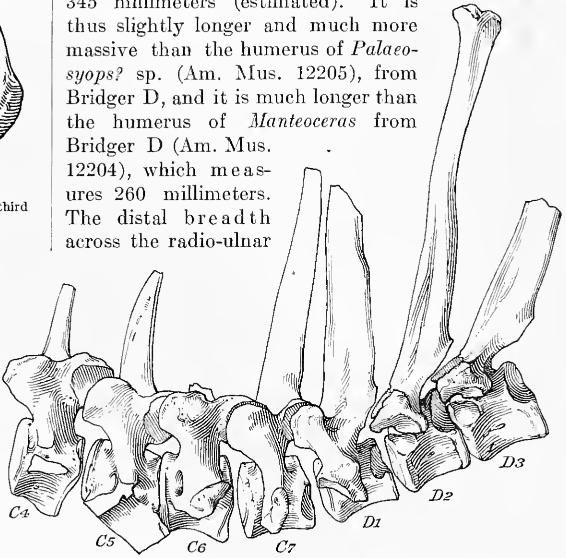

FIGURE 544.—Cervicals and dorsals of *Palaeosyops robustus*

Am. Mus. 1580; Bridger D (?). Cervicals 4–7, dorsals 1–3. One-third natural size.

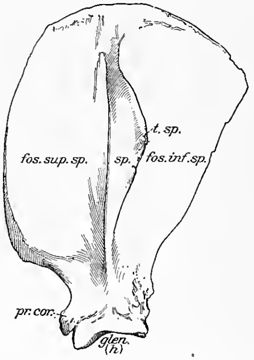

FIGURE 545.—Left scapula of *Palaeosyops robustus*

Am. Mus. 1580; Bridger C or D (?). One-sixth natural size.

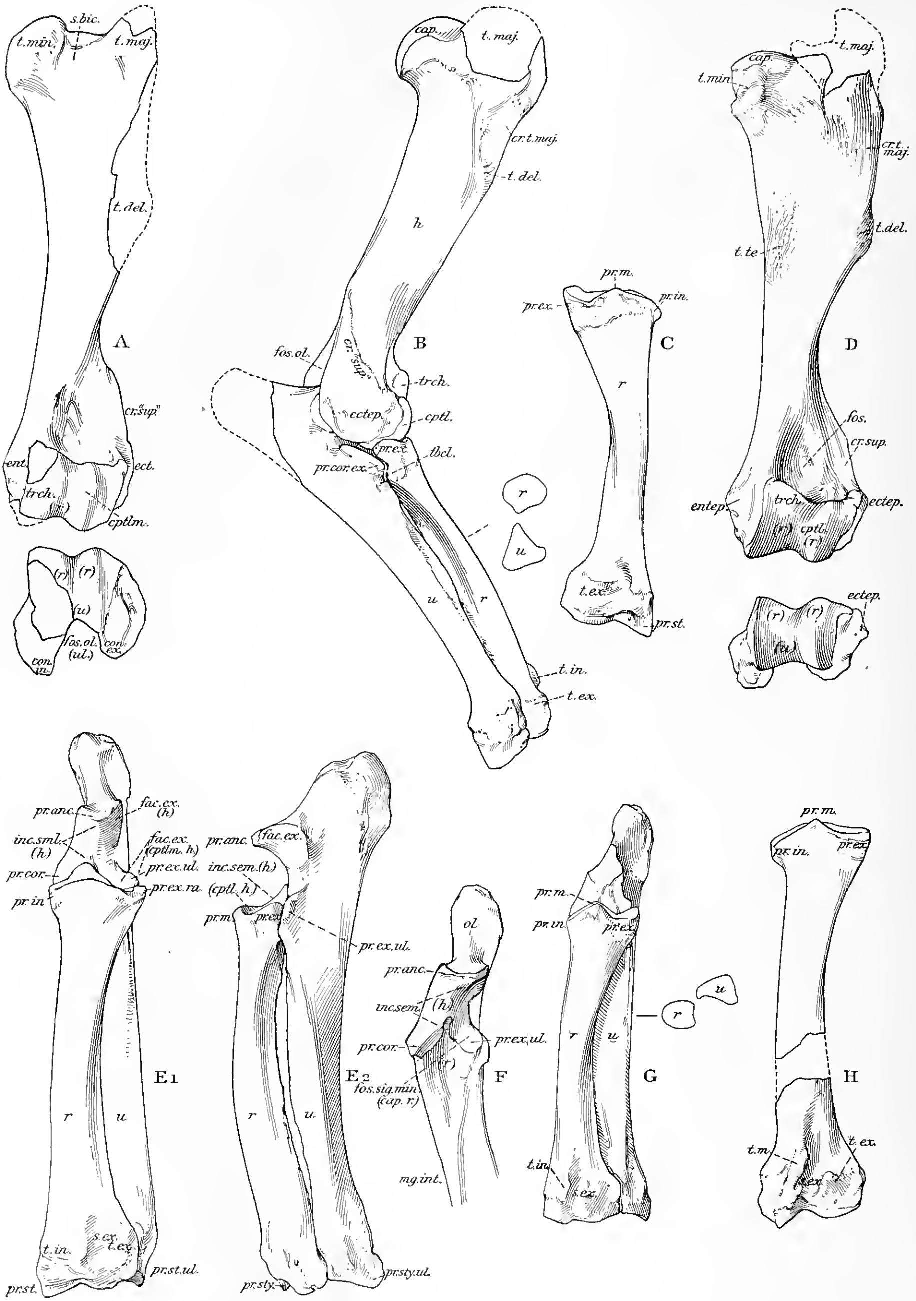

FIGURE 546.—Bones of forearm of *Palaeosyops*

A, *Palaeosyops robustus*, Am. Mus. 1580; Bridger C or D; left humerus, front and distal views. B, *Palaeosyops leidyi* (type), Am. Mus. 1544; Bridger C or D; right humerus and forearm; outer side view, with section of radius (*r*) and ulna (*u*). C, Right radius of same, front view. D, *Palaeosyops* sp., Am. Mus. 12386; Bridger C; left humerus, front and distal views. E₁, *Palaeosyops major*, Am. Mus. 13116; Bridger B 3; left radius and ulna, front view. E₂, The same, outer side view. F, *Palaeosyops robustus*, Am. Mus. 1580; Bridger C or D; left ulna, front view of proximal end. G, *Palaeosyops robustus*, Princeton Mus. 10360; Bridger Basin; left radius and ulna, with sections. H, *Palaeosyops robustus*, Am. Mus. 1580; Bridger C or D; left radius. All one-fourth natural size.

that of the manteoceratine group); lunar deep anteroposteriorly and broad laterally, resting broadly on magnum as well as on unciform; trapezium small, broadly articulating with trapezoid, and barely articulating with Mtc II, no facet apparent for scaphoid; trapezoid broad; magnum very broad, with six distinct faceted angles; large lunar facet appearing in front view, hook of magnum asymmetrical, pointed; unciform broadly horizontal, supporting more than half of the lunar; terminal phalanges cleft and somewhat rounded rather than spreading distally; the carpus while not ancestral is in general analogous to that of the heavy Oligocene titanotheres, namely, *Megacerops* and *Brontotherium*.

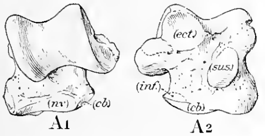

FIGURE 547.—Left astragalus of *Palaeosyops copei?*

Am. Mus. 12205a; Bridger D 1; front (A_1) and rear (A_2) views. One-third natural size.

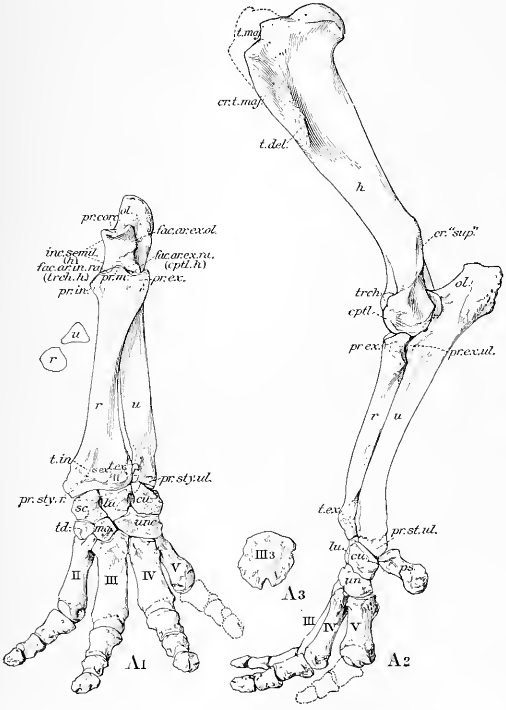

FIGURE 548.—Fore limb of *Palaeosyops copei?*

Am. Mus. 12205; Bridger D 1. A_1, Front view of left fore arm and manus, one-sixth natural size; A_2, outer view of same, with humerus, one-sixth natural size; A_3, right ungual phalanx of median digit, inferior view, one-sixth natural size.

Palaeosyops copei

Two skeletons found close together on level D 1 of the Bridger Basin (Am. Mus. 12205 and 12205a) are especially valuable because they give us the proportions of the limbs and the complete structure of the manus of an exceptionally short-footed type of *Palaeosyops*, the specific determination of which is doubtful; it may be provisionally referred to *P. copei*. One of these specimens (No. 12205a) belongs to a younger and smaller individual, the other (No. 12205) to an older and larger individual.

Skull and skeleton of the younger and smaller individual (No. 12205a)

Skull.—The skull belongs to a rather young individual. It exhibits the following especially important characters (fig. 281): (1) The nasals taper slightly anteriorly, much less so than in *Palaeosyops leidyi;* (2) the nasals are not deeply decurved at the sides as in *Limnohyops;* (3) the nasals exhibit V-shaped prolongations on the sides of the face as in *Palaeosyops;* (4) there are very slight and smooth prominences on the sides of the face at the junction of the nasals and frontals, occupying the same position as the rudimentary horns which have been observed in *Palaeosyops;* (5) there is a narrow and apparently deep sagittal crest.

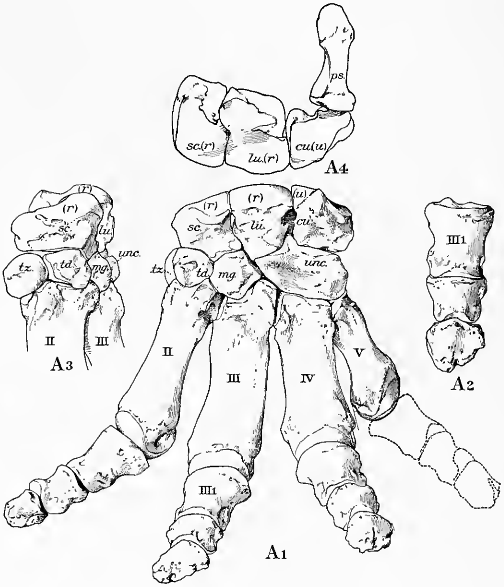

FIGURE 549.—Left manus of *Palaeosyops copei?*

Am. Mus. 12205; Bridger D 1. A_1, Front view of manus; A_2, upper view of phalanges of median digit; A_3, inner side view of carpus; A_4, upper or proximal view of carpus. One-third natural size.

Fore limb.—The chief upper limb character is that the humerus is longer (335 mm., estimated) than the radius (223 mm.), indicating slow speed, and we are surprised to find that the manus is shorter than in either *Palaeosyops leidyi* or *P. robustus*. The humerus measures about 63 millimeters across the distal trochlea. The ulna and radius are much less massive than in the type of *Palaeosyops leidyi* and slightly less massive than in the type of *L. laticeps;* the ulna, including the olecranon, measures 288 millimeters; the radial shaft 220. Distally the combined radio-ulnar facets for the carpus measure 70 millimeters. A part of the left manus is also preserved.

Hind limb.—The hind limb from the head of the femur to the ankle joint measures 642 millimeters. The pes is unfortunately unknown. The femur is a long (376 mm.), rather slender bone, greatly exceeding the tibia (270 mm.) in length, as in all slow-moving animals. Both these bones are readily distinguished from those of *Palaeosyops leidyi* by their more slender proportions. The femur has the long, straight form characteristic of titanotheres generally, with the second and third trochanters nearly opposite each other in the upper portion of the shaft; distally the patellar trochlea points obliquely forward. The patella is a relatively smaller element than in *Palaeosyops leidyi* (transverse 40 mm., vertical 56). The tibia also exhibits a slender shaft. In general these limbs are distinguished from those of *Palaeosyops leidyi* by their greater slenderness, from those of *Limnohyops laticeps* by their inferior length. The astragalus (fig. 547) is of palaeosyopine type.

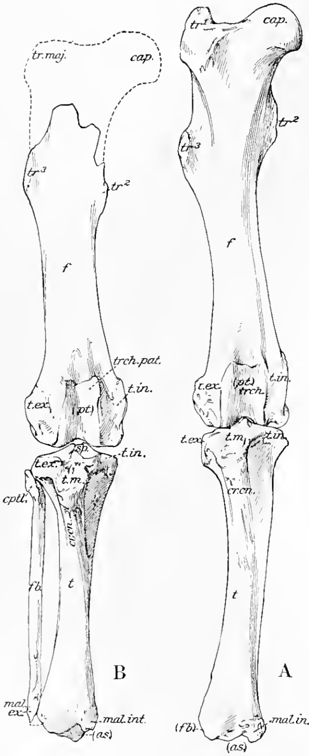

FIGURE 550.—Right hind limbs of *Palaeosyops major* and *P. copei?*

A, *P. major*, Am. Mus. 13116; Bridger B 3; femur and tibia. B, *P. copei?*, Am. Mus. 12205; Bridger D 1; femur, tibia, and fibula. One-sixth natural size.

Another more adult skeleton (Am. Mus. 12205)

Another skeleton (Am. Mus. 12205) was found with the one described above, at Lone Tree, Henrys Fork Bridger Basin, Wyo., level Bridger D 1. It is larger and belongs to a fully adult individual, the tibia measuring 300 millimeters as compared with 270 in the specimen just described.

Fore limb.—By far the most important part of this skeleton is the fore limb. The total length of the ulna is 326 millimeters, that of the radius 235; the transverse radio-ulnar carpal facets measure 85.

Manus.—Three very distinctive characters are found in the manus as compared with that of *Palaeosyops leidyi*—(1) the abbreviation of Mtc V; (2) the relatively elongate form of the distal phalanges as compared with those of *Palaeosyops;* (3) the broader displacement of the lunar on the unciform and its narrower facet on the magnum. These features are correlated with narrower hoofs, somewhat greater speed, and slightly more mesaxonic disposition of the metacarpals. The transverse measurement across the top of the carpus is 89 millimeters. The scaphoid rests on the trapezoid and magnum only, because the trapezium, though well developed, articulates with Mtc II and the trapezoid only. The lunar is narrower (32 mm.) superiorly than that of *P. leidyi* and inferiorly is readily distinguished by its narrow and nearly vertical facet for the magnum and relatively broad and horizontal facet on the unciform. The cuneiform measures 40 millimeters superiorly. The magnum is a much smaller bone than in *Palaeosyops leidyi*, subquadrate in form, with a short (16 mm.) oblique continuous facet for the lunar and unciform. The metacarpals measure, Mtc II, 96 millimeters; Mtc III, 106; Mtc IV, 93; Mtc V, 74. This animal was therefore decidedly short-footed; the median metacarpal in the contemporary *Palaeosyops leidyi* measures 116 millimeters. The form of the distal phalanges is somewhat more elongate and less expanded distally than in *Palaeosyops*.

Femur.—The femur exhibits the lesser and third trochanters directly opposite each other; distally it measures 90 millimeters across the condyles.

Tibia.—The tibia is finely preserved. The femoral facets measure 87 millimeters (tr.), the astragalar facets 43 (tr.) the shaft 31 (tr.) by 33 (ap).

Measurements of limb bones referred to Palaeosyops, in millimeters

	P. copei, Am. Mus. 12205 (adult), Bridger D 1	P. copei, Am. Mus. 12205a (young), Bridger D 1	P. leidyi, Am. Mus. 1544 (composite skeleton), Bridger C(?), D
Humerus, length	335	--------	325
Radius, length	233	223	235
Radius, breadth, proximal end	62	54	63
Radius, breadth, distal end	67	56	67
Ulna, length	325	290	315
Carpus, width	95	86	96
Mtc II, height	96	93	106
Mtc III, height	105	103	113
Mtc III, greatest width, distal	39	35	45
Mtc IV, height	93	89	102
Mtc V, height	75	73	75
Femur, length	376	370	370
Tibia, length	293	273	290

Palaeosyops copei?

From an uncertain level in the Washakie Basin comes an imperfect pes (Am. Mus. 5097) associated with other limb fragments, which Cope erroneously referred to his "*Palaeosyops vallidens*" but which is certainly a member of the Palaeosyopinae, whereas Cope's *P. vallidens* is now referred to *Dolichorhinus vallidens*, a member of the *Manteoceras-Dolichorhinus* group. Possibly this pes is referable to *P. copei*.

The astragalus in question agrees in most characters with those referred above to *Palaeosyops copei* (Am. Mus. 12205, 12205a) but is distinguished by the wider sustentacular facet, deeper navicular facet, and lower internal trochlear keel. The broad cuboidal facet also rounds off into the distal calcaneal facet; the pit on the inner face of the astragalus, below the internal trochlear keel, is very deep, and the internal distal protuberance for the lateral ligament is also very prominent; the depression for the tip of the fibula is wanting. The cuboid (absent) was elongate, and Mts IV does not articulate with the ectocuneiform (cf. *P. leidyi*, above).

Another palaeosyopine Washakie specimen from the Cope collection (Am. Mus. 5105) is an astragalus associated with fragmentary limb bones and bearing the same museum number as the upper dentition which was referred to above as allied to *Palaeosyops copei*. The characters of the astragalus do not support this association; it is about one-fourth smaller than that of *P. leidyi* and has a relatively narrower neck and narrower ectal and sustentacular facets, the ectal facet being shallow. It rather resembles a small *Limnohyops*.

SUBFAMILY MANTEOCERATINAE

Graviportal titanotheres of the upper deposits of the Bridger Basin, Wyo., the lower deposits of the Washakie Basin, Wyo., and the upper deposits of the Uinta Basin, Utah. Feet brachypodal. Ungual phalanges truncate. Tibia very short. Astragalus wide.

Manteoceras

General features.—Judging from its limb proportions, *M. manteoceras* was a slow-moving animal, much less alert than the tapir (*T. terrestris*) and less swift than its congeners of *Mesatirhinus*. All its known skeletal parts were found in Bridger D, so that it was contemporaneous with the larger and more massive species of *Palaeosyops*. These parts tend to confirm the view that *Manteoceras* was allied to *Mesatirhinus*, *Dolichorhinus*, and the Oligocene titanotheres. The *Manteoceras* of this period was a short, low-bodied animal. The skeleton, like the skull, is in many features prophetic of the Oligocene titanotheres; it is more paraxonic and tetradactylous, D. 5 being relatively longer than in *Palaeosyops;* the tibiae are relatively shorter ($\frac{68}{100}$ of the femur) than in any other Eocene titanothere; the humerus is intermediate in length and in its tuberosities foreshadows that of Oligocene type, there are broad flangelike pleurapophyses in the posterior cervicals. Many of the adaptive analogies ally it to *Palaeosyops*, although the deeper paleotelic resemblances ally it to *Dolichorhinus*.

Generic characters.—Atlas narrower than in *Palaeosyops* but broader than in *Mesatirhinus;* axis with a high spine; neural canal of cervicals and anterior dorsals rounded rather than angulate superiorly; anterior faces of cervical centra subcircular, lateral flange on C. 6 large, spines of cervical and dorsal vertebrae abbreviate as in *Palaeosyops*, second dorsal with prezygapophysis forming an angle with the neural spine. Humerus intermediate to short; manus mesatipodal; superior facets of carpals and metacarpals flatter, relatively wider posteriorly; scaphoid shallower anteroposteriorly; lunar with subvertical magnum facet; cuneiform flatter; trapezoid with facet for trapezium continuous with scaphoid facet. Magnum relatively narrow, with scaphoid facet subvertical, posterior hook spatulate; unciform relatively narrow, with subquadrate lunar facet. Metacarpals longer, narrower and more straight-sided than in *Palaeosyops*, but broader than in *Mesatirhinus;* proximal facets wide posteriorly; metacarpal V relatively longer than in *Palaeosyops;* phalanges smaller, shorter, and broader; distal phalanges broadly expanded, truncate, and deeply cleft. Femur of intermediate length. Tibia both relatively and absolutely short, with broad proximal end. Astragalus intermediate, rather broad, with broader convex tibial keel of the trochlea and broad cuboid facet, but also with straight-sided sustentacular facet and deep navicular facet.

Materials.—Material referable to this genus is rare. There are, in fact, only two specimens in which parts of the postcranial skeleton are certainly associated with the skull and dentition—Am. Mus. 1587, a young adult male from Bridger D, the skull of which is shown in Figure 303, and Am. Mus. 12204, a crushed skull of an old animal, possibly a female, from Bridger D 1 or D 2. A third specimen (Am. Mus. 12216), consisting of an incomplete manus, is not associated with a skull or with dentition but agrees so closely with Am. Mus. 1587 that it may be referred with confidence to *Manteoceras*.

From these three specimens we learn the principal characters of the cervical vertebrae, anterior dorsals, humerus, manus, femur, tibia, and astragalus. A pelvis is provisionally referred. The remaining vertebrae, ribs, sternals, and most of the pes are practically or wholly unknown.

Manteoceras manteoceras

A close examination of the vertebrae of *Manteoceras* in comparison with those of *Palaeosyops* and *Dolichorhinus* shows that the differences relate mostly to rather minor details and do not lend themselves to broad characterizations. It may be said, however, that in a general way the vertebrae of *Manteoceras* seem to be intermediate in form between those of *Palaeosyops* and of *Dolichorhinus*, sharing with those of *Palaeosyops* the high spine of the axis and the anteroposteriorly narrower spines of the anterior dorsals and sharing with those of *Dolichorhinus* the larger pleurapophysal flange of C. 6, the marked angulation between the prezygapophysis and the neural spine in D. 2, the inferior keels on D. 1, D. 2.

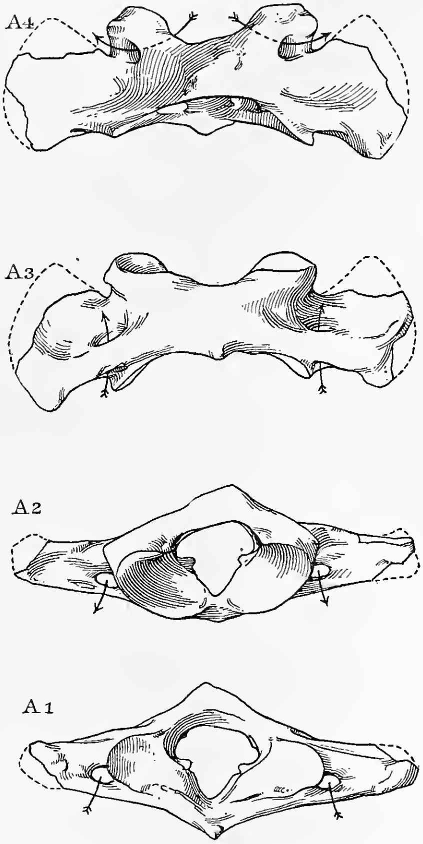

FIGURE 551.—Atlas of *Manteoceras manteoceras*

Am. Mus. 12204; upper Bridger. A1, Posterior view; A2, anterior view; A3, ventral view; A4, dorsal view. The arrows indicate the course of the first spinal nerve and vertebral artery. One-third natural size.

The atlas of *Manteoceras* has a larger vertebrarterial canal, the anterosuperior border of the cotylus is more deeply concave, the superior openings for the spinal nerve are nearer the lateral borders. The median hypapophysis is acuminate rather than peg shaped. The posterior root, or proximal portion of the pleurapophysis is thicker vertically. The atlas, on the whole, is intermediate in form between those of *Palaeosyops* and of *Dolichorhinus*, it being broader than that of *Dolichorhinus*, but sharing with it several of the characters already mentioned.

The axis probably had a taller spine than in *Palaeosyops;* the crura of the neural arch appear shorter anteroposteriorly; the postzygapophyses were larger and less inclined downward; the neural canal was more arched—that is, less angulate superiorly; the posterior face of the centrum was not so wide.

The third to seventh cervical vertebrae (see fig. 552) differ from those of *Palaeosyops* (Am. Mus. 1580, 1562). The neural canal is smaller and more roundly arched superiorly; the anterior faces of the centra are more circular instead of being broadly flattened at top; the posterior faces of the centra are also rounder superiorly and shallower vertically; the prezygapophyses and postzygapophyses are possibly larger. The neural spines seem to be of about the same relative size in the two genera, and lateral flanges or pleurapophyses appear on C. 3 to C. 6 in both genera, but the flange on C. 6 seems to have been larger in *Manteoceras* than in *Palaeosyops*.

The first dorsal had a spine of nearly the same relative size and proportions as in *Palaeosyops*; the neural canal is smaller and more arched superiorly, the front face of the centrum is rounder at top, and the rear face of the centrum, including the facets for the capitulum of the second rib, is more transversely oval. The oblique external buttress or column formed by the conjoined pedicles of the prezygapophysis and pleurapophysis in *Manteoceras* is shorter; the prezygapophysis seems more horizontal and broader anteroposteriorly. In the second dorsal both the anterior and posterior faces of the centrum are more transversely oval, the pleurapophyses spring from the sides of the centra at a lower level, the rib facets are smaller; the prezygapophyses face upward and form an open angle with the base of the neural spine, whereas in *Palaeosyops* the prezygapophyses of this vertebra face forward and upward and are nearly continuous with the base of the spine. The remaining vertebrae are too imperfectly known to warrant description.

The scapula (Am. Mus. 1587) is too insufficiently known to afford diagnostic characters.

The humerus (Am. Mus. 12204, fig. 553, B) is of intermediate length (290 mm.) between the long humerus of *Palaeosyops* (325) and the relatively short humerus of *Dolichorhinus* (255 to 315); it agrees nearly in length and general characters with the humerus of the *Limnohyops* skeleton Am. Mus. 11689, from Bridger B 2 (see above); it is massive proximally, with a heavy deltoid ridge; it apparently had a platelike crest for the infraspinatus muscle and stout tuberosities for the supraspinatus and deltoid muscles; the supinator crest is relatively short. The radius and ulna are not known.

The manus (Am. Mus. 12204, 1587, 12216) represents a broad-footed phase of the same stock that gave rise to *Mesatirhinus* and *Dolichorhinus*, and although broader than in *Mesatirhinus* is separated from that of *Palaeosyops* by many trenchant characters, the resemblances to that form being chiefly homoplastic or analogous. The width of the carpus (79 mm., estimated) is intermediate between that of *Mesatirhinus* (65 to 72) and of *Palaeosyops* (95), but nearer the former than the latter. The superior facets of the carpals and metacarpals are flatter than in *Palaeosyops* and relatively wider posteriorly. More in detail, the scaphoid (Am. Mus. 12204) in superior view is more shallow anteroposteriorly, being suboval, with broad ends, whereas in *Palaeosyops* it is elongate anteroposteriorly, with pointed ends; the facet for the magnum is relatively broader, that for the trapezoid more horizontal than in *Palaeosyops*. The lunar (No. 12204) has the facet for the magnum more vertical and that for the unciform more horizontal than in *Palaeosyops;* its posterior face is relatively deeper and much narrower, but not so much so as in *Mesatirhinus*. The cuneiform (Am. Mus. 12216) differs from that of *Palaeosyops* in the following particulars: The superior (radial) facet is not produced antero-internally into a ridged prominence, is deeper anteroposteriorly near the external end, and is separated from the broad pisiform facet by a high keel; of the two facets for the lunar the upper one is comparatively deep vertically, the lower one is very shallow; the unciform facet is deeper anteroposteriorly. As compared with that of *Mesatirhinus* the cuneiform is much broader, but a subfamily agreement is seen in the detailed characters of the facets. The pisiform is not preserved. In the trapezoid (Am. Mus. 1587, 12216) the trapezium facet is confined to the postero-external part of the bone and is broadly and roundly continuous above with the scaphoid facet, whereas in *Palaeosyops* it extends nearer to the front face of the bone and meets the scaphoid facet supero-anteriorly at an acute angle. In *Manteoceras* also the front face of the trapezoid is not carried obliquely downward and inward

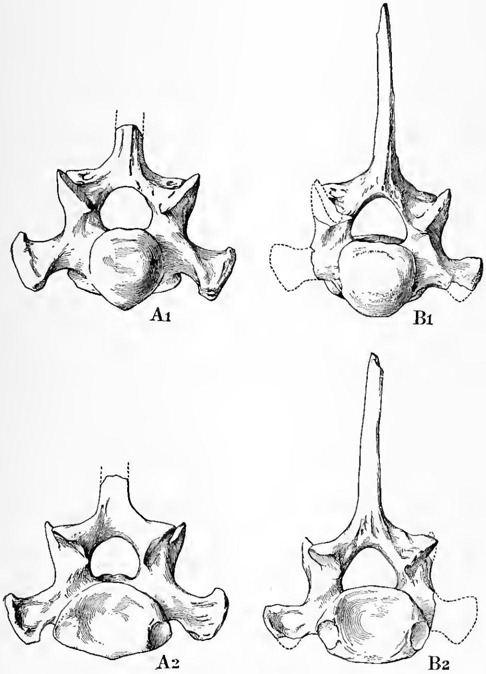

FIGURE 552.—Seventh cervical vertebra of *Manteoceras manteoceras* compared with that of *Palaeosyops leidyi*

A1, A2, *M. manteoceras*, Am. Mus. 12204; anterior and posterior views. B1, B2 *P. leidyi*, Am. Mus. 1562; anterior and posterior views. One-third natural size.

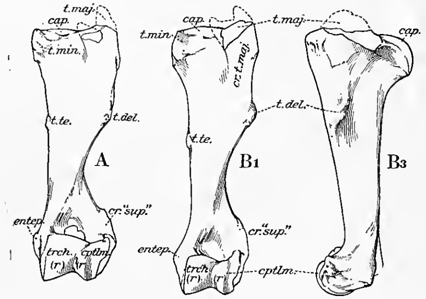

FIGURE 553.—Left humerus of *Manteoceras manteoceras*

A, Am. Mus. 12384; Bridger C 3; front view. B, Am. Mus. 12204; Bridger D 2; front (B1), and outer side (B3) views. One-sixth natural size.

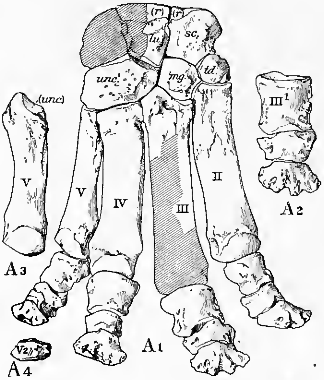

FIGURE 554.—Right manus of *Manteoceras manteoceras*

Chiefly from Am. Mus. 1587; Bridger C or D. Scaphoid, lunar, and magnum chiefly from Am. Mus. 12204. The magnum itself and the scapho-magnum contact as represented are somewhat too broad to fit well in 1587. A1, Front view of manus; A2, phalanges of median digit; A3, outer side view of metacarpal V; A4, second phalanx of digit V. One-third natural size.

into an angulate process, and in inferior view the bone is more oval, whereas in *Palaeosyops* it is more or less rhomboid. In most of these characters the trapezoid is, on the whole, nearer to that of *Mesatirhinus* than to that of *Palaeosyops*. The trapezium is not known, but to judge from the character of the trapezium facets on the trapezoid it probably approached nearer to the pear-shaped trapezium of *Mesatirhinus* than to the broad ovoid trapezium of *Palaeosyops*. The magnum (Am. Mus. 1587, 12204) has a relatively narrower front face than in *Palaeosyops*, and its scaphoid facet is more vertical than horizontal; the facet for Mtc II is larger, the facet for Mtc III in inferior view is more straight-sided, broader posteriorly, and less broad anteriorly; the posterior hook of the magnum is broadly spatulate instead of posteriorly pointed; the capitellum, or posterosuperior head for the scaphoid and lunar, in Am. Mus. 12204 appears more globose than in *Palaeosyops*, but this character is not so well shown in Am. Mus. 1587. The unciform (Am. Mus. 1587, 12216) is proportionately narrower than in *Palaeosyops* but broader and deeper vertically than in *Mesatirhinus*; in top view the lunar facet is subquadrate, whereas in *Palaeosyops* it is more rhomboid, being produced postero-externally and antero-internally; the cuneiform facet is not so wide supero-externally, being thus of more even diameter than in *Palaeosyops*, in which it is wide superointernally and narrow supero-externally. The tuber, or posterior process of the unciform, on its internal face meets the main body of the bone at right angles, whereas in *Palaeosyops* it slopes gently down and meets the posterior face on an open angle.

FIGURE 555.—Pelvis of *Manteoceras?*

Antero-inferior aspect of pelvis. Am. Mus. 2358; Washakie Basin, level B 1. One-sixth natural size.

The metacarpals (Am. Mus. 12216, 1587, 12204 in part) are relatively longer, narrower, and more straight-sided than in *Palaeosyops;* their distal (phalangeal) facets are transversely subcylindrical rather than subglobose; their proximal or carpal facets are relatively wider posteriorly, except in Mtc V; Mtc II is a little shorter than in *Palaeosyops*, but Mtc IV and V are as long or longer. The dimensions of the metacarpals compared with those of the supposed *Palaeosyops copei?*, Am. Mus. 12205, are as follows:

Measurements of metacarpals in Manteoceras manteoceras and Palaeosyops copei?, in millimeters

	M. manteoceras			P. copei, Am. Mus 12205
	Am. Mus. 12216	Am. Mus. 1587	Am. Mus. 12204	
II, length				96
II, proximal width (front)				35
II, distal width (maximum)				42
III, length	104			107
III, proximal width (front)	27	27		
III, distal width				38
IV, length	95	97	92	93
IV, proximal width (front)	27	27	25	31
IV, distal width (maximum)	[a] 30	30	29	40
V, length	82	82		75
V, proximal width (front)	17	17		24
V, distal width (maximum)	26	23		35

[a] Estimated.

The phalanges are much smaller, relatively shorter, broader distally, and deeper vertically than in *Palaeosyops:*

Comparative measurements of proximal phalanx of digit III in Manteoceras manteoceras and Palaeosyops copei?, in millimeters

	M. manteoceras, Am. Mus. 1587	P. copei, Am. Mus. 12205
Length	27	36
Transverse proximal	29	35
Vertical proximal	22	24
Transverse distal	29	27

The distal phalanges are short and widely expanded, truncate, and deeply cleft distally, in contrast to the longer, distally rounded to subpointed, rather feebly cleft unguals of *Palaeosyops*. These differences, considered in connection with the narrower, straight-toed manus, in contrast to the broad spreading-toed manus of *Palaeosyops*, point to tapir-like rather than hippopotamus-like habits and tend also to confirm not only the hypothesis that *Palaeosyops* was semiaquatic but also the hypothesis that *Manteoceras* was allied to *Mesatirhinus* and to the Oligocene titanotheres.

A well-preserved pelvis (Am. Mus. 2358) from the Washakie Basin is provisionally referred to *Manteoceras*. The measurements are as follows: Pelvis transverse 530 millimeters, anteroposterior 450; pubo-ischiadic symphysis 170. Only three sacral vertebrae are preserved out of the probable four. This specimen illustrates the deeply revolute character of the prezygapophyses of the first sacral vertebra, the transverse extent (170 mm.) of the sacral arcade, the flattened anterior (inferior) faces of the ilia, the vertical keel below the pubo-ischiadic symphysis, the deep acetabular notch. Its graviportal adaptation is indicated by the uniformly convex superior border of the broadly expanded ilia, in contrast with the indented border of the pelvis of *Limnohyops?* (Am. Mus. 2348) mounted in the skeleton of *P. leidyi* (see above).

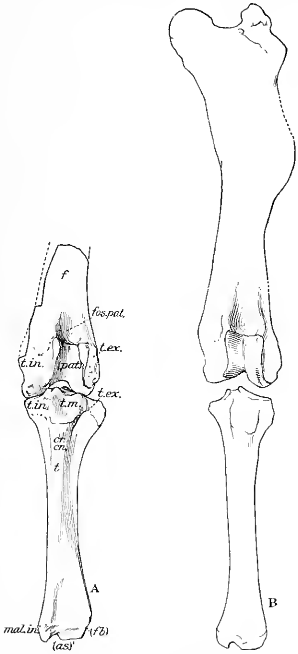

FIGURE 556.—Femora and tibiae of *Manteoceras manteoceras*

A, Left tibia and distal end of femur, Am. Mus. 12204, Bridger D 2, front view; B, left femur and tibia, Am. Mus. 1587, Bridger C or D, front view. One-sixth natural size.

The femur (Am. Mus. 1587, 12204) is not very well preserved. Its length (400 mm.) is somewhat less than that (435 mm.) of a large *Palaeosyops major* (Am. Mus. 13116) from Bridger B 3; it is relatively stouter than in the large *Mesatirhinus petersoni* (No. 11659); the third trochanter is large; the distal condyles are more sharply keeled than in *Palaeosyops major*.

The tibia (Am. Mus. 1587, 12204) is much shorter (length 265 mm.) than in *Palaeosyops major* (325 mm.); it is somewhat shorter and much stouter than in *Mesatirhinus*, and the proximal end is relatively broad (87 mm).

The astragalus (Am. Mus. 1587, 12204) parallels that of *Limnohyops* and *Palaeosyops* in the following characters: Trochlea broad with very convex tibial keel, neck relatively broad, cuboid facet broad, sustentacular facet not very long vertically. It differs, however, from that of the Palaeosyopinae and shows the subfamily kinship with *Mesatirhinus* in the following: Neck not so broad in proportion to the total height, navicular facet deep anteroposteriorly, sustentacular facet straight-sided, forming with the cuboid facet a broad L, its internal or tibial edge set nearly flush with the internal face of the bone; depression on internal face beneath the tibial keel not forming a deep pit; process on internal face near distal end forming a marked protuberance; articular surface of the trochlea extending down antero-internally on to the pedicle of the trochlea. The astragalus is distinguished from that of *Mesatirhinus* not only by its greater breadth and stoutness throughout, but especially by the greater breadth of the cuboid facet, the more convex tibial keel of the trochlea, the shorter and broader sustentacular facet. Of the two astragali Am. Mus. 12204 is much the smaller and differs from Am. Mus. 1587 in minor details, differences which may be connected with the fact that No. 12204 is an old and possibly female animal, whereas No. 1587 is a very large young male.

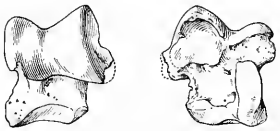

FIGURE 557.—Left astragalus of *Manteoceras manteoceras*

Am. Mus. 1587; Bridger C or D; front and rear views. One-third natural size.

The rest of the pes is unknown.

Comparative measurements of limb bones referred to Limnohyops, Manteoceras, and Mesatirhinus, in millimeters

	Limnohyops monoeonus?			Manteoceras manteoceras			Mesatirhinus petersoni		
	Am. Mus. 11689, Bridger B 2	Am. Mus. 11699, Bridger B 2	Am. Mus. 11690, Bridger B 1	Am. Mus. 1587, Bridger D	Am. Mus. 12204, Bridger D 2	Am. Mus. 12216, Bridger D	Am. Mus. 11659, Bridger C 5	Am. Mus 1571, Washakie A	Princeton Mus. 10013, Bridger
Humerus, length, head to interior condyle	295				290				
Humerus, width (across trochlea)	52								
Radius, length	228–233	230					258	233	245
Radius, width proximal end	58	55						49	50
Radius, width distal end	56	57						49	50
Radius, circumference of shaft, just above middle	74	74						72	75
Ulna, length	298–308	305					[a] 310	300	310
Carpus, width	[a] 75			[a] 79			72		65
Mtc II, height	99	99						103	101
Mtc II, width, maximum distal	31	32						25	25
Mtc III, height	109	103				105	118		112
Mtc III, width, maximum distal	33	34					31		28
Mtc IV, height	98	97		97	91	95		106	98
Mtc IV, width, maximum distal	29	29		30	29	[a] 31		24	22
Mtc V, height		79		82		83	88	85	82
Mtc V, width, maximum distal		24		22		26		20	19
Femur, length	[a] 357		387	[a] 395			358		
Tibia, length	285		297	268	265		283–287		
Tibia, width, proximal end	71		83		87		72		
Astragalus, height, inner face	53		55	56	50		53		
Astragalus, width, proximal end	39		42	49	42		40		
Astragalus, width, distal end	44		44	44	40		41		
Calcaneum, height (length)	98		108				95		
Calcaneum, width (including sustentaculum)	53		55				46		
Mts II, length			114				110		
Mts II, width, maximum distal			24				23		
Mts III, length	112		126				121		
Mts III, width, maximum distal	32		34				29		
Mts IV, length	105			97	91		111		
Mts IV, width, maximum distal	27			30	28				

[a] Estimated.

SECTION 4. THE POSTCRANIAL SKELETON OF UPPER EOCENE TITANOTHERES

SUBFAMILY DOLICHORHININAE

Slender to mediportal titanotheres of the upper deposits of the Bridger Basin, Wyo., the deposits of the Washakie Basin, Wyo., and the deposits of the Uinta Basin, Utah. Feet mesatipodal to brachypodal. Ungual phalanges truncate. Tibia slender to short. Astragalus narrow.

The general adaptations of the limbs and other parts of the skeleton of the Dolichorhininae have already been stated. The main features of the adaptive radiation of the skulls and feet and the geologic succession are as follows:

Mesatirhinus: Mesaticephalic; mesatipodal; Bridger C and D, Washakie A.

Metarhinus: Mesaticephalic; mesatipodal; Washakie B, Uinta B 1.

Dolichorhinus: Dolichocephalic; brachypodal; Washakie B, Uinta B 2.

In the treatment of these forms it is convenient to begin with the tapir-like *Mesatirhinus*, on the whole the most primitive and central, and then to describe *Metarhinus*, a dwarfed, aberrant form. This will be succeeded by the description of the extremely long-headed *Dolichorhinus*, which is further distinguished from the above animals by the possession of short feet.

Mesatirhinus

GENERAL FEATURES

The parts of the skeleton of *Mesatirhinus* are readily distinguished by the collector and student as belonging to the most slender-limbed of the known middle Eocene titanotheres.

It is a striking proof of the generally heavy-bodied proportions of the Eocene titanotheres that even these most light-limbed members of the family are somewhat heavier in their proportions than the modern tapirs, animals which we are accustomed to think of as rather heavy-bodied, forest-living, and certainly not cursorial. In brief, *Mesatirhinus* in limb structure is proportioned much as *Tapirus indicus*, but the fore and hind feet were somewhat broader and flatter, the back was more arched, the neck was relatively shorter, the head more elongate, thus bringing the lips closer to the ground.

Yet, as compared with the other middle Eocene titanotheres, *Mesatirhinus* is mediportal, and all parts of the skeleton which are known are relatively narrow and deep in their proportions, including the atlas, the limbs, the carpals and tarsals, and the metapodials. We observe at once (figs. 512, 520) that the digits of the manus are more compressed laterally and at the same time more paraxonic and tetradactylous—that is, the fifth digit of the manus is relatively longer than in the above-described *Palaeosyops* and *Limnohyops*.

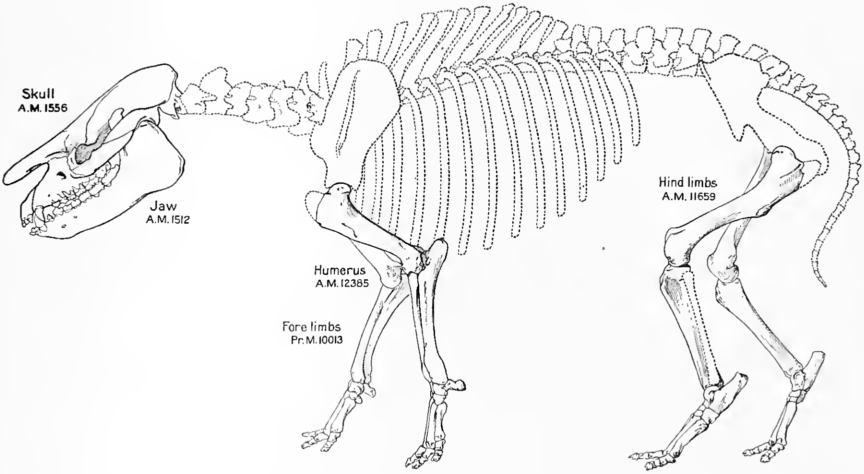

FIGURE 558.—Restoration of the skeleton of *Mesatirhinus petersoni*

A provisional reconstruction of this light-limbed titanothere of Bridger D, based on specimens in the American Museum pertaining to various individuals. The backbone, scapula, and pelvis are restored in broken lines from *Dolichorhinus;* the ribs from *Palaeosyops.* One-twelfth natural size.

The above diagnosis is important because this type of skeleton is broadly ancestral to the mediportal and brachypodal *Dolichorhinus*.

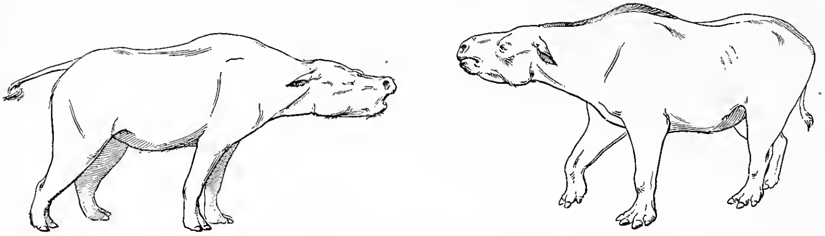

FIGURE 559.—Restorations of *Mesatirhinus petersoni* (left) and *Palaeosyops leidyi* (right)

By Mrs. E. M. Fulda. Bridger C and D. About one-thirtieth natural size.

The skeletal material of *Mesatirhinus*, like that of *Manteoceras*, is rarely associated with parts of the skull or teeth, so that identifications are difficult; parts only of two skeletons have been found associated. The specimens listed below have been collected.

Mesatirhinus petersoni, Princeton Mus. 10013, Figures 563, 565, 566; Bridger D.
Mesatirhinus petersoni?, Am. Mus. 11659 (fore and hind limbs not associated), Figure 564; Bridger C 5.
Mesatirhinus petersoni, Am. Mus. 1571; Washakie A.
Mesatirhinus megarhinus, Am. Mus. 1523 (associated), Bridger C?

The above individuals include only a single vertebra, the atlas. The scapula and pelvis are still unknown. When found they will furnish us with very significant characters.

In the following description of the skeleton it seems best to describe together the parts belonging to the different species of *Mesatirhinus*. The geologically oldest specimen named in the above table is *M. megarhinus*, from the Bridger formation, level unknown (Am. Mus. 1523), consisting of a skull with incomplete axis. From Spanish John's Meadows, Bridger Basin, Wyo. (level Bridger C or D), came the very well-preserved radius, ulna, and manus (Princeton Mus. 10013) that were describedand figured by Earle (1897.1, pp. 358–364) as belonging to *Limnohyops laticeps*.

These unassociated bones agree very well with those of Am. Mus. 1571. In Bridger C 5 was found Am. Mus. 11659, including the radius, ulna, manus, femur, tibia, and pes, which afford a knowledge of the relative proportions of the fore and hind limbs. These bones are considerably larger than those of any of the other specimens and apparently pertain to a large individual of *M. petersoni*. In beds of the same age (Washakie A) was found the leading associated specimen (Am. Mus. 1571), including the front part of the skull and upper dentition of *Mesatirhinus petersoni*, together with the radius, ulna, incomplete manus, astragalus, and fragments of the pelvis.

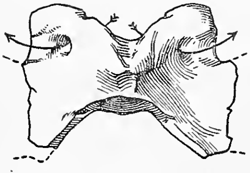

FIGURE 560.—Atlas of *Mesatirhinus megarhinus*

Am. Mus. 1523; upper Bridger. The arrows indicate the course of the first spinal nerve and vertebral artery. Dorsal view. One-third natural size.

GENERAL CHARACTERS OF THE SKELETON OF MESATIRHINUS AS COMPARED WITH OTHER EOCENE TITANOTHERES

Atlas relatively narrow and deep, elongate, facets for axis facing inward. Humerus relatively shorter, radius relatively longer than in *Palaeosyops* or *Manteoceras;* radius long, slender, with narrow extremities proximal, and distal articular facets shallow anteroposteriorly. Ulna slender, with erect, subtruncate olecranon. Manus high and narrow, straight-sided parallel metacarpals, and short phalanges; carpals in general narrow, vertically deep. Scaphoid shallow anteroposteriorly, broad posteriorly. Lunar narrow, lower end sharply wedge-shaped; magnum facet subvertical; cuneiform facet broad; cuneiform narrow, not extended postero-externally. Pisiform with proximal end sharply constricted from the shaft. Trapezium small, pear shaped, articulating with scaphoid. Trapezoid wide anteroposteriorly, shallow, truncate posteriorly. Magnum small, scaphoid facet broad. Unciform narrow, vertically deep, lunar facet quadrate. Metacarpals with carpal facets shallow and truncate (rather than extended backward as in *Palaeosyops*), elongate, straight-sided; fifth metacarpal long and narrow, proximal end embracing unciform externally. Proximal phalanges relatively shorter than in *Limnohyops* and *Palaeosyops*, longer than in *Manteoceras;* distal phalanx of D. III widely spreading and sharply truncate distally, longer than in *Manteoceras*, median cleft fairly marked. Femur slender with prominent trochanters, with patella facet oblique to long axis of shaft. Tibia long and slender, about $\frac{79}{100}$ of the length of the femur, with deeply concave facet for astragalus. Pes with high tarsals, slightly divergent digits, narrow, straight-sided metatarsals. Astragalus relatively high and narrow, with narrow trochlea and elongate neck, cuboid facet narrow, sustentacular facet narrow, vertically elongate. Calcaneum elongate with narrow sustentaculum and deep, laterally compressed tuber. Navicular relatively deep vertically, forming a quadrant in superior view. Entocuneiform vertically oval, pointed at top. Mesocuneiform anteroposteriorly elongate, narrow. Ectocuneiform relatively deep, shallow anteroposteriorly, and narrow transversely. Cuboid deep vertically, shallow anteroposteriorly, with subquadrate superior and inferior facets. Metatarsals long, straight sided, distal facet of Mts III transversely cylindrical, proximal facets truncate posteriorly (not deep as in Palaeosyopinae). Phalanges: Proximal phalanx of Mts III relatively long, narrow; middle phalanx wide and shallow; distal phalanx relatively long, very broad distally, sides obliquely truncate.

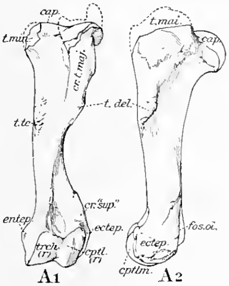

FIGURE 561.—Humerus of *Mesatirhinus megarhinus*

Am. Mus. 12385; Bridger C or D. A1, Front view; A2, outer side view. One-sixth natural size.

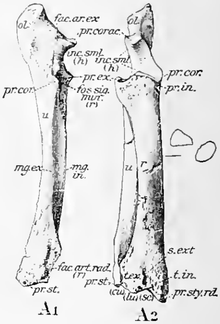

FIGURE 562.—Radius and ulna of *Mesatirhinus petersoni*

Am. Mus. 1571; Washakie A. A1, Right ulna, outer side view; A2, right radius and ulna, front view. One-sixth natural size.

The atlas (Am. Mus. 1523) shows (fig. 560) a subfamily agreement with that of *Manteoceras* and with that of *Dolichorhinus* and contrasts with that of *Palaeosyops* in the following characters: The cotylus is narrow transversely (93 mm.) but deep vertically (40 mm.); its superior border is deeply concave anteriorly; the neural arch is produced above into a circular rather than an elongate hillock; the neural tunnel is more roundly arched above; the postero-median inferior process below the odontoid is acuminate, not peg-shaped; the axis facets do not diverge so widely—that is, they face more inward; the pleurapophysial flanges are not preserved; the vertebrarterial canal was large. The atlas is distinguished from that of *Manteoceras* by its relative narrowness and depth, both anteroposteriorly and vertically.

A humerus (Am. Mus. 12385) provisionally referred to *Mesatirhinus megarhinus* from Bridger C 3 agrees in most characters with that of *Manteoceras* (Am. Mus. 12204) but is smaller and more slender. In length (260 mm.) it is far shorter than the humerus of

Palaeosyops leidyi (325 mm.). The supinator crest is relatively shorter. It is sharply separated from the humerus of the contemporary cursorial rhinoceros *Hyrachyus* by the marked asymmetry of the radial facet, the marked downward extension of the deltoid ridge, the stouter supinator crest, and the heavier proximal end. It is smaller than even the smallest (Am. Mus. 1571) of the three forearms referred to *Mesatirhinus petersoni.*

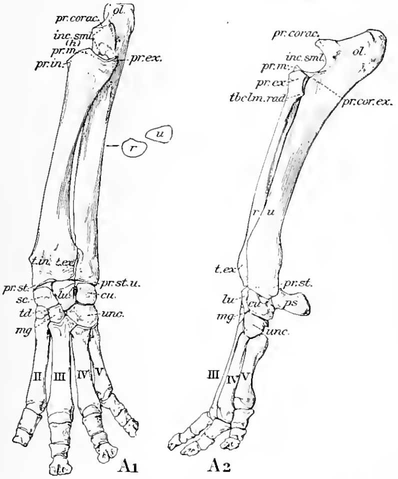

FIGURE 563.—Left forearm and manus of *Mesatirhinus petersoni?*

Princeton Mus. 10013; Bridger C or D. A_1, Front view; A_2, outer side view. One sixth natural size.

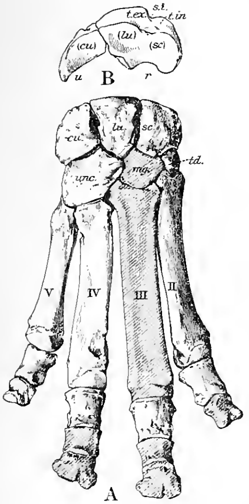

FIGURE 564.—Right manus and fragments of radius and ulna of *Mesatirhinus petersoni*

Am. Mus. 1571; Washakie A. A, Right manus; B, distal end of radius and ulna. Facets for scaphoid (sc), lunar (lu), and cuneiform (cu). One-third natural size.

The radius of *M. peterson* (Am. Mus. 1571, Princeton Mus. 10013) is remarkable for its length (233–245 mm.), its slenderness (circumference of shaft just above middle, 72–75), and the narrowness of its proximal end (tr. 49, 50) and distal end (tr. 49, 50). By way of comparison, in *Palaeosyops copei* (Am. Mus. 12205) the corresponding measurements are length 237 millimeters, breadth proximal end 62, distal end 67, circumference of shaft 87. The proximal end of the radius of *M. petersoni* is also shallower (ap. 30 mm.) than in *Palaeosyops* sp. (35). The external proximal facet for the capitellum of the humerus is much shallower anteroposteriorly (20 mm.), more deeply concave anteriorly, and continues externally into a high anteroposterior ridge which is higher than that in *Palaeosyops.* This ridge is supported inferiorly by the angulate external border of the shaft, which slopes downward and inward at a gentle angle, whereas in *Palaeosyops* the rounded external border rapidly contracts into the shaft so that the proximal end of the bone expands widely. The shaft of the radius arches forward a little less strongly than in uncrushed specimens of *Palaeosyops*, but, as already noted, is much more slender. The distal end is much less expanded transversely and relatively deeper anteroposteriorly; the internal distal process is sharply prolonged downward. The radius of *M. petersoni* (Am. Mus. 11659) is badly crushed but differs from those above de-

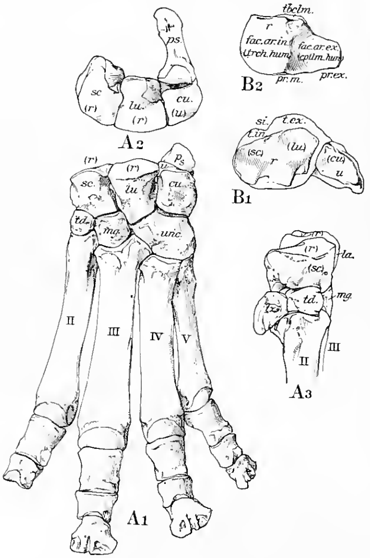

FIGURE 565.—Left manus, radius, and ulna of *Mesatirhinus petersoni*

Princeton Mus. 10013; upper Bridger. A_1, Front view of manus; A_2, top view of carpus; A_3, inner side view of carpus; B_1, radius and ulna, distal view; B_2, radius, proximal view. One-third natural size.

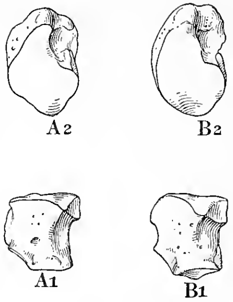

FIGURE 566.—Right scaphoid of *Mesatirhinus* and *Manteoceras*

Front and top surfaces. A_1, A_2, *Mesatirhinus petersoni*, Princeton Mus. 10013; B_1, B_2, *Manteoceras manteoceras*, Am. Mus. 12204. One-half natural size.

scribed in its greater length (258 mm.) and heavier shaft.

The ulna of *M. petersoni* (Princeton Mus. 10013) is slender (length 310 mm.) and slightly more curved anteroposteriorly than in *Palaeosyops*. The olecranon is relatively thicker transversely and is subtruncate rather than pointed posterosuperiorly; the dorsal extension of the humeral facet is narrow. The antero-external face of the shaft faces more obliquely outward; this is partly because the external longitudinal ridge is much lower than in *Palaeosyops*. The distal end of the shaft curves backward more sharply. The distal cuneiform facet is nearly at right angles to the main axis of the shaft, and the external or styloid process is not pronounced, whereas in *Palaeosyops* the cuneiform facet is more inclined to the shaft, and the styloid process is more pronounced.

Manus (Am. Mus. 1571, Princeton Mus. 10013): The chief characteristics of the manus in comparison with those of *Palaeosyops* are its narrowness and vertical height, the straight-sided character of the metacarpals, and the shortness of the phalanges, so that it represents the extreme dolichopodal stage known among the Bridger titanotheres. It shares several of these characters with *Manteoceras*, as well as many of the more detailed characters of the carpals and metacarpals, and differs from that form chiefly in its greater narrowness. The general measurements are given on page 636. In the measurements given below more in detail the first always refers to Princeton Mus. 10013, the best-preserved specimen, and the second to Am. Mus. 1571. The scaphoid is relatively deeper vertically (25, 27 mm.), shallower anteroposteriorly (36, 35), and broader posteriorly (23) than in *Palaeosyops* (Am. Mus. 12205); the radial facet is flatter, the trapezoid and scaphoid facets form a more open angle (Princeton Mus. 10013 only); the facet for the capitellum of the magnum is wider; there is a close general agreement with the scaphoid of *Manteoceras* (Am. Mus. 12204), save that the bone is narrower and the trapezoid facet smaller. The lunar is relatively narrow (27 mm.) and deep (32, 33 mm.) on both the anterior and posterior faces; the inferior end is more sharply wedge shaped, the magnum facet being subvertical in front view; the lower facet for the cuneiform is broader. In *Palaeosyops* the lunar is separated in front from the cuneiform by the dorsal ridge of the unciform. The cuneiform is narrow (26 mm.), not extended postero-externally, with ulnar and unciform facets comparatively deep anteroposteriorly (Princeton Mus. 10013, crushed in Am. Mus. 1571); facet for pisiform less elongate; cuneiform narrower than in *Manteoceras* (Am. Mus. 12216). The pisiform contrasts in many characters with that of *Palaeosyops:* the distal end of its tuber is less expanded vertically and thicker transversely; its ulnar facet is concave and triangular, that of *Palaeosyops* is convex and with rounded contour; inferiorly its cuneiform facet is rounded, that of *Palaeosyops* is deeply angulate; the head, or proximal end, is sharply constricted from the shaft, that of *Palaeosyops* rises gently from the shaft. The trapezium is small (greatest length 22 mm.), pear-shaped (resembling a small patella) rather than broadly ovate (*Palaeosyops*); a distinctive feature is that it articulates with the scaphoid. Trapezoid relatively wide (tr. 19 mm.), flat, anteroposteriorly shallow (16 mm.), and more truncate posteriorly, not produced anteroposteriorly into an oblique projection; also shallower anteroposteriorly than in *Manteoceras*. Magnum (Princeton Mus. 10013) rather small, scaphoid facet broad, flat, and subhorizontal; posterior hook broadly spatulate (Am. Mus. 11659); facet for Mtc II large and sharply ridged; magnum thus agreeing in general with that of *Manteoceras* but smaller and with narrower capitellum. The unciform is narrow (extreme width 37 mm.) and deep vertically (diameter at right angles to long axis 25 mm.); lunar facet subquadrate, ridge separating lunar from cuneiform low and not greatly produced posteriorly; postero-external process with relatively slender base and subpyramidal top, agreeing in facets with unciform but entire bone narrower. As noted above, the metacarpals (Am. Mus. 1571, Princeton Mus. 10013) are elongate, straight-sided, subcylindrical rather then flattened, and more nearly parallel with each other than in the spreading manus of *Palaeosyops;* the distal facets are somewhat flatter (less subglobose); the fifth metacarpal (Mtc V) is relatively much longer and narrower. Distinctions from *Manteoceras* are found chiefly in the greater narrowness and in the obliquely triangular rather than the posteriorly truncate broad proximal facet of Mtc II and III.

Considered more in detail: The first metacarpal, as in other perissodactyls, is entirely wanting, unless it is represented possibly by the distal part of the trapezium. The second metacarpal (length 110 mm., maximum distal width 25) has the trapezoid facet deeply concave in front and produced postero-internally into a blunt tip, unlike both *Palaeosyops* and *Manteoceras;* the trapezium facet, as in *Manteoceras,* is small and confined to the postero-external border; the facet for the magnum forms an elongate rectangular, nearly plane surface rather than an irregularly warped band, it is also more shallow posteriorly than in *Manteoceras;* the facet for Mtc III is quite small (contrast *Palaeosyops*). The third metacarpal has the proximal facet (for the magnum) pointed posteriorly instead of roundly truncate, as in *Manteoceras* and *Palaeosyops;* the facet for Mtc II is very small; the facet for the unciform is broadly triangular, whereas in *Manteoceras* it is intermediate; the facet for Mtc IV is relatively smaller than in *Palaeosyops* and faces more downward than outward (Princeton Mus. 10013); in *Manteoceras* it is intermediate. Mtc IV has the proximal facet very different from that in *Palaeosyops;* the unciform is flatter on top, and its posterior part is not decurved so sharply; posteriorly this facet is not so broad; the facet for Mtc III is nearly divided into two triangular facets, whereas in *Palaeosyops* it forms a broad half ring; the facet for Mtc V is much shallower; in all these characters Mtc IV approaches that of *Manteoceras.* The fifth metacarpal offers a very wide contrast to that of *Palaeosyops;* it is actually much longer (82 mm. as compared with 75) while only about half as wide (19 as compared with 36); the proximal end is produced externally into a high ridged prominence, which embraces the unciform externally and causes the unciform facet to face obliquely upward and inward; the facet for Mtc IV is relatively narrow. In all these characters except the extreme slenderness the fifth metacarpal, like the fourth, approaches *Manteoceras manteoceras.*

Although the third metacarpal is considerably longer than in *Palaeosyops* the first phalanx of the same digit is only about two-thirds as long (24 mm.) as that in *Palaeosyops* (37); it is, however, nearly as broad (23, estimated) as it is long (24) and therefore has about the same proportions as in *Palaeosyops* (ap. 37, tr. 36); this phalanx is thus proportionately longer than in *Manteoceras.* The distal phalanx of the same digit is widely spreading and sharply truncate distally, with a fairly marked distal cleft; in these features it approaches the corresponding phalanx in *M. manteoceras* but is longer in proportion to its distal breadth (ap. 19 mm., tr. 28, as compared with 17 by 33 in No. 1587, *M. manteoceras*). The remaining phalanges call for no special remark.

Mesatirhinus petersoni?

The manus Am. Mus. 11659, a part of the larger skeleton from Bridger C 5, differs from those of Am. Mus. 1571 and Princeton Mus. 10013 chiefly in its larger size, as shown in the table of measurements. It is pretty badly crushed but agrees well in most details of the facets, etc.

The hind limb is preserved only in the larger skeleton Am. Mus. 11659. The femur approaches that of *Hyrachyus*, first, in the large size of the third trochanter, which is relatively a little farther down the shaft than in *Palaeosyops major;* second, in the position of the patellar facet, which is more nearly at right angles to the long axis of the bone, whereas in *Palaeosyops major* it is prolonged upward and backward and becomes nearly parallel to that axis. But these characters are approached in the femur of *Manteoceras* and besides being associated with a manus and an astragalus of *Mesatirhinus* type, the femur itself is separable from that of *Hyrachyus* by various differences in the shape of the head, great trochanter, and distal end. The femur (length 358 mm.) is shorter than in *Palaeosyops leidyi* (370 mm.), but its relative length as compared with the tibia (T 79, F 100) is the same as in *Palaeosyops.* The chief distinctions from the femora of *Palaeosyops*, *Telmatherium*, and *Manteoceras* lie in the greater slenderness of the shaft and probably also in the position of the patellar facets (see above).

The tibia, though somewhat crushed, was long (283 mm.) and slender; its distal third was relatively steeper anteroposteriorly and narrower transversely than in *Palaeosyops major;* a marked difference is seen in the region of the astragalar facets; in front view the facet for the internal keel of the trochlea is deeply incised and bounded internally by a prominent vertical malleolar process; in inferior view the same facet is broad posteriorly, whereas in *Palaeosyops* it is narrow posteriorly; the facet for the external half of the trochlea is deeper anteroposteriorly and less produced antero-externally.

The pes (Am. Mus. 11659), like the manus, is of the long, narrow type, with high tarsals and straight-sided metatarsals.

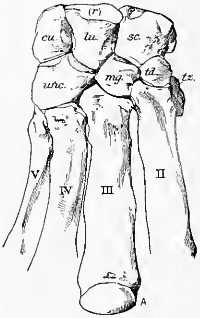

FIGURE 567.—Right manus of *Mesatirhinus petersoni?*

Am. Mus. 11659; Bridger C 5. One-third natural size.

The astragalus (Am. Mus. 11659) is considerably larger than the one that is associated (Am. Mus. 1571) with teeth of *M. petersoni* type; the navicular facet is also relatively deeper anteroposteriorly; the cuboid facet, the sustentacular facet, and the neck all seem relatively a little wider. But notwithstanding these differences, generic affinity is indicated by the following characters in common, which serve to separate these two astragali from those of other genera. As compared with that of *Palaeosyops* the whole bone is long (vertically high) and narrow, with relatively narrower trochlea and neck; internal or tibial keel of trochlea sharply rather than roundly convex, inner slope of external trochlear keel flatter, ridge bounding navicular facet superiorly not sharply projecting, navicular facet shallower anteroposteriorly, cuboid facet narrower, less sharply inclined to the long axis of the navicular facet; sustentacular facet narrow, straight-sided, lying on the extreme internal (tibial) side of the posterior face, broadly continuous below with the cuboid facet, with which it forms a well-defined L. The astragalus is distinguished from that of *Manteoceras* by the characters noted above, chiefly the greater narrowness of the bone as a whole, the sharper internal keel of the trochlea, the narrower cuboid and sustentacular facet. The astragalus approaches those of the forerunners of *Limnohyops* from Bridger B (Am. Mus. 11689, 11690), the principal differences noted above being the relative narrowness of the bone as a whole, the truncate inner border of the navicular facet, the somewhat narrower and straighter sustentacular facet.

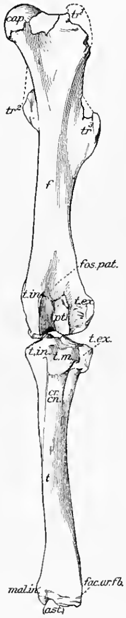

FIGURE 568.—Left femur and tibia of *Mesatirhinus petersoni?*

Am. Mus. 11659; Bridger C 5. Front view. One-sixth natural size.

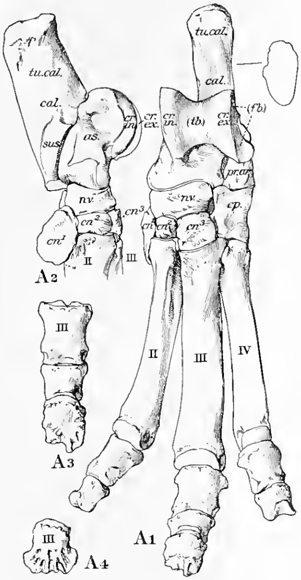

FIGURE 569.—Left pes of *Mesatirhinus petersoni?*

Am. Mus. 11659; Bridger C 5. A₁, Front view; A₂, inner side view; A₃, phalanges of digit III, front view; A₄, ungual phalanx of digit III, top view (a different individual from A₃). One-third natural size.

The calcaneum (Am. Mus. 11659) in its total length (93 mm.) is nearly as long as that of *P. leidyi* (101 in Am. Mus. 1589), but its total width across the sustentaculum is only 47 millimeters as compared with 60 in *P. leidyi;* the tuber calcis as seen from above is more straight-sided and its distal end less expanded and rugose than in *Palaeosyops;* the sustentacular facet is elongate-oval (vertical diameter 32 mm., tr. 13) rather than broadly oval, as in *Palaeosyops.*

The navicular is nearly as deep vertically as in *Palaeosyops* but is much smaller both anteroposteriorly and transversely; in superior view it forms a quadrant.

The entocuneiform (Am. Mus. 11659) forms a vertical oval (vertical 29 mm., tr. 22), which is broad below, pointed at top, and obliquely truncate anterosuperiorly by the facet for the navicular; in *Palaeosyops* (Am. Mus. 1589) this bone is much wider below, not so high vertically, and ends above either in a sharp angle or in a low, rounded hillock. The navicular facet is subcircular, especially at its upper end, whereas that of *Palaeosyops* is either large and ovoid (Am. Mus. 1589) or broadly rounded (Am. Mus. 11682); the facet for the mesocuneiform forms a decided angle with the navicular facet, while in *Palaeosyops* it is more nearly in the same plane. The lower end of the posterior or internal face shows two prominent features—an oval facet for Mts II near the anterior border, and near the posterior border a large, rounded protuberance, probably for the attachment of a ligament; this protuberance is wanting in *Palaeosyops* and at first adds to the difficulty of homologizing the widely different borders and facets in the entocuneiform of the two genera.

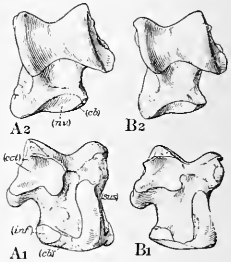

FIGURE 570.—Left astragali of *Mesatirhinus petersoni?*

A, Am. Mus. 11659; B, Am. Mus. 1571. A₁, B₁, Back view; A₂, B₂, front view. Astragalocalcaneal facets; ectal (ect), sustentacular (sus), and inferior (inf). One-third natural size.

The mesocuneiform (Am. Mus. 11659) is a small, anteroposteriorly elongate (20 mm.), narrow (10 mm.) bone, in top view differing widely from the triangular mesocuneiform of *Palaeosyops.*

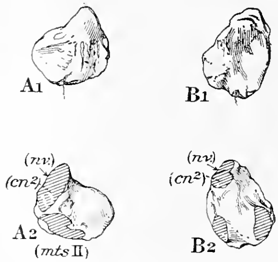

FIGURE 571.—Left entocuneiform tarsi of *Palaeosyops* and *Mesatirhinus*

A, *P. robustus*, Am. Mus. 1550; B, *M. petersoni?*, Am. Mus. 11659. A₁, B₁, inner side view; A₂, B₂, outer side view. One-half natural size.

The ectocuneiform (Am. Mus. 11659, fig. 523) as compared with that of *Palaeosyops* is deep vertically (18 mm.; 19 in *P. leidyi*), shallow anteroposteriorly (33 mm.; 40 in *P. leidyi*), and narrow transversely (21 mm.; 25 in *P. leidyi*); there are corresponding differences in the facets, and the antero-external facet for the cuboid is lacking.

The cuboid (Am. Mus. 11659) as compared with that of *Palaeosyops* is also deep vertically (31 mm.) and much more shallow anteroposteriorly (27 mm.); the superior and inferior facets are subquadrate rather than anteroposteriorly elongate. As compared with that of *Limnohyops* from Bridger B (Am. Mus.

11690) the cuboid is narrower transversely, with somewhat differently shaped facets and a larger postero-external process.

The metatarsals are long and straight-sided. The measurements show that Mts III, although several millimeters longer than in *P. leidyi* (Am. Mus. 1589), is only $\frac{69}{100}$ as broad near its distal end; the proximal facet (for the ectocuneiform) is more truncate posteriorly; as in the manus the distal facet of Mts III is more transversely cylindrical and less convex transversely than in *Palaeosyops*, but the distal facets of Mts II and IV, being narrower, are more convex or subglobose transversely.

The proximal phalanx of Mts III as in the manus is relatively longer (ap. 30 mm.), narrower (tr. 28 mm.), and vertically shallower (17 mm.) than in *Palaeosyops*. The middle or second phalanx, on the contrary, is relatively wider (tr. 25 mm.) and much shallower (13 mm.). The distal or ungual phalanx of Mts III is again rather long (27 mm.), narrow proximally (19 mm.), and very broad distally (28 mm.), the extreme tip being transversely and the sides obliquely truncate. This phalanx therefore differs widely from that of *Palaeosyops leidyi* (Am. Mus. 1550), which is shorter (23 mm.) anteroposteriorly and roundly spatulate distally.

Comparative measurements of the pes in Dolichorhininae, in millimeters

	Mesatirhinus sp., Am. Mus. 2352; Washakie (B?)	Mesatirhinus petersoni?, Am. Mus. 11659; Bridger C 5	Metarhinus sp., Am. Mus. 2058; Uinta B 2	Dolichorhinus hyognathus, Am. Mus. 13164; Washakie B	Dolichorhinus hyognathus, Am. Mus. 1845; Uinta B 2
Astragalus, height of inner face	65	53	[a]58		69
Astragalus, breadth of trochlea	50	40	[a]44		55
Astragalus, height of sustentacular facet	39	35	29		30
Astragalus, width of cuboid facet	11	9	10		12
Calcaneum, height	128	94			
Calcaneum, width across sustentaculum	54	48			
Mts II, length		110			
Mts II, distal width					
Mts III, length	147	120		120	
Mts III, distal width	37	28		37	
Mts IV, length	136	110		108	
Mts IV, distal width	26			21	

[a] Estimated.

Mesatirhinus?

A large unassociated pes from the Washakie Basin (Am. Mus. 2352), of uncertain level, resembles in many ways that of the referred *Mesatirhinus petersoni* (Am. Mus. 11659) described above but is much larger, as shown by the measurements given below. The proportions tend to dolichopody. As compared with that specimen the astragalus is a little broader in proportion to its height, and the cuboid facet is a little more prominent, both progressive characters; the sustentacular facet agrees with that of *Mesatirhinus* and contrasts with those of *Dolichorhinus* and *Metarhinus* in its long, straight-sided character; but it is sharply separated from the cuboid facet, a very exceptional condition. The calcaneum has the stout neck, unexpanded head, and narrow sustentaculum characteristic of *Mesatirhinus*. The third and fourth metatarsals and the second phalanges of D. III and D. IV agree closely with those of *Mesatirhinus* save in the larger size. The pes is thus distinguished from those of *Dolichorhinus hyognathus* and *Metarhinus* by the greater length of the metatarsals and by the character of the sustentacular facet of the astragalus; it is also distinguished from that of *Manteoceras* by the characters of the astragalus, in which the internal keel of the trochlea is narrowly rather than broadly convex, the cuboid facet is relatively narrower, the sustentacular facet vertically longer, and the neck not so short.

The pes, therefore, appears to represent a large species of *Mesatirhinus* perhaps allied to *Dolichorhinus vallidens*.

The question of the generic reference of this pes is one of great morphologic interest, which must be finally determined by the discovery of another skeleton. Its detailed characters (see fig. 572) are as follows: (1) General proportions high and narrow; (2) Mts II measures 145 millimeters, as against 118 in *Dolichorhinus hyognathus;* (3) Mts IV measures 136 millimeters as compared with 108 in *D. hyognathus;* (4) the astragalus exhibits an exceptionally high and narrow sustentacular facet separated inferiorly from the small inferior facet; (5) the calcaneum exhibits an elongated tuber calcis (138 mm. as compared with 114 in *D. hyognathus*).

Another large pes from Washakie B (Am. Mus. 13175) is of the same dolichopodal type and apparently of the same species. It is certainly a member of the *Manteoceras-Dolichorhinus* group rather than of the palaeosyopine group. It does not belong to the short-footed *Dolichorhinus hyognathus*, but like the foregoing (Am. Mus. 2352) may represent a long-footed representative of this genus or of *Mesatirhinus*.

Metarhinus?

Provisionally referred pes from Uinta B 1.—To *Metarhinus* are referred provisionally three hind feet doubtfully recorded from the *Metarhinus* zone (Uinta B 1), as follows: Am. Mus. 1950, a plaster cast from a lost original; Am. Mus. 1947, including chiefly the astragalus, calcaneum, and navicular; Am. Mus. 2058, including among other fragments the astragalus and metatarsals II and IV, from the top of horizon B. These feet are referred to *Metarhinus* because no skulls of *Mesatirhinus* but abundant skulls of *Metarhinus* have been found at the geologic levels in which they occur.

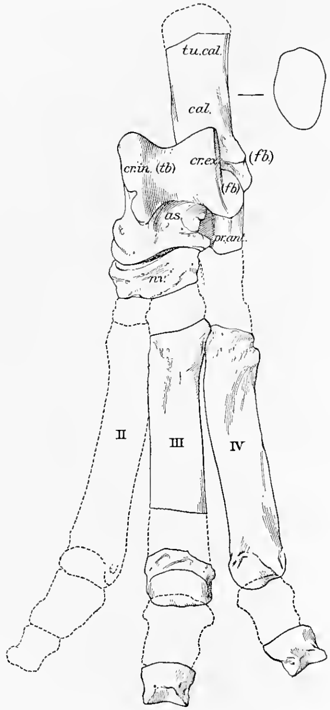

FIGURE 572.—Pes referred to *Mesatirhinus*

Am. Mus. 2352; Washakie B (?). One-third natural size.

The astragalus represents an advance upon the *Mesatirhinus* type, from which it differs in the following progressive characters: Trochlea a little more flattened on the anterior face and a little wider in proportion to the length (vertical diameter) of the bone; process for ligament on posterosuperior border of internal face very pronounced; cuboid facet wider (Am. Mus. 2058), sustentacular facet vertically shorter and narrowing instead of broad superiorly, ectal facet shallower. All these characters are seen also in *Dolichorhinus*, in which, however, the astragalus is larger, the sustentacular facet shorter and even more pointed above, and the cuboid facet wider. The calcaneum (Am. Mus. 1947) has a long neck, narrow sustentaculum, and in general resembles that of *Mesatirhinus*, but the sustentaculum is smaller and more oblique and the top of the prominence bearing the ectal facet also shows a considerable facet for the tibia; the ectal facet itself is flatter; in most points except size it resembles the calcanea referred to *Dolichorhinus*.

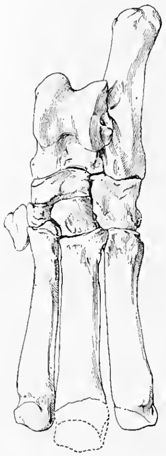

FIGURE 573.—Pes of *Metarhinus* cf. *M. earlei*

Am. Mus. 1950. Cast of left pes, partly restored. One-third natural size.

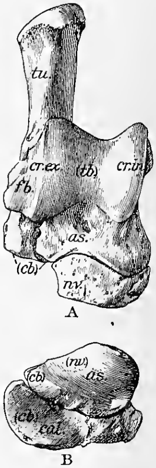

FIGURE 574.—Astragalus, calcaneum, and navicular of *Metarhinus* cf. *M. earlei*

Am. Mus. 1947. A, Front view of right astragalus, calcaneum, and navicular; B, distal view of astragalus and calcaneum. One-half natural size.

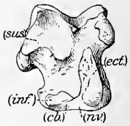

FIGURE 575.—Astragalus of *Metarhinus* cf. *M. earlei*

Am. Mus. 1947. Rear view (drawing from left astragalus reversed). One-third natural size.

The second metatarsal (Am. Mus. 2058, 1950), closely resembles that of *Mesatirhinus*, and the same is true of the third (No. 1950) and the fourth (No. 2058). In the shape of the facets they also resemble *Dolichorhinus*, but they are distinguished by their slenderness. From this close similarity in the pes to that of *Mesatirhinus* and also from the similarity in the dentition and other parts we are led to expect that the manus of *Metarhinus* will also be found to resemble that of *Mesatirhinus*.

Comparative measurements of the supposed hind feet of Metarhinus sp., in millimeters

	Metarhinus?			Mesatirhinus petersoni?, Am. Mus. 11659, Bridger C 5
	Am. Mus. 1950 (cast), Uinta B 1	Am. Mus. 1947, Uinta B 1	Am. Mus. 2058, top of Uinta B 1	
Astragalus, height of inner face	55	53	57	53
Astragalus, breadth of trochlea	40	39	44	40
Astragalus, height of sustentacular facet	------	29	32	35
Astragalus, width of cuboid facet	------	8	10	9
Calcaneum, height	88	87	------	94
Calcaneum, width across sustentaculum	45	44	------	48
Mts II, vertical length	108	------	------	110
Mts II, distal width	21	------	------	------
Mts III, vertical length	------	------	------	120
Mts III, distal width	------	------	------	28
Mts IV, length	106	------	------	110
Mts IV, distal width	22	------	------	------

Juvenile skeleton.—A skeleton of a newly born or fetal animal, from Uinta B 1 (formerly called Uinta upper A) was described in 1914 by Peterson (1914.2) under the name *Heterotitanops parvus*. It consists (fig. 578) of the greater part of the skeleton (Carnegie Mus. 2909) including the skull and lower jaw, lacking only the feet. As noted in Chapter VI (p. 426) the skull and deciduous dentition of this animal present important indications of relationship with some of the smaller Dolichorhininae, presumably *Metarhinus*.

The vertebral formula, according to Peterson, is approximately as follows: Cervicals 7, dorsals 16 or 17, lumbars 3 (?), sacrals 4 or 5, caudals 14 or 15. This may therefore be practically the same as in *Dolichorhinus*—namely, cervicals 7, dorsals 17, lumbars 4 (?), sacrals 4.

The anterior face of the sacrum is quite even with the supra-iliac border of the pelvis, a characteristic of the titanotheres generally. The thoracic cavity was of large size, as indicated by the rather long ribs. There are apparently six bones in the sternum. The scapula is titanotheroid in its general outline, the spine being less overhanging than usual, which is probably a juvenile character (Peterson). The other limb bones are in a very immature condition but so far as preserved suggest the limb proportions of Uinta Basin titanotheres (Peterson).

Dolichorhinus

GEOLOGIC HORIZON AND GENERAL FEATURES

These peculiar long-skulled, short-footed animals are known only from the *Eobasileus-Dolichorhinus* zone (Washakie B 2 and Uinta B 2). They are readily distinguished by their very long skulls, and so far as we know they had short necks and relatively short, heavy limbs. As they are partly adapted in the skull and dentition to grazing habits we should expect to find them long-legged, or subcursorial, but they were not. The fortunate discovery in Washakie B 2 of a specimen of *D. hyognathus* (Am. Mus. 13164), in which the skull and parts of the skeleton are associated, proves that the hind foot of *Dolichorhinus* was brachypodal (fig. 585). The contemporary perissodactyls of similar size are *Manteoceras* and *Sphenocoelus* (an aberrant titanothere). Another contemporary is the peculiar rhinoceros *Amynodon*, which is readily distinguished by its long, slender feet.

SKELETONS REFERRED TO DOLICHORHINUS HYOGNATHUS

Materials.—Our knowledge of the skeleton of *D. hyognathus* is very slight; it is based chiefly on remains of two individuals. The first American Museum specimen (No. 1843) was found by Mr. O. A. Peterson in 1894, in horizon B 2 of the Uinta Basin, Utah. It consists of a nearly complete vertebral series, a part of the pelvis, the anterior part of the skull, the humerus, and one rib. The second specimen (Am. Mus. 13164) was found by Mr. Paul Miller in 1906, in Washakie B; it consists of the finely preserved skull already described, with which were associated parts of the atlas and axis, one lumbar, parts of the scapula, the humerus, the proximal half of the ulna-radius, the femur, two metatarsals, and isolated foot bones. Another specimen also found in Uinta B 2 (Am. Mus. 1836) consists of parts of the radius and ulna, associated with the jaw. An atlas (Am. Mus 1837) was found associated with the skull of *D. intermedius*. A number of other bones not associated with cranial material have been referred to this genus, especially an atlas (Am. Mus. 1844); also a part of the scapula (Am. Mus. 1833) and a radius and ulna (Am. Mus. 1831). The manus, unfortunately, is not known. The materials above enumerated enable us to make a

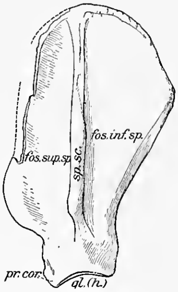

FIGURE 576.—Left scapula of *Metarhinus?* sp.

Am. Mus. 1873; Uinta B 1. One-sixth natural size.

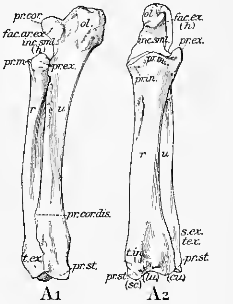

FIGURE 577.—Left radius and ulna of *Metarhinus earlei?*

Am. Mus. 2363; Washakie B 1. A1, Outer side view; A2, front view. One-sixth natural size.

partial and provisional restoration (fig. 579) of this peculiar animal. This tentative restoration is undoubtedly incorrect in many details, especially in the limbs, which were very incompletely known at the time the restoration was made. The tibia as restored is too long, the femur as preserved in No. 13164 is much shorter than in *D. longiceps*. The restoration of the skeleton of *D. longiceps*, figured in 1924 by Peterson (Carnegie Mus. Mem., vol. 9, pt. 4), is based on much better material and is doubtless more accurate.

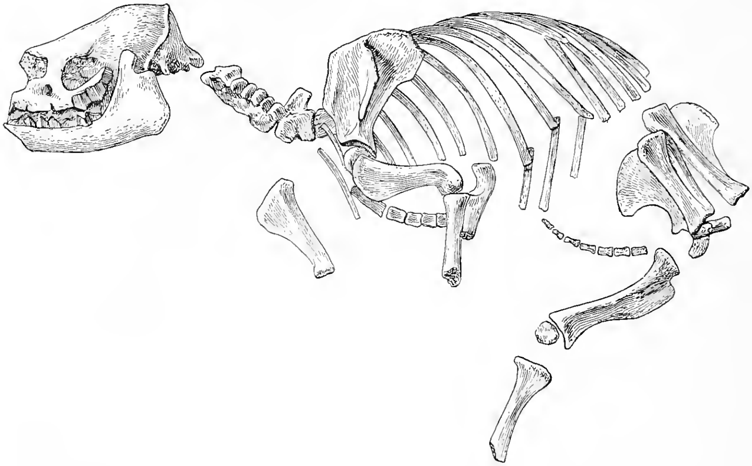

FIGURE 578.—Skeleton of a newly born animal, provisionally identified as *Metarhinus* sp.

Carnegie Mus. 2909; Uinta B 1; type of *Heterotitanops parvus* Peterson. After Peterson. One-fourth natural size.

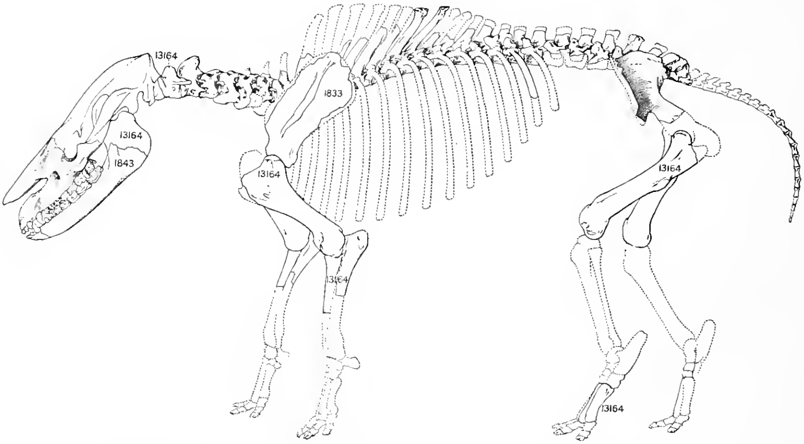

FIGURE 579.—Provisional restoration of the skeleton of *Dolichorhinus hyognathus*

One-fifteenth natural size. Based on the following specimens in the American Museum of Natural History: 1843, Uinta B 2, anterior half of skull with lower jaw, vertebral column, sacrum, and part of pelvis; 13164, Washakie B, remaining parts of skull, humerus, portions of radius and ulna, femur, Mts III, IV; 1833, Uinta B 2, scapula. The remaining parts, which are more or less hypothetical, are based on *Mesatirhinus*, with modifications supplied by fragments from Uinta B 2. The number of dorsolumbar vertebrae shown in this restoration (19) is incorrect, for the last two dorsal vertebrae are omitted. The complete vertebral column of *Dolichorhinus longiceps* in the Field Museum, Chicago, has 17 dorsals and 4 lumbars. The manus as restored is too high and slender. (Compare Pl. XXXII.)

General proportions as displayed in the composition of the two principal skeletons (fig. 579).—The total length of the animal with the head outstretched—that is, measured from the premaxillaries to the ischium—is estimated at 2.02 meters (6 feet 8 inches), the height

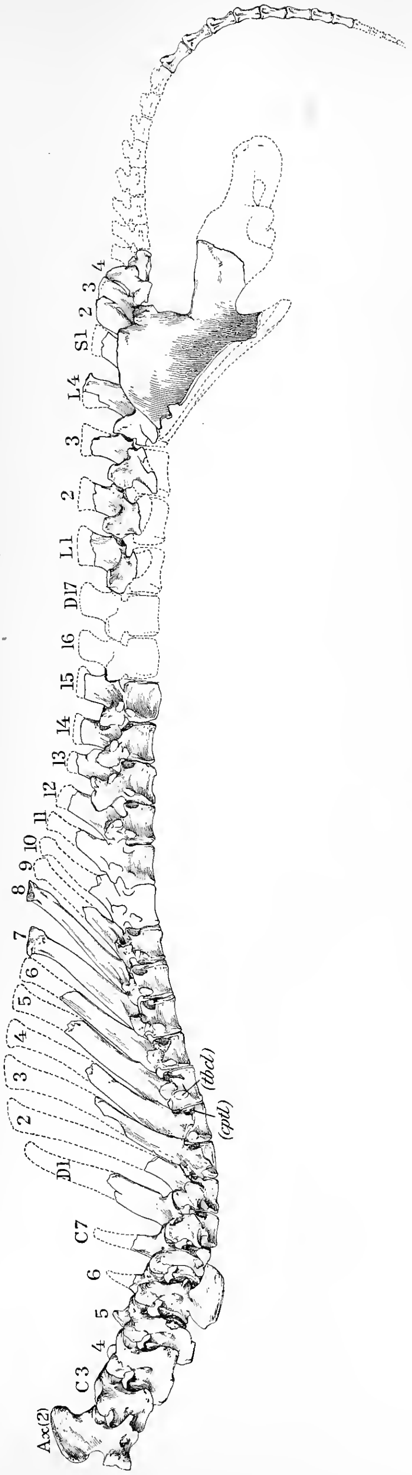

FIGURE 580.—Vertebral column of *Dolichorhinus hyognathus*

Am. Mus. 1843; Uinta B 2. Two dorsal vertebrae may be missing and are here restored in outline. One-eighth natural size.

at the shoulder 1.09 meters (3 feet 6 inches). Altogether the vertebral column is mechanically superior in the strength of its muscular attachments to that of *Palaeosyops*. We observe certain analogies to the spinal column of *Equus*. The backbone is adapted to the support of the long, depressed head; the broad neural spines of the dorsal vertebrae serve for the attachment of the ligaments and muscles supporting the cranium. The spines in the lumbar region were also deep, indicating the presence of powerful running muscles. This apparent adaptation of the backbone in the lumbar region to a strong running action is to our surprise not correlated with length of limb or of foot, because both the humerus and the hind feet are relatively abbreviated. The median metatarsal measures only 120 millimeters. Other striking characters of the restoration are the broad inferior lamellae of the cervical vertebrae (C. 3–C. 6). The measurements in Am. Mus. 1843 are:

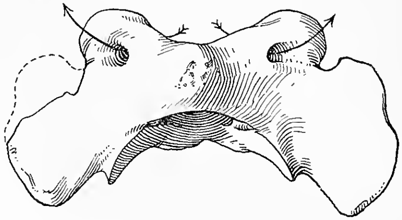

FIGURE 581.—Atlas referred to *Dolichorhinus* sp.

Am. Mus. 1844; Uinta C; dorsal view. The arrows indicate the course of the first spinal nerve and vertebral artery. One-third natural size.

	Meters
Actual length curve of back, axis to spine of posterior sacral	1. 35
Length of neck lacking axis—that is, C. 2–C. 7	. 30

Vertebral column.—The vertebral formula as preserved in Am. Mus. 1843 appears to be cervicals, 7; dorsals, 15 +; lumbars, 4; sacrals, 3–4. The exact number of dorsals is not revealed by this specimen. In the specimen of *Dolichorhinus longiceps* described by Riggs (1912.1, p. 31), the formula is, dorsals, 17; lumbars, 4; sacrals, 4. In *Palaeosyops* the number is not certainly known. In two genera of Oligocene titanotheres (*Brontotherium*, *Menodus*) the number of dorsolumbars is believed to be 20.

The atlas (fig. 581) is partly known from a specimen in the American Museum (No. 13164) and fully known by comparison of this specimen with a much larger atlas (Am. Mus. 1844). It is moderately elongate; its breadth is 203 millimeters. The vertebrarterial canal traverses the base of the transverse processes. The atlas is narrower transversely than that of *Palaeosyops* and it has narrower pleurapophyses (201 mm. in *Metarhinus* as compared with 240 in *P. robustus*); the superior border of the cotylus is deeply concave anteriorly, the dorsal prominence (neural spine) is larger, the cotyli are larger, and the articular surfaces for the axis form a more deeply concave sinus.

As compared with *Palaeosyops* the cervicals had slightly longer and relatively smaller centra, slightly longer prezygapophyses and postzygapophyses and perhaps larger pleurapophysial flanges on C. 1– C. 6; the spines are broken off but may have been more slender at the base. The anterior dorsals had relatively somewhat smaller centra with pronounced inferior keels; the neural spines were broader anteroposteriorly; the anterior zygapophyses of D. 2 faced upward and inward, making a decided angle with the neural spine as in *Manteoceras*, whereas in *Palaeosyops* the zygapophyses were nearly continuous with the spine.

The neck, which measures only 320 millimeters in length, is short, especially when compared with the remarkably long skull, which is estimated at 540 millimeters.

The remainder of the column all belongs to one animal (Am. Mus. 1843). The axis (fig. 580) does not exhibit so high a spine as in *Palaeosyops* or *Manteoceras*, but we recall the fact that *Dolichorhinus* has a low occiput. There is little evidence of high spines on C. 3–C. 5; the powerful ligamentum nuchae was supported by the high and extensive spines of D. 1–D. 8. Cervicals 1–6 are characterized by widely expanding and actually overlapping inferior lamellae, distinct in C. 6 from the pleurapophysis above (thus unlike *Palaeosyops*). The centra are quite deeply opisthocoelous and laterally compressed. The zygapophyses face vertically and obliquely outward and inward from C. 3 to the anterior face of D. 1; they face horizontally downward and upward in D. 1 to D. 12; beginning with the posterior face of D. 12 to L. 4 the zygapophyses are vertically placed, facing outward and inward and more or less sigmoid or revolute in curvature, as in certain lumbars of *Palaeosyops*. The neural spines from D. 1 to L. 4 are extended anteroposteriorly in marked contrast to the feeble spines of *Palaeosyops*. The metapophyses are unusually broad; that of L. 4 articulates with the front border of the ilium as in *Equus*. The centra throughout are relatively deep; the depth equals the height in the posterior cervicals and anterior dorsals, but in the lumbars the height slightly exceeds the depth. The centra are compressed, or keeled inferiorly. There are apparently but three true sacrals in this specimen, but the number can not be ascertained positively.

The upward curvature of the dorsolumbar region of the column is greater than that represented in Figure 580 but is correctly indicated in the restoration, Figure 579.

Arches and limb bones.—A scapula (fig. 582) is doubtfully associated with *Dolichorhinus;* it presents rather high and narrow proportions and measures 320 millimeters vertically.

The humerus is known from two specimens. It is a highly characteristic and progressive bone, closely resembling that of the large lower Oligocene titanotheres, such as *Brontotherium leidyi.* The most distinctive Oligocene titanothere character is the very high, thin, and platelike great tuberosity (tub. maj.) with an erect anterior process. The humerus associated with Am. Mus. 1843 (fig. 583) is short; it measures 285 millimeters to the tip of the great tuberosity, while the length of the shaft is 255 millimeters. The humerus of the other specimen (Am. Mus. 13164) belongs to an animal of larger size; length of shaft, head to distal extremity, 315 millimeters; extreme distal width 95. The disparity in size of the two humeri as compared with the approximate equality in size of the respective skulls is a puzzling feature.

The length of the forearm or ulna and radius can only be estimated; it certainly is considerably less than that of the humerus (estimated humeroradial ratio 81). This indicates (see p. 733) that *Dolichorhinus* was an animal capable of more speed than *Palaeosyops* but of less speed than *Mesatirhinus*, in which the humerus and radius are more subequal. The most highly characteristic feature of the ulna is the form of the olecranon process, which is obtuse, highly rugose, and incurved, as shown in Figure 584, a character which relates this animal to *Mesatirhinus.* The manus of *D. longiceps*, figured by Peterson (Carnegie Mus. Mem., vol. 9, pt. 4, pl. 54), is remarkably like that of *Mesatirhinus* but relatively somewhat shorter and more massive.

Little is certainly known of the pelvis beyond the outline indicated in Figure 580.

The femur (Am. Mus. 13164, fig. 579) exhibits a total length of 387 millimeters as compared with the length of the humerus, 315, and with the total basilar length of the skull, 540. The femur has the characteristic straight shaft of the titanotheres generally and is readily distinguished from that of the contemporary *Amynodon* (fig. 518) by the more vertical position of its patellar facet (in *Amynodon* these facets are placed very obliquely) and the lesser development of the third trochanter, which is very prominent in *Amynodon,* as in all other rhinoceroses.

Mts III and IV (Am. Mus. 13164, fig. 585) are of almost brachypodal proportions, being no longer than those of *Mesatirhinus petersoni* but much broader (dimensions are given above). They show syngenetic resemblances to *Mesatirhinus* and *Metarhinus.*

COMPARISON OF THE FORE LIMB OF DOLICHORHINUS AND AMYNODON

Before it was learned that *Dolichorhinus* was brachypodal a finely preserved fore limb (Am. Mus. 1961, from Uinta B 2, figs. 586, 587) was provisionally referred to that genus. It differs from *Dolichorhinus*, however, and agrees with *Amynodon* in the detailed characters of the upper arm and forearm, especially in relative length and slenderness, form of the great tuberosity and supinator crest of the humerus and of the olecranon. The manus has the deep carpus, relatively long metacarpals, and extremely abbreviate ungual phalanges of *Amynodon;* metacarpal III is enlarged, the foot being functionally mesaxonic.

UNASSOCIATED ASTRAGALI PROVISIONALLY REFERRED TO DOLICHORHINUS AND MESATIRHINUS

The tarsus is known from unassociated specimens only. The structure of the tarsus is uncertain. Three types of relatively large astragali are found in the *Eobasileus-Dolichorhinus* zone (Washakie B 2 = Uinta B 2). These are sketched in Figure 588. B (Am. Mus. 1845) is said to be associated with part of a *Dolichorhinus* skull. It differs from *Mesatirhinus* in the short sustentacular facet, deeply grooved above; also in the short neck. Of this type another astragalus (Am. Mus. 1838, fig. 588, C) has a broader cuboidal facet and is wider. A (Am. Mus. 2352, from Washakie B 2), which is not associated with other remains, agrees with *Mesatirhinus* in the long neck and long sustentacular facet. D (Am. Mus. 1962), although not associated with other remains, possibly belongs to *Telmatherium*. (See above.) If B belongs to *Dolichorhinus* it is certainly distinctive.

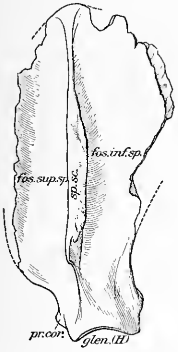

FIGURE 582.—Left scapula of *Dolichorhinus? hyognathus*

Am. Mus. 1833; Uinta B 2. One-sixth natural size. Compare Figure 590.

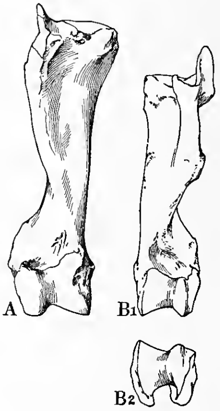

FIGURE 583.—Humerus of *Dolichorhinus hyognathus*

A, Am. Mus. 13164, Washakie B, right humerus, front view; B, Am. Mus. 1843, Uinta B 2, left humerus, front (B_1) and distal (B_2) views. One-sixth natural size.

SKELETONS REFERRED TO DOLICHORHINUS LONGICEPS

Three partial skeletons that have been referred to this species are known. Two are in the Carnegie Museum at Pittsburgh. They were discovered in 1912 by Peterson (1914.3) in the upper levels of horizon B 1 of the Uinta Basin Eocene, on White River, Utah. The skull, mandible, and hyoid bones of this specimen have been described in Chapter V; the vertebrae, limbs, and feet, as described by Peterson,[37] are noticed below. The third skeleton referred to this species is in the Field Museum at Chicago and was discovered in 1910 by Riggs (1912.1) in the "upper *Metarhinus* beds" (upper level of *Metarhinus* zone = Uinta B 1, formerly included in Uinta A). A photograph (Pl. XXXII) and numerous measurements (see below) of this skeleton were kindly supplied for this monograph through the courtesy of Mr. Riggs.

SKELETON OF DOLICHORHINUS LONGICEPS COMPARED WITH THAT OF EOTITANOTHERIUM (DIPLACODON?) OSBORNI

The description by Peterson (1914.1, pp. 132–137) of the vertebrae and limbs of the specimen of *Dolichorhinus longiceps* in the Carnegie Museum (No. 2865) may be abstracted and restated as follows:

The atlas.—In comparing the atlas with that of *Eotitanotherium osborni* Peterson, it is at once observed that the bone is proportionally higher and longer but of a less transverse diameter, which is due chiefly to the shorter transverse process in the present genus. The anterior cotyle is on the whole very nearly as large as but is deeper than in *Eotitanotherium,* and its inferior surface is more distinctly separated. The odontoid process of the axis is proportionally longer and reaches nearly through the inferior arch of the atlas, while in *Eotitanotherium* it does not. The articulation for the axis is much deeper than in *Eotitanotherium* and not nearly as broad, in this respect more nearly suggesting the condition found in some Oligocene rhinoceroses (*Diceratherium*) than the horned titanotheres. The transverse process is pierced by a large foramen, unlike *Eotitanotherium,* in which this canal is small, or completely absent.

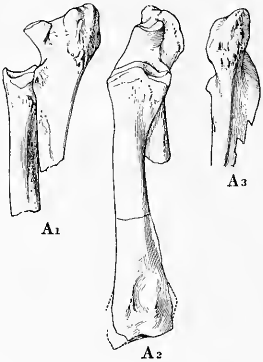

FIGURE 584.—Radius and ulna of *Dolichorhinus hyognathus*

A_1, Outer side view of proximal end of left radius and ulna, Am. Mus. 13164, Washakie B; A_2, front view of same, combined with distal end of radius, Am. Mus. 1831, Uinta B 2; A_3, rear view of left olecranon shown in A_1. One-sixth natural size.

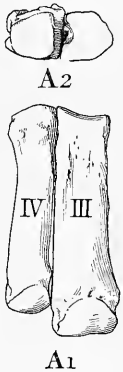

FIGURE 585.—Metatarsals of *Dolichorhinus hyognathus*

Am. Mus. 13164; Washakie B. Right metatarsals III and IV. A_1, Front view; A_2, proximal view. One-third natural size.

The axis.—The body of the axis is possibly somewhat longer than in *Eotitanotherium,* the anterior opening of the arterial canal located farther back, and the postzygapophysis is smaller and less rounded in outline, while the neural spine and the ventral keel have approximately the same general proportions.

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[37] Peterson's final description of these skeletons (Carnegie Mus. Mem., vol. 9, No. 4, 1924) was received too late for extended notice in this monograph.

The other cervical vertebrae present no characters of sufficient importance to mention in this connection.

The dorsal vertebrae.—The first dorsal has a short depressed centrum and a prominent keel. The spine and transverse processes are broken off. The other dorsal vertebra belongs well back in the series and has a higher and more evenly rounded centrum, without ventral keel, but with the indication of a heavy neural spine.

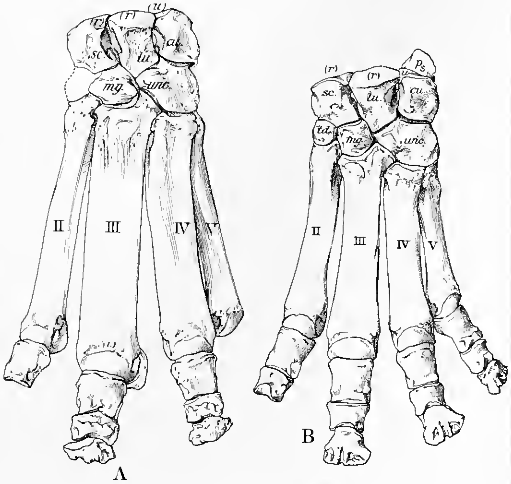

FIGURE 586.—Manus of *Amynodon* and *Mesatirhinus* compared

A, The amphibious rhinoceros *A. intermedius?*, Am. Mus. 1961; B, the terrestrial mediportal titanothere *M. petersoni?*, Princeton Mus. 10013. One-third natural size.

The lumbar vertebrae.—The two last lumbar vertebrae are present; the body of the last being depressed, as is usual in the case of the last lumbar, and has also the neural spine suddenly reduced in the fore-and-aft direction. The transverse process of the same vertebra is quite heavy and projects outward and forward. Near the base of the process on the posterior face there is a heavy and rounded process, which possibly came in close contact with a similar process on the anterior face of the pleurapophysis of the first sacral vertebra.

When the vertebrae described above are compared with the vertebral column of *Dolichorhinus hyognathus* it appears that the neural spine of the atlas of the specimen in New York is more prominent, while the position of the transverse process and the anterior exit of the vertebrarterial canal of the axis appear to be the same in the two specimens. The cervical series as a whole appear to be slightly shorter in the specimen preserved in New York (*D. hyognathus*).

Measurements of Dolichorhinus longiceps

	Millimeters
Atlas, greatest anteroposterior diameter	105
Atlas, greatest transverse diameter, approximately	180
Atlas, greatest vertical diameter	88
Axis, anteroposterior diameter of centrum, odontoid process included	95
Axis, height, including neural spine	125
Cervical region, total length, approximately	395

The scapula.—The scapula is little if any shorter than in *Eotitanotherium*, as figured by Peterson, but its general outlines differ from those shown in that genus. The lower portion of the coracoid border is more deeply notched than in *Eotitanotherium.* The coracoid border above the notch is more curved forward, as is also the glenoid border. The general outlines of the scapula are on the whole more suggestive of the Rhinocerotidae than the titanotheres.

The humerus.—The humerus is short and heavy. The bone is comparatively shorter than in *Eotitanotherium.* Unfortunately, the greater tuberosity is broken on the posterolateral face, but near the deltoid groove the superior face is complete and indicates very plainly that the tuberosity is not as high as in *Eotitanotherium.* The lesser tuberosity accords more nearly with that shown in the latter genus. The deltoid groove is also of about the same size in the two genera here compared. The deltoid ridge is less prominent in *Dolichorhinus*, while the distal end of the bone is quite nearly alike in the two genera.

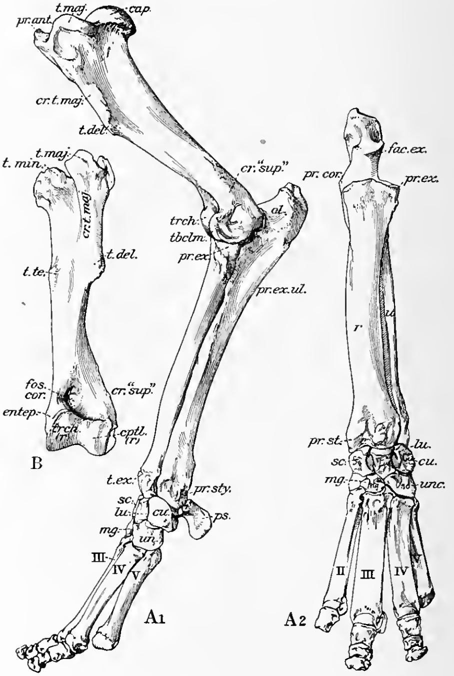

FIGURE 587.—Left fore limb of the amphibious rhinoceros *Amynodon intermedius?*

Am. Mus. 1961, Uinta B 2. Formerly referred to *Dolichorhinus.* A1, Outer side view; A2, front view of forearm and manus; B, front view of humerus. One-sixth natural size.

The radius and ulna.—The radius and ulna are much shorter than in *Eotitanotherium* and proportionally also much heavier. There is a tendency to coossification of the two bones in the present specimen, the shaft is rounder, and the articulation for the humerus is less deeply excavated than in *Eotitanotherium.* In comparing the ulnae of the two genera in more detail, it is seen that there is a less developed tubercle on the outer margin of the tendinal groove of the olecranon process in *Dolichorhinus* than in *Eotitanotherium.* In consequence the groove is not as well defined in the genus under description, though the termination of the olecranon process is fully as well developed. In *Dolichorhinus* there is a greater constriction of the olecranon between the upper border of the great sigmoid notch and the termination of the process than is seen in *Eotitanotherium.* Otherwise the ulna is quite similar in the two genera.

The manus.—The manus of the specimen under description is complete with the exception of the ungual phalanges and the proximal phalanges of digits III and IV, which were not recovered. The foot as a whole is short and broad, and, when compared with the manus of *Eotitanotherium*, it may be said to be heavier. In comparing the carpal elements of the two genera it is at once observed that they are all of greater height in the present genus than in *Eotitanotherium.*

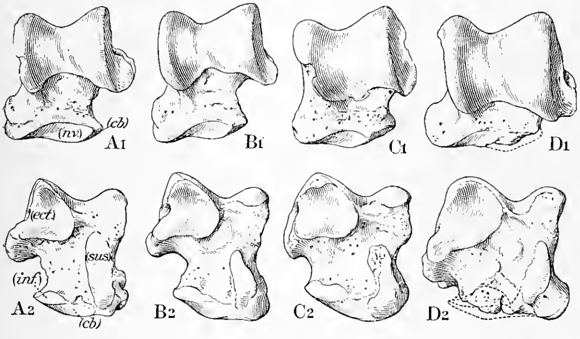

FIGURE 588.—Left astragali of *Dolichorhinus* and allied types

Front (A_1, etc.) and rear (A_2, etc.) views. A, *Mesatirhinus?*, Am. Mus. 2352, Washakie B? (cf. figs. 569, 570, 572); B, *Dolichorhinus hyognathus?*, Am. Mus. 1845, Uinta B 2 (probably associated with a skull of *Dolichorhinus* sp.); C, *Dolichorhinus?*, Am. Mus. 1838, Uinta B 2; D, *Telmatherium?*, Am. Mus. 1962, Uinta B 2. One-third natural size.

The metacarpals, in proportion to the carpals, are shorter than in *Eotitanotherium.* The metapodial keel of Mtc II is less oblique to the long axis of the bone than that in *Eotitanotherium*, otherwise the differences between these two genera are slight. The head of Mtc III differs from that in *Menodus* by having the ulnar portion more squarely truncated and by the much smaller size of the facet for Mtc II on the radial angle. Mtc IV presents only slight differences from the corresponding bone in Oligocene titanotheres. In its general details Mtc V is quite similar to the same bone in *Eotitanotherium* but proportionally shorter.

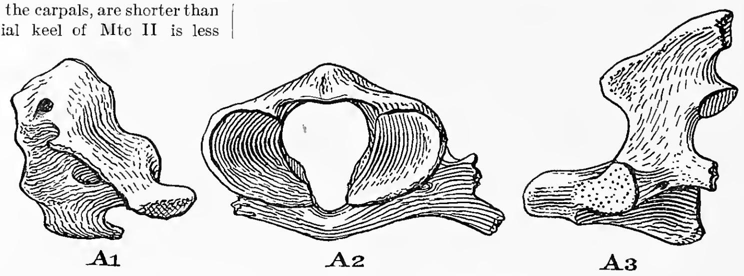

FIGURE 589.—Cervical vertebrae of *Dolichorhinus longiceps?*

Carnegie Mus. 2865. A_1, Left side of atlas; A_2, anterior view of atlas; A_3, left side of axis. After Peterson. One-third natural size.

Measurements of Dolichorhinus longiceps (by Peterson)

	Millimeters
Total length of scapula	337
Total length of humerus, head to distal end	285
Total length of ulna	340
Total length of radius	295
Total length of manus, approximately	200
Height of carpus at unciform and cuneiform	59
Transverse diameter of carpus at proximal row of carpals	90
Greatest length of Mtc II	116
Greatest length of Mtc III	124
Greatest length of Mtc IV	109
Greatest length of Mtc V	95

As in *Eotitanotherium* and the titanotheres generally, the phalanges are short, broad and depressed. In comparing Osborn's restoration of *Dolichorhinus* (fig. 579) with the above-described fore limb it appears that the foot of the present specimen is shorter, while the radius, ulna, and scapula are longer. There are considerable variations in the length of the limb of the genus *Dolichorhinus.* The humerus and the radius and ulna of specimen No. 1961 [38] in the American Museum very nearly agree in general length with those of No. 2865 in the Carnegie Museum, while the fore foot of the former specimen is considerably longer than in the latter.[39] On the other hand, the specimen No. 13164 (Am. Mus.) from the ?Washakie B level indicates that the humerus is relatively longer and the fore foot shorter than in the fore limb of *Dolichorhinus* in the Carnegie Museum, which is described in this paper.

In conclusion this Carnegie Museum skeleton shows that *Dolichorhinus* had a relatively shorter and wider manus than that of *Mesatirhinus*—that it was in fact almost brachypodal.[40]

SKELETON OF DOLICHORHINUS LONGICEPS IN THE FIELD MUSEUM

The skeleton of *Dolichorhinus longiceps* in the Field Museum (No. 12200), from Riggs's "upper *Metarhinus* beds" (=upper part of Uinta B 1), comprises a well-preserved skull and jaws associated with a vertebral column which is complete from the atlas to the last sacral vertebra; together with the left scapula, both humeri, the left radius and ulna, and the complete pelvis.

This important skeleton furnishes the proof that in *Dolichorhinus longiceps* there were 21 dorsolumbar vertebrae, 17 dorsals and 4 lumbars. In the preliminary reconstruction of *Dolichorhinus*

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[38] The dimensions of the metacarpals of this specimen in millimeters as measured by W. K. Gregory are as follows:

	Length of middle of shaft	Breadth above distal condyle
Mtc II	112	33
Mtc III	117	32
Mtc IV	105	29
Mtc V	91	23

[39] The manus referred to, Am. Mus. 1961 (fig. 587), is probably referable to *Amynodon* sp. Its resemblances to *Dolichorhinus*, however, are remarkably close.

[40] Peterson's final illustrations of the manus of *D. longiceps* (Carnegie Mus. Mem., vol. 9, pl. 54, 1924) show that it is strikingly similar to that of *Mesatirhinus*, only somewhat broader. Mtc III is relatively longer and narrower than Mts II. The manus as a whole is of the compressed, straight-sided type, presenting a great contrast to the spreading manus of *Palaeosyops.*

hyognathus by Osborn and Gregory only 19 dorsolumbars were assigned to this animal, but probably the last two dorsal vertebrae were missing in the specimen upon which this restoration was based (Am. Mus. 1843, figs. 579, 580).

Without placing the specimens of *D. hyognathus* and the more ancient *D. longiceps* side by side it is difficult to determine from a comparison of the illustrations what are the really significant differences between these two sets of vertebrae. In the *D. longiceps* specimen the spine of the axis appears to be more acute posteriorly, the spines of dorsals 6, 7, 8, and of the posterior dorsals and lumbars seem to be wider anteroposteriorly.

Measurements of the skeletons of Dolichorhinus longiceps and D. hyognathus, in millimeters

	D. longiceps		D. hyognathus	
	Field Mus. 12200; Uinta B 1	Carnegie Mus. 2865	Am. Mus. 1843; Uinta B 2	Am. Mus. 13164; Washakie B
Distance from tip of nasals to last vertebra, as mounted, on straight line; right side	1, 910	-------	-------	-------
Length of skull, pmx to condyles	533	-------	-------	542
Length of skull, nasal tip to lambdoid crest	[a] 570	-------	-------	580
Width of skull across zygomata	[b] 210	-------	-------	250
P^1–m^3	184	-------	-------	205
M^1–m^3	122	125	-------	119
P_1–m_3	195	-------	207	230
Lower jaw, incisors to angle	423	-------	-------	[a] 420
Length of neck as mounted	360	-------	348	-------
Scapula, length	375	337	-------	-------
Humerus, length	275	285	248	[b] 308
Radius, length	287	295	-------	-------
Ulna, length	330	340	-------	-------
Os innominatum, right, length from crest of ilium to tuberosity of ischium	290	-------	-------	-------
Number of dorsals	17	-------	(?)15+	-------
Number of lumbars	4	-------	4	-------
Number of sacrals	4	-------	4	-------

[a] Estimated.

[b] Modified by distortion.

SUBFAMILIES TELMATHERIINAE, BRONTOPINAE?, AND DIPLACODONTINAE

Nothing was known of the skeleton of Uinta C (true Uinta) titanotheres until the publication of the memoir "The Mammalia of the Uinta formation," by Scott and Osborn, in 1890 (Osborn, 1890.51). Parts of four skeletons were described in this memoir—Princeton Mus. 10393, 10395, 10396, 10396a. These were all attributed to *Diplacodon elatus.* It is now evident that this specific reference is somewhat doubtful, because, as we have already seen (p. 96), *Diplacodon elatus* is only one of four or five kinds of titanotheres that were living contemporaneously during the period of deposition of Uinta C. Since the original Princeton expedition the Princeton, American, and Carnegie Museums have sent parties into the same field, which discovered parts of many additional but very incomplete skeletons. Unfortunately not any of these skeletons are associated with teeth or skulls in such a manner as to enable us to determine them specifically or generically. It may be said, therefore, that the skeletal characters of the Uinta C titanotheres are assigned only provisionally.

FIGURE 590.—Right fore limb of *Dolichorhinus longiceps?*

Carnegie Mus. 2865. After Peterson. One-tenth natural size.

As there were no less than five kinds of titanotheres in Uinta C, such skeletal remains as are found there may belong to any one of the following phyla: (1) Successors of the *Telmatherium* phylum; (2) members of the true *Diplacodon* phylum, in which the skull is long and slender, resembling in some respects that of the Menodontinae, in others that of ancestors of *Brontotherium;* (3) descendants and members of the *Manteoceras* phylum, so far as known only in the lower beds of Uinta C; (4) members of the *Protitanotherium* phylum, animals of robust and large size, skeleton progressive upon that of *Manteoceras,* believed to be ancestral to *Brontops* of the Oligocene; (5) descendants or relatives of *Eotitanotherium,* a progressive titanothere so far known only from Uinta B 2.

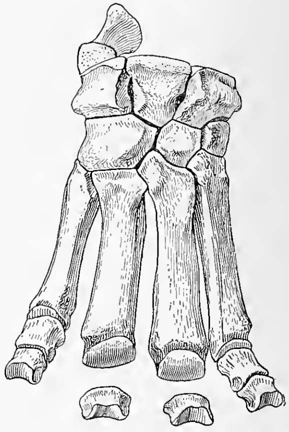

FIGURE 591.—Manus of *Dolichorhinus longiceps?*

Carnegie Mus. 2865. Front view. After Peterson. One-third natural size.

With these precautions clearly in mind, we may now describe the parts as provisionally referred.

SUBFAMILY TELMATHERIINAE

Telmatherium ultimum (referred)

The hind limb of *Telmatherium ultimum* (Am. Mus. 1942), from Uinta C, includes the femur, tibia, and pes. It is evidently of palaeosyopine rather than manteoceratine affinity. Its association with the genus *Telmatherium* of the palaeosyopine group is provisional and rests mainly on the characters of the femur, tibia, and pes, especially on the short neck and facets of the astragalus, which are of the palaeosyopine rather than of the manteoceratine type. The tibiofemoral ratio is 70.

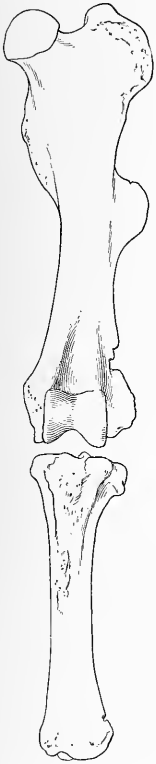

FIGURE 592.—Hind limb referred to *Telmatherium ultimum*

Am. Mus. 1942; Uinta C. One-sixth natural size.

The entire length of the hind limb from the head of the femur to the extremity of Mts III is estimated at 965 millimeters, distributed as follows: Femur, crushed, estimated, 400; tibia, actual length, 323; pes, estimated, 240.

The femur exhibits a very prominent third trochanter, which is considerably lower down on the shaft than the second trochanter. The palaeosyopine character is seen especially in the broad patellar facet, which is elongate and faces anteriorly. The tibia presents a slight anterior depression in the cnemial crest.

The pes (fig. 593) is more distinctive. It is of an advanced type in many details; its reference to *Telmatherium* rather than to any of the Manteoceratinae is due to the character of the astragalus, which is of the short-necked type, with a broad oval sustentacular facet; the very large tibio-astragalar trochlea is broad and flat, presenting anteriorly; the navicular facet spreads well on the front face of the astragalus; the cuboidal facet is narrower than in *Protitanotherium*. The navicular and ectocuneiform are also low and broad elements of graviportal type.

All these bones are deep anteroposteriorly, and all facets are subhorizontal or subvertical rather than oblique. The metatarsals are likewise broad and in detailed characters suggest those of the Bridger Palaeosyopinae on a larger scale. The proximal facets of the metatarsals are deeply extended anteroposteriorly, as in the Palaeosyopinae, and unlike those of *Dolichorhinus*, which are shallow, as in the Manteoceratinae.

Skeletal remains originally referred to Diplacodon elatus by Scott and Osborn

In 1890 parts of four separate skeletons from Uinta C 1 (Princeton Mus. 10393, 10395, 10396, 10396a) were described by Scott and Osborn (1890.1) and were all attributed to *Diplacodon elatus*. It has been demonstrated in Chapter V that Marsh's type of *D. elatus* shows affinities to both *Menodus* and *Brontotherium*. The elongate proportions of the skeletons now to be described, moreover, resemble those of the Oligocene *Menodus* rather than those of the Oligocene *Brontops;* consequently it appears improbable that they belong to *Protitanotherium*, which in cranial characters resembles *Brontops*. The generic and specific references are therefore uncertain.

The principal characters are as follows: (1) Short neck, cervical vertebrae flattened and abbreviated; (2) long limbs, pelvis and feet elongated as in *Menodus;* (3) prominent and recurved hook on the humerus; (4) metapodials of manus elongated, stilted, functionally tetradactyl in proportion; (5) radius long and slender (Am. Mus. 2035); (6) tibia short and massive (Am. Mus. 2056).

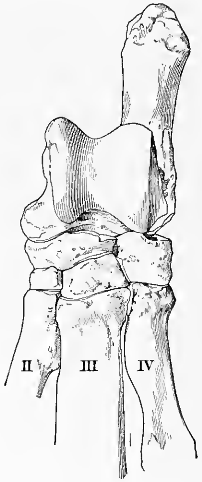

FIGURE 593.—Pes of *Telmatherium? ultimum?*

Doubtfully referred left pes, Am. Mus. 1942; Uinta C. One-third natural size.

Cervicals.—It is noteworthy that the cervical centra, although belonging to an animal nearly double the size of *Palaeosyops* in height and breadth, are only a trifle longer, a fact which points to the progressive abbreviation of the neck. The axis (Princeton Mus. 10396a) exhibits a broad spine overhanging the postzygapophyses, laminae very slightly notched, postzygapophyses of elongate oval form, transverse processes hooked and perforated at the base, centrum with a sharp inferior keel. The remaining cervicals and dorsals (Princeton Mus. 10396) probably belong to a single individual. The cervicals are probably the third, fourth, fifth, and sixth. Of these C. 5 is the most complete, spine pointed, vertically placed and grooved posteriorly, zygapophyses very stout, facets placed at angles of 45°, vertical diameter of the centra much greater than the transverse, opisthocoelous, transverse processes not extending below the level of the centrum. The centra of seven dorsals are preserved. Figure 594 represents one between the seventh and tenth exhibiting the following characters: Centrum opisthocoelous and considerably excavated at the sides; anterior, posterior, and transverse diameters about the same; lower half of the spine triangular, indicating a considerable elongation and strongly oblique inclination;

zygapophyses almost horizontal. The single lumbar centrum preserved is considerably longer than the above-described dorsal vertebrae and exhibits a stout keel; spine broad and grooved posteriorly; zygapophyses rounded and vertically placed.

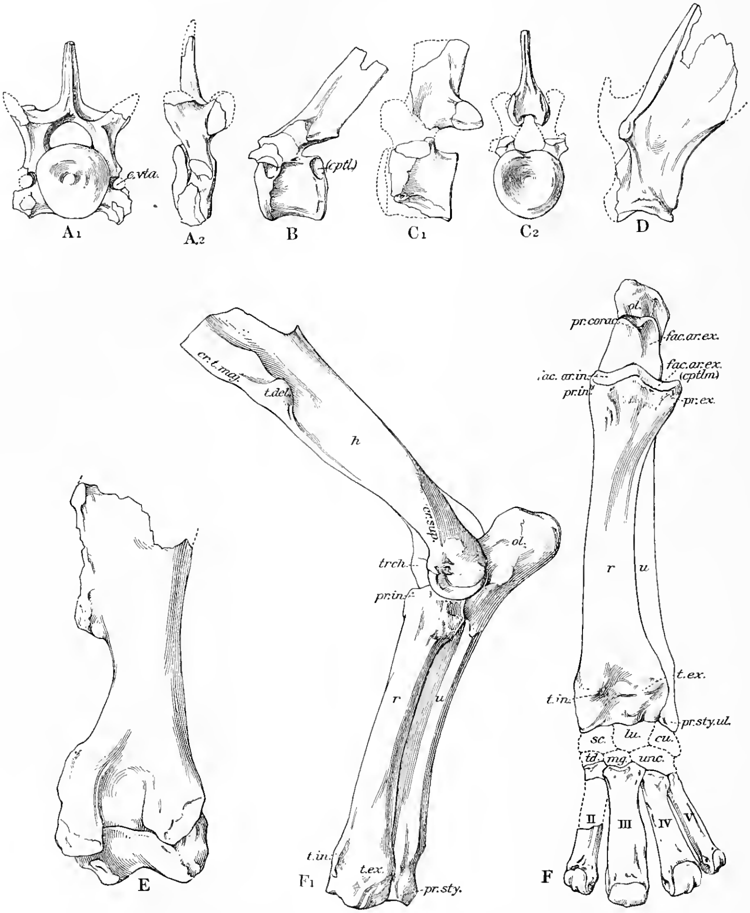

FIGURE 594.—Vertebrae and fore limb of *Diplacodon* or *Protitanotherium*

Princeton Mus. 10396; Uinta C. After Scott and Osborn. A_1, A_2, Front and side views of a cervical vertebra; B, a dorsal vertebra (D. 7–10?), side view; C_1, C_2, side and rear views of a lumbar vertebra; D, incomplete left scapula; E, rear view of left humerus; F_1, left humerus, radius, and ulna, outer side view; F, left radius and ulna with manus, front view, oblique perspective. One-sixth natural size.

The scapula of the same individual (Princeton Mus. 10396) is preserved, its total length being estimated at 600 millimeters (fig. 594). The characters are as follows: Coracoid process a stout tuberosity; glenoid fossa elongate, a rather shallow oval; spine ascending gradually from the neck and passing without an acromion process into a deep, recurved ridge; in midsection the spine much expanded along the border and overhanging the postscapular fossa. The parts preserved indicate that the scapula was lofty, with a rounded suprascapular border unlike the somewhat angular border of the Oligocene *Menodus* scapula.

The humerus (fig. 594) of the same specimen (Princeton Mus. 10396) lacks the head, lesser tuberosity, and bicipital groove. Its chief characters are as follows: Stout deltoid ridge, terminating in a prominent recurved hook; the inner length is estimated at 450 millimeters; shaft twisted upon itself, as in *Rhinoceros;* supinator ridge less distinctly marked and less prominent than in *Menodus;* pronator ridge rugose but not projecting; supratrochlear fossa deeply excavated, and trochlear process somewhat oblique to main axis of shaft.

The ulna and radius are complete in the same specimen (Princeton Mus. 10396, fig. 594) and taken together indicate a rather long and slender forearm. Other characters are as follows: Relative diameters of distal facets of radius and ulna about as 5 to 2, ulna with a very stout, rugose olecranon, with the posterior border presenting a single concave curvature, with shaft triangular in midsection, and a deep groove on the anterior face. The radius in midsection of the shaft is suboval anteriorly and flattened posteriorly. Facet for the entocondyle of the humerus with a deep anteroposterior diameter. The manus (Princeton Mus. 10396, fig. 594) lacks the carpus. The metacarpus exhibits a high, stilted tetradactyl or digitigrade type, the distinctive feature of the foot consisting in the subequal size of the second and fifth metacarpals, which brings the working median axis of the manus between the third and fourth digits instead of through the middle or third digit. This is a decided progression upon any known Bridger type. The measurements are as follows: Mtc III, length 180 millimeters; Mtc V, 130. Other measurements may be taken from the figure.

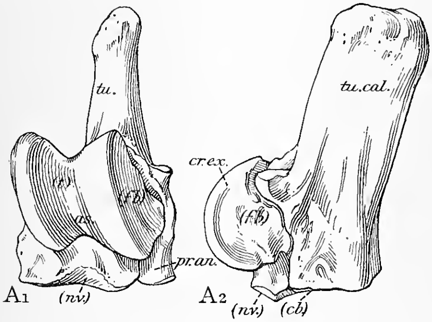

FIGURE 595.—Astragalus and calcaneum of *Diplacodon* or *Protitanotherium*

Princeton Mus. 10396; Uinta C. Left astragalus and calcaneum, crushed (?). A_1, Front view; A_2, outer side view. One-third natural size.

The femur belongs to another animal (Princeton Mus. 10395). The original drawing represents bones belonging to two individuals of the same size drawn in combination. This bone presents the essential characters of the femora of titanotheres.

The tibia of the same animal (Princeton Mus. 10395) is about five-sevenths the length of the femur; the cnemial crest is moderately prominent; there is the usual triangular section of the shaft just below the crest passing into an oval section in the lower third; the proximal and distal faces are too much worn to admit of description.

The somewhat crushed astragalus and calcaneum o a tarsus in the Princeton Museum (fig. 595) are of great interest. The principal feature of the calcaneum is the extremely narrow, deep, and elongate tuber calcis, which has an unusually flattened section. There is also a distinct fibular facet, and the calcaneum forms part of the tibial trochlea. The astragalus rests upon over one-third of the upper surface of the cuboid; the three astragalar facets—the ectal, sustentacular, and inferior—are entirely distinct.

An ilium (Am. Mus. 2084) may also be referred to this species. The measurements (estimated) are as follows: Transverse width across ossa innominata 665 millimeters, total width of superior border of ilium 340, length of anterior border to acetabulum 335. The superior border is well rounded.

A tibia (Am. Mus. 2056), rather short and massive, having a total length of 325 millimeters, is provisionally referred to the same species, *P. emarginatum.*

SUBFAMILY BRONTOPINAE?

Bones provisionally referred to Protitanotherium superbum

A radius (Am. Mus. 2035) exhibits a length of 425 millimeters and perhaps may be referred to *P. superbum.* The length of the radius in the Princeton Museum provisionally referred to *Diplacodon elatus* is 350 millimeters.

A large astragalus (Am. Mus. 2030) has the breadth (width across trochlear keels, 700 mm.) that seems appropriate for this species. The cuboid facet is very progressive (fig. 596).

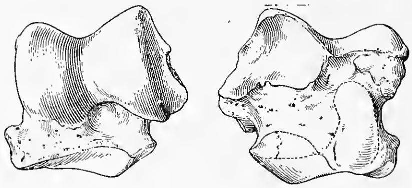

FIGURE 596.—Left astragalus of *Protitanotherium superbum*

Am. Mus. 2030; Uinta C. Front and rear views. One-third natural size.

SUBFAMILY DIPLACODONTINAE

Pelvis referred to Diplacodon elatus

The only portions of the skeleton certainly associated with the type of *D. elatus* are the cervical vertebrae associated with the type skull in the Yale Museum (No. 10320).

The pelvis (Princeton Mus. 10393, fig. 597) originally referred to *Diplacodon elatus* by Scott and Osborn in "The Mammalia of the Uinta formation" (1890.7, pp. 516, 517) may still be referred provisionally to that species. The marked characteristic of this pelvis is the great length of the ossa innominata as compared with their breadth. The ilia did not expand immediately above the acetabulum, but there is a long and rather slender neck of the ilium beyond which the borders begin to expand. The acetabular border of the ilium (a) presents a short, sharp curvature and is relatively much shorter than in *Palaeosyops*. The ischiac border (b) is much longer, with a gradual curvature. It follows that the supra-iliac border apparently presented outward more than directly upward and forward. Below the acetabulum the ischium has a triangular section, then expands in a plane directly perpendicular to that of the ilium.

FIGURE 597.—Incomplete ilium and ischium of *Diplacodon elatus*

Princeton Mus. 10393; Uinta C; provisionally described. After Scott and Osborn. One-sixth natural size.

Eotitanotherium Peterson

Although the type specimens of *Eotitanotherium osborni* Peterson were found in the upper part of horizon B 2 of the Uinta Basin, Utah, rather than in horizon C (true Uinta formation), this animal is in a stage of evolution in many respects similar to that of the titanotheres of horizon C and therefore may be conveniently described with them.

Peterson's description of the skull and dentition of the type and paratype and comparison with the Princeton specimen of *Diplacodon* or *Protitanotherium*, figured above, have been cited in Chapter V; his description of the rest of the skeleton (1914.1, pp. 37–51), with modifications in the nomenclature, is as follows:

> The atlas of the type (No. 2859) is quite complete. There is also the greater portion of an atlas with the paratype (No. 2860). With regard to the posterior division of the arterial canal it may be said that there appears to be some variation in the Uinta species. Thus it is seen that in the type the base of the transverse process is pierced by a small foramen (see fig. 598), while in the paratype there is no evidence of this foramen on the posterior face of the transverse process. Of the later Uinta forms there is apparently no atlas known. In comparing the Oligocene titanotheres with the Uinta specimens before us, there is a corresponding variation. The atlas of the Oligocene types further varies in the anteroposterior diameter and in the prominence of the neural spine and the transverse processes.
>
> In *Eotitanotherium osborni* the anteroposterior diameter of the atlas is rather small, while transversely it is proportionally greater than in the Oligocene forms. This is due in a great measure to the longer transverse process of the Uinta form. The cotyle for the occipital condyle is also deeper and the groove for the odontoid process of the axis extends farther forward on the inferior arch, due probably to the proportionally longer odontoid in *Eotitanotherium osborni*.
>
> The axis of the type is represented by a portion of the centrum, the complete neural arches, and the spinous process. The arch is somewhat depressed by crushing, but it is evidently of rather large size. The vertebra as a whole possibly has a smaller anteroposterior diameter than is the case in most of the titanotheres of the Oligocene; the articulating surface for the atlas is located more laterally, and the postzygapophysis has a greater vertical obliquity and a more nearly rounded outline than in the latter. In the Princeton specimen[41] it is seen that the arterial canal is located back of the posterior edge of the articulation for the atlas, while in *Eotitanotherium osborni* the foramen is, on a direct side view, partially hidden by the backwardly

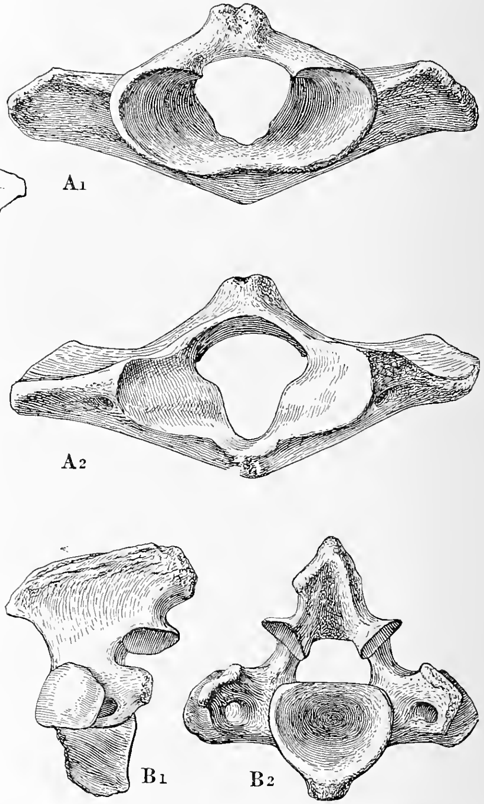

FIGURE 598.—Atlas and axis of *Eotitanotherium osborni*

Carnegie Mus. 2859 (type); Uinta B 2. A1, Anterior view of atlas; A2, posterior view of atlas; B1, posterior view of axis; B2, lateral view of axis. One-third natural size.

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[41] Scott, W. B., and Osborn, H. F., The Mammalia of the Uinta formation: Am. Philos. Soc. Trans., vol. 16, pt. 3, p. 514, pl. 9, fig. 15, 1889.

extended process of the articulation. I judge that the axis as a whole, in the present form, is relatively shorter than in the Princeton specimen. In more minute details the description of Scott and Osborn (op. cit., p. 514) agrees well with the parts preserved, in the specimen before me—that is, the heavy spine overhanging the postzygapophyses, the inner turn of the transverse process, and a prominent inferior keel.

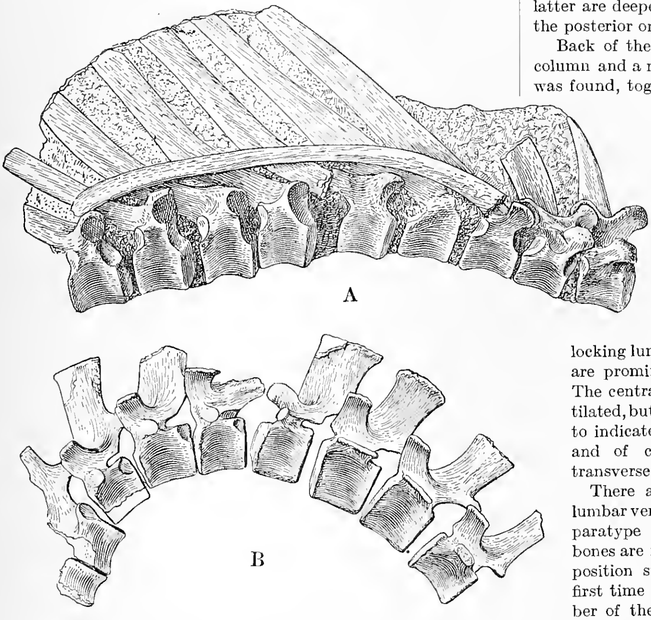

FIGURE 599.—Vertebrae of *Eotitanotherium osborni*

Carnegie Mus. 2860 (paratype); Uinta B 2. After Peterson. A, Last cervical and dorsal vertebrae, right side; B, posterior dorsal and lumbar vertebrae, left side. One-sixth natural size.

The succeeding four cervical vertebrae in the paratype (No. 2860) are represented only by fragments. They appear to have short opisthocoelian centra, as in *Diplacodon* described by Marsh and Osborn, and a prominent ventral keel.

The seventh cervical vertebra is completely worked out in half relief and shows the chief characteristic features [fig. 599]. The long and pointed spinous process is well shown, as is also the neural arch and the centrum. The pre- and post-zygapophyses are, as in the axis, located quite laterally and face directly upward and downward as in *Menodus*. The transverse process shows a tendency to develop the broad round termination found in *Brontops validus* of the Oligocene.

There are eight dorsal vertebrae, which are worked out in half relief and rest on the original block of sandstone on which they were found. The neural spine of the first dorsal is broken off about 10 centimeters above the neural arch, but judging from the size of the fracture, the spinous process attained a length equal, and perhaps even proportionally greater, than was the case in *B. validus*, with which the Uinta remains have been compared. The second, third, fourth, and fifth dorsals have their spines very nearly complete. In proportion they agree quite well with those of the Oligocene genus but are more strongly inclined backward. As in *Menodus* the transverse processes are not extremely heavy and the capitular facets for the ribs are of large size, while the sides of the centra are deeply concave. The latter are deeper than broad, and the inferior borders, especially the posterior ones, are distinctly more keeled than in *Menodus*.

Back of the eighth dorsal there is a break in the vertebral column and a number of bones are lost. A second block which was found, together with the one just described, contains portions of six posterior dorsals and three lumbar vertebrae. [See fig. 599.] The neural spines of the dorsal series are prominent and quite lumbar-like in their general character. The zygapophyses are also of the interlocking lumbar type, and there are prominent metapophyses. The centra are somewhat mutilated, but enough is preserved to indicate that they are deep and of comparatively small transverse diameter.

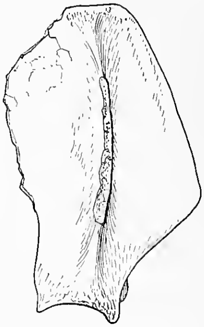

FIGURE 600.—Scapula of *Eotitanotherium osborni*

Carnegie Mus. 2859 (type); Uinta B 2. After Peterson. One-sixth natural size.

There are, as stated, three lumbar vertebrae present in the paratype (No. 2860). These bones are fortunately found in position succeeding the last dorsal vertebra, and for the first time apparently furnish data as to the correct number of the lumbar vertebrae of the titanotheres. That the last one of this series is the last lumbar vertebra there is but little or no doubt, inasmuch as the neural spine

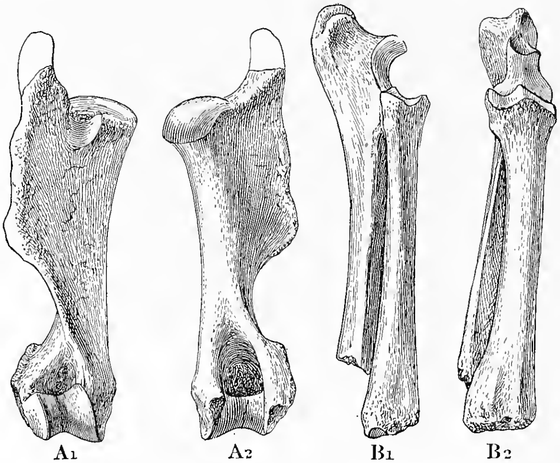

FIGURE 601.—Humerus, radius, and ulna of *Eotitanotherium osborni*

Carnegie Mus. 2860 (paratype); Uinta B 2. A_1, Anterior view of humerus; A_2, posterior view of humerus; B_1, lateral view of radius and ulna; B_2, anterior view. One-sixth natural size.

is very suddenly reduced in its fore-and-aft dimension and also shows the presence of the very heavy transverse process and the well-expanded postzygapophysis to meet the correspondingly broad surfaces of the sacrum. Unfortunately the greater portion of the centrum is weathered away, but from what remains it appears that it was more depressed than are those in front of it. Of the first and second lumbars the centra are large, sharply keeled, and the transverse processes, though generally broken off, are seen to have been prominent, though attenuated. There are large metapophyses, and the neural spines are high and of great anteroposterior diameter.

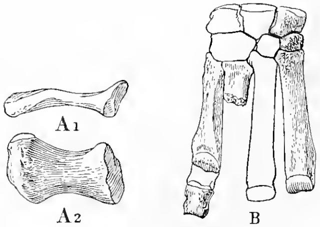

FIGURE 602.—Manus of *Eotitanotherium osborni*

Carnegie Mus. 2860 (paratype); Uinta B 2. A1, Superior view of pisiform; A2, lateral view; both one-third natural size. B, Dorsal view of manus, one-sixth natural size. After Peterson.

Measurements of Eotitanotherium osborni, in millimeters

	No. 2859	No. 2860
Atlas		
Greatest anteroposterior diameter	90	95
Greatest transverse diameter	250	250
Greatest transverse diameter of articulation for occipital condyle	140	138
Vertical diameter of articulation for occipital condyle	60	60
Axis		
Greatest height	[a]138	------
Greatest transverse diameter	158	------
Transverse diameter of postzygapophyses	70	------
Length of centrum of a median cervical vertebra	------	37
Depth of centrum including inferior keel, approximately	------	45
Seventh cervical, greatest height when vertebra is in position	------	195
Seventh cervical, length of spine	------	120
Seventh cervical, anteroposterior diameter of centrum	----	70
Second dorsal, greatest height when vertebra is in position	------	300
Second dorsal, length of spine	------	[a]325
Seventh dorsal, greatest height when in position	------	200
Seventh dorsal, length of spine	------	165
Last dorsal, greatest height when in position	------	165
Last dorsal, length of spine	------	90
Second lumbar vertebra, greatest height when in position	------	165
Second lumbar vertebra, length of spine	------	[a]95
Caudal belonging to middle region of tail, length	------	29

[a] Approximate.

The sacrum is not represented. The caudals appear to be short and heavy and in other respects like those of the Oligocene forms.

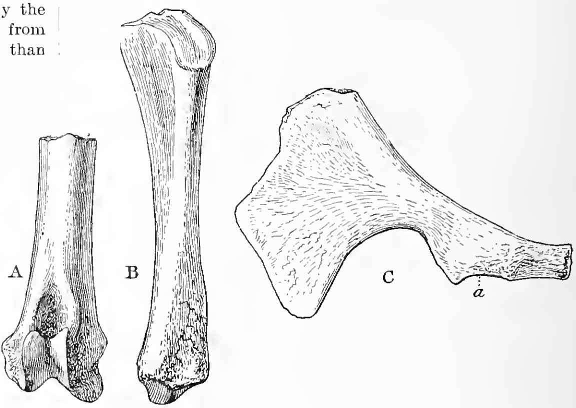

FIGURE 603.—Femur, tibia, and pelvis of *Eotitanotherium osborni*

A, Distal end of femur, Carnegie Mus. 2860 (paratype); B, dorsal view of tibia, Carnegie Mus. 2862 (paratype); C, lateral view of pelvis, Carnegie Mus. 2859 (type). After Peterson. One-sixth natural size. *a*, Acetabulum.

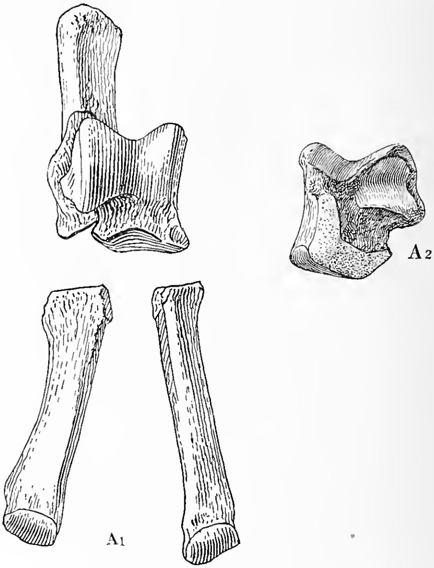

FIGURE 604.—Pes of *Eotitanotherium osborni*

Carnegie Mus. 2860 (paratype). A1, Dorsal view of pes; A2, posterior view of astragalus. After Peterson. One-third natural size.

The ribs are represented only by a few fragments, and there are no sternebrae.

The greater portion of the scapula is represented with No. 2859. The upper and lower ends were found separately embedded in the sandstone ledge, but in working out the two portions it is seen that they pertain to the same side of two individuals. The bone as a whole, so far as comparison may be

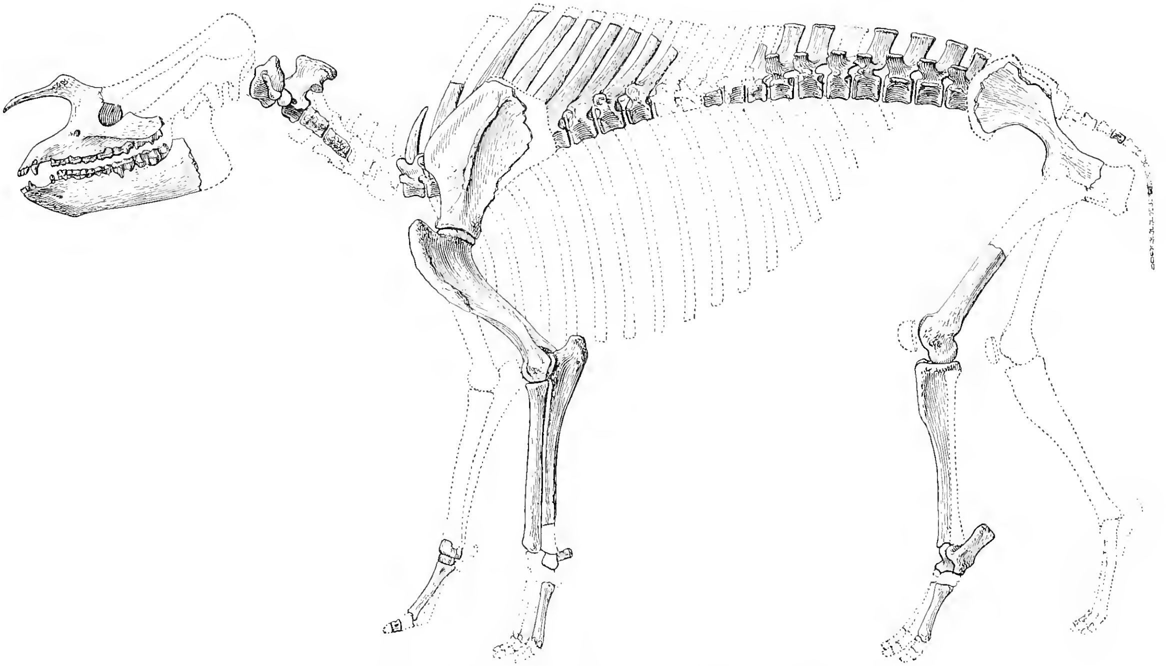

FIGURE 605.—Restoration of skeleton of *Eotitanotherium osborni*

This represents the type (Carnegie Mus. 2859) and the paratypes. After Peterson. One-twelfth natural size.

made, presents characters not unlike those in the Princeton specimen referred to *Diplacodon elatus* (see above). However, in the specimen under description (possibly a female) the coracoid is seen to be relatively smaller than in the latter. The groove between the base of the coracoid and the border of the glenoid cavity is larger in proportion than in *Menodus*, and the excavation on the coracoid border, immediately above the coracoid, has a less abrupt curvature. This is due to the smaller development of this angle in *Eotitanotherium*. The coracoid border is otherwise quite straight as in *Menodus*. The superior portion of the glenoid border is broken off, but in the region of the break there is a similar broad extent of the superior portion of the blade. The spine is damaged, but it was apparently overhanging like that in *Diplacodon* described by Osborn, and thus less extended over the postscapular fossa than in *Menodus*.

In comparing the humerus of the present form with that of *Brontops validus*, the difference most noticeable is the relative robustness and the length. In the Oligocene form the bone is short and very heavy, while in the present genus the bone is longer in proportion and also lighter. Superiorly the greater tuberosity extends higher above the head than in *Menodus* but is not so robust, the proximal end as a whole being more delicately proportioned. The bicipital groove is deep and well defined, as in the Oligocene genus. On the other hand the deltoid ridge, though very prominent, does not terminate in the heavy recurved process as in *B. validus* but descends much more gently toward the supratrochlear fossa. Distally there is less variation between the two forms here compared. The anconeal fossa in the species under description is relatively broader, and the supinator ridge is less rugose. The trochlea is slightly deeper but not more oblique than in *B. validus*.

The humerus as described and figured by Osborn holds an intermediate position between the Oligocene genus and the present form. This is especially shown in the development of the deltoid ridge, which in the Princeton specimen is considerably more developed than in the genus under description.

Measurements of humerus of Eotitanotherium, in millimeters

	No. 2860	No. 2861
Length from head to distal end	365	365
Transverse diameter of lower part of deltoid ridge	[a] 108	[a] 110
Transverse diameter at broadest portion of supinator ridge	115	113
Transverse diameter of distal trochlea	------	78

[a] The shafts of the two bones are more or less crushed, and the measurement is only approximately correct.

Both radii and ulnae are represented in No. 2860. A third radius was also found in the same sandstone ledge in close proximity to the spot where Nos. 2858 and 2859 were found.

The radius and ulna are long and relatively slender when compared with those of the Princeton specimen of *Diplacodon* and the Oligocene genus *B. validus*. Thus the forearm of the new genus is actually a little longer than in *Diplacodon* and is very nearly as long as that of *B. validus*, notwithstanding the much smaller size of the Uinta form of which we are speaking. Another striking difference between the forms here compared is the lateral expansion of the proximal and distal ends of the radius. In the Oligocene form the shaft of the radius is more rounded in the middle region, while more proximally and distally a sudden expansion takes place, which is also well displayed in the Uinta specimen described and illustrated by Scott and Osborn. In *Eotitanotherium osborni* the shaft is flatter, more uniform throughout, and the proximal and distal ends comparatively little expanded.

The proportions of the ulna conform to the radius, and it is consequently slenderer and proportionally longer than in *Diplacodon* and *Menodus*. In detail the bone is otherwise quite similar to that in the two latter genera, including the well-defined tendinal groove on the anterior superior angle of the olecranon process so characteristic of the ulna of *Brontops validus*, but apparently less developed in the Princeton specimen, judging from the illustration (Pl. IX, figs. 10–10^{c}).

Measurements of No. 2862

	Millimeters
Radius, greatest length	380
Radius, transverse diameter at middle of shaft	40
Radius, transverse diameter of head	78
Radius, transverse diameter of distal end	77
Ulna, length of olecranon process	100

The forefoot of No. 2860 is represented by the scaphoid, pisiform, trapezoid, Mtc II, IV, and V, and one or two phalanges. No. 2859 has also Mtc IV and V represented.

As might be anticipated from the description of the limb, it is found that the foot is higher than in *B. validus* of the Oligocene. Thus the scaphoid is higher in proportion and narrower than in the latter species but is of considerable fore-and-aft diameter. In detail there are only such differences as one might expect from the general outlines described—that is, the different articulating surfaces of the distal face are narrow and long, while the articulation for the radius is less concave anteroposteriorly than in the Oligocene form. The pisiform has a similar long attenuated shaft terminating in an obtuse tuberosity of considerable vertical diameter but transversely rather thin. Besides the greater height of the trapezoid, the small posterior superior facet for the magnum, which is characteristic of *Menodus*, is practically wanting in the present form. Judging from the facet on the posteroradial angle there is present in the new Uinta genus a trapezium of considerably larger size.

Mtc II is long, quite broad, but of small anteroposterior diameter, which is in part due to crushing. The proximal end is partly broken off, so that the different facets can not be accurately compared. The shaft is of quite uniform width until the distal articulating surface is reached, where there is on the radial face a sudden expansion. This character is less apparent in the Oligocene forms and also apparently less than in the metacarpus of the Princeton specimen from the Uinta, as figured by Scott and Osborn. Mtc IV is, as stated, represented by fragments in both type and paratype and displays no features of especial importance.

Mtc V is longer and slenderer than the same element in *B. validus* and that referred to *Diplacodon* (Pl. IX, fig. 13). Proximally and distally the bone is expanded much as in *Menodus*, and the shaft, though relatively longer, is of a similar cylindroid character. The facet for Mtc IV is located more laterally than in the Oligocene genus, and the dorsal and ulnar faces are less deeply grooved for muscular attachments. Near the distal end is a flange on the postero-ulnar angle, which is similar to that already described on Mtc II and is not generally present in the Oligocene titanotheres.

There is apparently more inequality in size between Mtc II and Mtc V than represented in the figure of the manus of *Diplacodon* by Scott and Osborn. This is very probably due, to some extent, to the crushing of Mtc II of the specimen in the Carnegie Museum. In the specimen at Princeton the complete length of Mtc V is apparently represented. Its measurements appear to be only about 13 millimeters longer though nearly one-third broader than that of the specimen before us.

The phalanges are short, broad, and in every respect titanotheroid.

Measurements of No. 2860

	Millimeters
Scaphoid, vertical diameter	35
Scaphoid, transverse diameter	33
Scaphoid, anteroposterior diameter	53
Pisiform, total length	60
Trapezoid, vertical diameter	20
Trapezoid, transverse diameter	26
Trapezoid, anteroposterior diameter	36
Mtc II, greatest length	153
Mtc II, transverse diameter of head, approximate	37
Mtc II, transverse diameter of middle of shaft, approximate	30
Mtc II, transverse diameter of near distal end, approximate	42
Mtc V, greatest length	125
Mtc V, greatest transverse diameter of head	36
Mtc V, greatest transverse diameter of middle of shaft	20
Mtc V, greatest transverse diameter of near distal end	33
Proximal phalanx, length	31
Proximal phalanx, transverse diameter of proximal end	29
Proximal phalanx, transverse diameter of distal end	26

The pelvis of No. 2859 is represented by the greater portion of the ilium. It is quite broad across the gluteal surface, but the point of the ilium probably did not project laterally as much as in *B. validus*. The constricted portion of the neck is actually longer than in the latter species and also longer than in the Princeton specimen of *Diplacodon* as represented on Plate VIII in Scott and Osborn's work. The pelvis as a whole was consequently proportionally longer and probably narrower than in the Oligocene genus. The ischium and pubis are not represented.

In No. 2860 the lower half of the femur is present. The tibial and dorsal faces of the shaft are convex, while posteriorly it presents a flat surface. On the fibular angle may be seen the lower portion of the prominent ridge below the third trochanter, which decreases in prominence in its downward course. Near the distal end the fibular border presents a roughened area for muscular attachment, back and below which is the rather shallow supracondylar fossa. Distally the condyles are rather well separated by the deep and broad intercondylar fossa. The lateral sides of the distal end (especially the fibular) is well marked by the rugose attachment for muscles. The rotular trochlea is proportionally deeper and narrower than in *Menodus*, and the fossa immediately above it is much deeper and better defined. In this respect the present genus agrees better with Figure 5 on Plate VIII of Scott and Osborn's publication.

Measurements of femur of No. 2860

	Millimeters
Total length of the fragment	280
Transverse diameter of shaft about the middle region of the fragment	60
Transverse diameter of distal end	108
Anteroposterior diameter of distal end	110

The greater part of the tibia is represented in the paratype No. 2860, but it is badly crushed. Another individual, No. 2862, has both tibiae present and is approximately of the same size as the individuals we are describing. The bone is very nearly as long as in *B. validus*. The ends are not expanded as in the latter form, while the shaft is flatter, due in part to crushing. The superior end carries a heavy and bifid spine, while the upper anterior extremity displays the broad groove for the patellar ligament as in *Menodus*. The cnemial crest, though prominent, does not descend low on the shaft, another feature recalling what may be observed in *B. validus* and in the Uinta specimen figured by Scott and Osborn.[42] The anterior border of the distal trochlea was found weathered off, but the posterior surface is complete and presents a very prominent descending process on the median ridge of the articulating trochlea very similar to what is seen in the later Uinta form and in *Menodus*.

From the material in hand it is shown that the hind limb of *Eotitanotherium osborni* corresponds well in length with the fore limb.

Measurements of tibia of No. 2862

	Millimeters
Greatest length, approximate	415
Transverse diameter of head	100
Transverse diameter of shaft, middle region	48
Transverse diameter of distal end, approximate	75

The hind foot of No. 2860 is represented by the calcaneum, the astragalus, and the second and fourth metatarsals.

When compared with the Princeton specimen from a higher Uinta level and also with the Oligocene genera, the tuber of the calcaneum in the present form is seen to be as long in proportion and compressed laterally to the same extent, while that portion carrying the sustentacular facets is longer. The fibula also apparently articulates with the calcaneum, but the posterior portion of the tibial trochlea did not touch the calcaneum as in *Diplacodon* and in *Menodus*. The astragalus is higher and narrower, and the metatarsals are longer and much slenderer than in the latter genera.

When compared in more detail there are a number of differences between the genera here compared. On the calcaneum of the genus under description the proximal astragalar facet is not raised as high above the surface as in *Menodus*. The greater process of the distal end extends lower down and the facet for the cuboid is more oblique than in *Menodus*. As already stated, the astragalus is higher and narrower, the trochlear groove is deeper, with the articular surfaces of the two condyles steeper, and the neck separating the distal end from the trochlea longer than in the astragalus of the Oligocene form and also somewhat longer than in *Diplacodon* as figured by Scott and Osborn. Furthermore, the distal end of the astragalus of the present form is more unequally divided by the navicular and cuboid facets than in the Oligocene genus. These facets of the astragalus in *Menodus* are more nearly subequal in size, the cuboid facet having increased in size as well as being located more distally on the bone, while in *Eotitanotherium* this facet occupies a comparatively narrow area on the fibular angle and is placed laterally.

The most noticeable difference of the astragalus of *Eotitanotherium osborni* and that of the Princeton specimen as figured (Pl. VIII, fig. 8*b*) seems to be in the three distinct astragalar facets (viz, ectal, sustentacular, and cuboidal) of the latter, while in the present form the ectal, besides extending higher, unites with the cuboidal facet without distinct separation, the two forming a perfect right angle apparently similar to that in *Mesatirhinus*.[43]

Aside from the greater proportionate length the metatarsals differ from those in *Menodus* by being arched forward to a greater degree. The shaft of Mts IV is more cylindrical, and the facet for the cuboid more oblique.

Measurements of No. 2860

	Millimeters
Astragalus:	
Total length	71
From lower end of external condyle to distal end	26
Greatest transverse diameter	68
Transverse diameter of trochlea	56
Calcaneum:	
Greatest length	124
Length of tuber	64
Vertical diameter of tuber	45
Transverse diameter of tuber	22
Transverse diameter at sustentaculum	70

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[42] If the illustration on Pl. VIII, Fig. 6, in Scott and Osborn's publication is one-fifth of nature, as is that of the femur in the same plate, the tibia of that form is actually shorter than that in the genus here described.

[43] Osborn, H. F., Am. Mus. Nat. Hist. Bull., vol. 24, p. 68, 1908.

Mts II:	Millimeters
Length	150
Transverse diameter at head	28
Transverse diameter of shaft, median region	21
Transverse diameter of distal end	26
Mts IV:	
Length	41
Transverse diameter of head	38
Transverse diameter of shaft, median region	22
Transverse diameter of distal end	34

The restoration of *Eotitanotherium osborni* here attempted (Pl. X) is obtained from the material described in the preceding pages, and it is chiefly based on two individuals. As previously stated, the front of the skull, the lower jaws, atlas, axis, pelvis, and a few fragments of the feet pertain to one individual, the type, while the rest of the vertebral column, a few ribs and limb bones, as well as a number of foot bones, belong to a second individual, one of the paratypes.[44] The dotted lines represent estimated diameters and are consequently conjectural as to proper contour outlines. This is especially true of the posterior portion of the skull, the sacrum, the ischium, the upper half of the femur, and the caudal region. There are inserted two cervicals, two dorsals, the sacrum, and the greater part of the caudal region. The vertebral formula as represented in the illustration is the same as that of the articulated skeleton of *Menodus* from the Oligocene now in the Carnegie Museum. The vertebral formula of *Eotitanotherium osborni* is in part therefore tentative and is as follows: Cervicals 7, dorsals 17, lumbars 3, sacrals 4, caudals 18. The ribs are conjectural.

The illustration is effected for the purpose of ascertaining at a glance the general proportions of the animal. Each part represented by the solid lines is drawn directly from the bones themselves, by the assistance of the pantograph, and the illustration as a whole is fairly reliable.

Measurements

	Centimeters
Total length of the vertebral column from the premaxillary to the end of the sacrum, all curves of the backbone included	252
Height of skeleton at fore limb	138
Height of skeleton at hind limb	114

SECTION 5. THE POSTCRANIAL SKELETON OF OLIGOCENE TITANOTHERES

Five factors have conspired to limit our knowledge of the postcranial skeleton of Oligocene titanotheres and to make it unsatisfactory.

First, owing to the conditions of preservation and deposition, the skulls of Oligocene titanotheres are rarely found in association with the rest of the skeleton, so that only a few skeletons have been mounted. Marsh's type of *Brontops robustus* in the Yale Museum and the skeleton of *Menodus trigonoceras* in the Munich Museum are nearly complete. The skeleton of *Brontops dispar* in the Carnegie Museum is nearly complete, but it lacks the skull. The skeleton of *Brontops robustus* in the American Museum includes the skull, fore limbs, and thorax of one individual, but the pelvis and hind limbs are supplied from another individual.[44a] A few skulls were found in association with parts of the limbs or of the backbone, but by far the greater part of the collections consist of unassociated skulls, jaws, and parts of skeletons.

Second, the natural scarcity of well-associated material was intensified by the hasty methods of early collectors, who, with certain exceptions, through eagerness to secure the conspicuous and highly prized skulls, neglected the opportunity to collect skulls and skeletal parts in association or failed to make careful records of such association. Still further damage was done through crude methods of packing and transportation.

Third, an unfavorable condition arises from the crushing and distortion suffered by the skeletal parts of titanotheres during the structural alteration and displacement of the ancient strata in which they are entombed. A skeleton in the American Museum of Natural History (No. 1064), in which there is a good association of dentition, vertebrae, and limbs, is rendered practically useless for systematic study through the crushed condition of the bones. Such distortion often alters the natural contours and proportions in a deceptive manner, as noted by the late J. B. Hatcher (1902.1), who showed that in the Carnegie Museum skeleton certain limb bones on one side were much lengthened, while on the opposite side the corresponding elements were shortened, the former having been crushed laterally, the latter longitudinally. As a result of distortion, added to the great difficulty of securing uniformity in the methods of measuring such large skeletons, it follows that many of the measurements given below would hardly be a safe basis for precise quantitative distinctions between supposedly different species.

Fourth, a difficulty arises from the wide differences between males, females, and young of the same species and at different ages, which even in the study of well-preserved skulls causes considerable uncertainty as to the correct identification of certain specimens. Besides this it is probable that fully adult male titanotheres of the same species would show considerable variation in minor characters and measurements of the vertebrae and limbs, as in the case of modern rhinoceroses.

Fifth, the postcranial skeleton of titanotheres has not hitherto been used to any extent by authors in defining the genera and species, so that, from a systematic point of view, the vertebrae and limbs have not been regarded as sufficiently important to require the degree of intensive study which has been made of the skull and dentition.

As a result of these unfavorable conditions we have as yet only an incomplete knowledge of the generic characters of the vertebrae and limbs of Oligocene titanotheres, while we have hardly begun to recognize specific differences. The following studies are preliminary and should be supplemented by a more systematic and intensive study of the material available comparable with that which has been made upon the skulls.

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[44] There was no other material found with the remains of *Eotitanotherium* described in the preceding pages, except a few fragments of turtles. All the material was found within a radius of about 20 feet.

[44a] Since this was written the Colorado Museum of Natural History, at Denver, Colo., has mounted an unusually fine skeleton of *Megacerops acer*, and the U. S. National Museum, at Washington, has mounted a partial skeleton of *Brontotherium hatcheri*.

Chief skeletal characters of the Oligocene phyla

Brontops phylum	Allops phylum	Menodus phylum	Brontotherium phylum
Progressively graviportal, brachypodal. Scapula and pelvis less broad than in *Brontotherium*. Tall and ponderous animals.	Relatively small, short-limbed.	Relatively long, slender-limbed. Scapula and pelvis of high, slender type. Neck relatively long.	Progressively increasing in size and weight. Skulls very large. Necks relatively short and massive. Scapula and pelvis extremely broad, graviportal type. Limbs very broad and massive. Feet relatively short as compared with Menodus.

Skeletons and parts of skeletons of Oligocene titanotheres here described [a]

Genus and species	Specimen	Museum
Brontops ?brachycephalus	Referred partial skeleton with skull. Mounted.	Victoria Memorial Museum, Ottawa.
Brontops dispar	Referred skeleton without skull. Mounted.	Carnegie Museum, Pittsburgh, No. 92.
Brontops robustus	Type skeleton with skull. Mounted.	Peabody Museum, Yale University, No. 12048.
Brontops	Referred incomplete skeleton with skull. Mounted.	American Museum of Natural History, New York, No. 518.
Diploclonus tyleri	Type incomplete skeleton with skull	Amherst Museum, No. 327.
Allops marshi	Referred partial skeleton with skull. Mounted.	Field Museum of Natural History, Chicago, No. P6900.
Allops crassicornis	Referred partial skeleton with skull	British Museum (Natural History), London, No. 5743M.
Menodus trigonoceras	Referred skeleton with skull. Mounted.	Munich Palaeontological Museum.
Do	Referred manus and pes	American Museum of Natural History, New York, No. 1079.
Menodus ?heloceras	Referred pes	American Museum of Natural History, New York, No. 1080.
Menodus giganteus	Referred pelvis and hind limbs	University of Nebraska, Lincoln, No. 3296.
Do	Referred ulna and radius	Carnegie Museum, Pittsburgh, No. 120.
Do	Referred skull and cervicals	Field Museum of Natural History, Chicago, No. 5927.
Brontotherium leidyi	Referred partial skeleton with skull	Carnegie Museum, Pittsburgh, No. 93.
Do	do	Carnegie Museum, Pittsburgh, No. 114.
Brontotherium hatcheri	Referred manus and pes	American Museum of Natural History, New York, No. 1047.
Brontotherium gigas	Referred manus	American Museum of Natural History, New York, No. 1443.
Do	Referred partial skeleton with skull	American Museum of Natural History, New York, No. 492.
Brontotherium gigas hatcheri	Referred partial skeleton with skull. Mounted.	U. S. National Museum, Washington, No. 4262.

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[a] In addition to those listed there are two well-mounted skeletons of titanotheres (*Megacerops acer*) in the Colorado Museum of Natural History, Denver, Colo. (1928). (See Pl. CCXXXVI.)

Comparative measurements of the skeletons of lower Oligocene titanotheres, in millimeters

	Brontops dispar, Carnegie Mus. 92	Brontops robustus, Yale Mus. 12048 (type)	Brontops robustus?, Am. Mus. 518	Brontops robustus?, Am. Mus. 1046	Diploclonus tyleri, Amherst Mus. 327 (type)	Allops marshi, Field Mus. P6900	Allops crassicornis?, British Mus. 5743M	Menodus trigonoceras, Munich Mus.	Menodus trigonoceras, Am. Mus. 1079	Menodus giganteus?, Carnegie Mus. 120	Monodus giganteus?, Univ. of Nebraska 3296	Brontotherium leidyi, Carnegie Mus. 93	Brontotherium ?hatcheri, Am. Mus. 1047	Brontotherium gigas, Nat. Mus. 4262	Brontotherium gigas, Am. Mus. 492	Brontotherium ?gigas, Am. Mus. 1443	Brontotherium gigas, Yale Mus. (?part of type)
Height at shoulder (top of third dorsal)	1, 855	2, 502	2, 311	----	[a]2, 230	----	----	[a,b]2, 120	----	----	----	----	----	----	----	----	----
Skull, length, pmx to condyles	-----	765	-----	----	[a] 768	655	637	700	----	----	----	----	----	770	830	----	----
Skull, breadth across zygomata	-----	667	-----	----	------	465	----	------	----	----	----	----	----	----	740	----	----
Atlas, width	-----	460	440	----	320	----	275	------	----	----	----	305	----	----	----	----	----
Second dorsal, length of spine above centrum	-----	580	612	----	------	----	----	------	----	----	----	----	----	----	600	----	----
Scapula, length	600	690	657	----	690	----	570	[a] 640	----	----	----	475	----	593	----	----	----
Scapula, greatest breadth	-----	-----	-----	----	------	----	----	------	----	----	----	----	----	407	----	----	----
Humerus, length (head to entocondyle)	545	615	530	----	------	425	450	557	----	----	----	380	----		----	----	----
Radius, length	404	495	455	----	490	355	350	525	----	475	----	305	----	----	460	----	----
Radius, width at top	-----	170	165	----	------	----	----	------	----	----	----	93	----	----	168	----	----
Ulna, length	535	680	610	----	[a] 620	475	----	------	----	595	----	410	----	----	642	----	----
Carpus, width, proximal row (facets)	167	200	207	205	170	142	----	149	155	----	----	----	168	160	----	200	----
Lunar, width	65	-----	90	89	74	----	50	65	59	----	----	----	----	62	84	80	----
Mtc II, height	155	220	212	----	------	144	----	214	196	----	----	----	----	----	----	207	----
Mtc II, maximum width near distal end	-----	74	-----	----	------	----	----	------	----	----	----	----	----	----	----	----	----
Mtc III, height	173	225	218	----	250	155	----	233	199	----	----	----	----	187	----	----	160
Mtc III, maximum width near distal end	72	88	-----	----	------	----	----	------	----	----	----	----	----	----	----	----	76
Mtc IV, height	163?	210	204	----	------	138	----	225	188	----	----	----	----	174	210	----	----
Mtc IV, maximum width near distal end	59	84	-----	----	------	----	----	------	----	----	----	----	----	----	----	----	----
Pelvis, width	935 +	1, 220	-----	----	------	----	----	830	----	----	----	----	----	----	1, 170	----	----
Pelvis, length, ilium crest to ischium	809	900	-----	----	------	----	----	------	----	----	902	----	----	----	820	----	----
Femur, length	[c] 686	820	-----	----	785	590	560	703	----	----	762	----	----	----	----	----	----
Tibia, length	[c] 432	430	-----	----	446	350	345	430	----	----	432	300	----	----	----	----	----
Calcaneum, length	-----	230	-----	----	208	147	140	------	155	----	----	----	----	152	----	--	----
Astragalus, width	-----	110	-----	----	105	70	82	------	----	----	----	----	----	----	----	----	----
Astragalus, height (fibular side)	-----	86	-----	----	------	----	----	------	----	----	----	----	----	80	----	----	----
Tarsus, width (astragalus and calcaneum)	-----	144	-----	----	------	90	100	------	105	----	----	----	126	120	----	----	----
Mts II, length	-----	180	-----	----	------	----	----	------	173	----	----	----	----	----	----	----	----
Mts II, width near distal end	-----	-----	-----	----	------	----	----	------	----	----	----	----	----	----	----	----	----
Mts III, length	164	208	-----	----	205	----	155	------	200	----	----	----	170	----	----	----	----
Mts III, width near distal end	-----	96	-----	----	------	----	----	------	----	----	----	----	----	----	----	----	----

[a] Estimated. [b] After correcting position of scapula. [c] Crushed.

SUBFAMILY BRONTOPINAE

Lower Oligocene titanotheres, progressively graviportal and brachypodal; trapezium lost in later forms.

Brontops dispar Marsh

Materials.—Our knowledge of *Brontops dispar* is based chiefly upon the remarkably complete skeleton in the Carnegie Museum (No. 92), which lacks the skull and three anterior cervicals. The skeleton was discovered by J. B. Hatcher in Sioux County, Nebr., in 1900 and described by him in 1902 (1902.1). The locality is Warbonnet Creek; the geologic level is near the base of the *Titanotherium* zone as exposed at that point, about 30 feet above the Pierre shale; the matrix fine clays. The skull had been destroyed by weathering; the skull and jaws mounted with the specimen belong to another animal.

Limb distortion by crushing.—An interesting feature connected with the discovery is the distortion due to the various positions of the several bones as they lay embedded. The right femur, which was embedded vertically, is some 6 inches shorter than the left, which was embedded horizontally. The right and left humeri similarly differ widely in proportion. This striking discrepancy shows what extraordinary care must be taken to avoid conclusions based merely on measurements. The calcanea of the opposite sides are of entirely different shape, although there is little external sign of crushing. Had these femora been found in different localities they would certainly have been referred to different species if not to different genera.

Comparison with Brontops robustus.—As Hatcher observes, not only is this skeleton smaller and somewhat less robust than that of *B. robustus*, but there are primitive characters of importance. (1) Compare the slender, pointed neural spine of the first dorsal vertebra, which although much longer resembles that of the last cervical in form, with the broad, heavy neural spine of the first dorsal in *B. robustus* or in *Menodus.* (2) In the carpus of *B. dispar* a well-developed trapezium is present, while it is absent in *B. robustus.* In this connection Hatcher observes that in all titanotheres from the lower *Titanotherium* zone the trapezoid shows a trapezium facet.

The measurements are given in the table above.

Summary of primitive characters.—This skeleton presents the following primitive characters as compared with *Brontops robustus:* (1) Less development of neural spines on cervicals and dorsals, smaller neural spines on cervicals; (2) relatively more elongate scapula and innominate bones; (3) slightly less elevated humeral tuberosity; (4) a trapezium; (5) lunar resting more subequally on magnum and unciform; (6) tarsus less compressed vertically; (7) less displacement in manus and pes; (8) limited metacarpal displacements—that is, Mtc II without large magnum facet; (9) Mtc III with small ectocuneiform facet.

Size and proportions.—The total linear proportions of this skeleton to that of the *Brontops robustus?* skeleton in the American Museum (No. 518, fig. 606) can not be given owing to the absence of the skull, but a few comparisons can be made:

Comparative measurements of Broniops dispar and B. robustus?

	B. dispar, Carnegie Mus. 92			B. robustus?, Am. Mus. 518		
	Millimeters	*Ft.*	*in.*	*Millimeters*	*Ft.*	*in.*
Shoulder height, to spine of third dorsal	1, 855	6	1	2, 300	7	7
Breadth of pelvis	935	3	¾	1, 220	4	
Length of fore limb, including scapula	1, 743	5	9	2, 050	6	9
Length of hind limb	1, 500	4	11	1, 670	5	6
Presacral vertebrae	2, 275	7	5½	2, 640	8	8
Length of femur	686	2	3	790	2	7

The skeleton of *B. robustus* is thus throughout between one-sixth and one-eighth larger.

Vertebrae.—The vertebral formula is C. 7, D. 17, L.?, S. 4, C. 18. The atlas (partly restored) exhibits a hypophysial backward spur beneath the axis.

More in detail, the fourth to seventh cervical vertebrae resemble those of *B. robustus* in the lateral processes but differ markedly in the comparatively small spines on C. 6 and C. 7. D. 1 differs also in its relatively slender spine; in D. 2–5 the spines are approximately equal, that of D. 2 being the broadest and somewhat the longest; in D. 7–14 the spines gradually diminish in height; in D. 15 to L. 2 the spines are relatively lower and broader than in *B. robustus;* in D. 3–12 the zygapophyses are horizontal; in D. 13–17 the zygapophyses become obliquely vertical. In L. 2 (the only lumbar preserved) the transverse processes are rather narrow; the spine is relatively broader and larger than in *B. robustus.* Twelve caudals are preserved, of which the third bears a chevron but not the second.

Ribs.—The first rib is less massive than in *B. robustus.* The ribs increase steadily in length from R. 1 to R. 8; R. 8 to R. 10 are the longest and of nearly equal length; R. 11–17 steadily diminish in size.

Sternals.—The manubrium is restored. S. 2 and S. 3 are laterally compressed. The xiphisternum is partially restored.

Scapula and fore limb.—As compared with that of *Brontops robustus* the scapula is relatively higher and narrower, the anterior and posterior borders being more nearly parallel, and the general form more quadrate than triangular; this is due to the relatively larger supraspinous fossa, the long, straight anterior border for the attachment of the levator anguli scapulae, the inferior angle of which above the supracoracoid notch is placed on a lower level than in *B. robustus;* similarly the infraspinous fossa for the infraspinatus muscle is relatively smaller; as characterized by a very prominent rugosity at the posterior superior angle (latissimus dorsi), the superior or vertebral border is less arched than in *B. robustus.*

The humerus exhibits a highly convex great tuberosity (supraspinatus and infraspinatus insertion), which is relatively as elevated as in *B. robustus;* the deltoid ridge and tuberosity are equally prominent and the external or supinator crest rises very prominently, the shaft being deeply excavated between. The internal face of the radius is somewhat less elevated than in *B. robustus;* its total length (404 mm.) is double the circumference (202). The ulna exhibits a broadly flattened anterior face; the olecranon lacks the deep vertical cleft at the summit so characteristic of the upper Oligocene titanotheres.

The carpus shows the following characters: Breadth 167 millimeters, lunar resting broadly on the magnum facet (28 to 32 mm.) as well as on the unciform facet (34 to 40 mm.), more primitive or less displaced than in *B. robustus*, much more primitive than in *Menodus.* The trapezium is present; it is attached above to the scaphoid but reaches only halfway down the inner face to the trapezoid; it is not in contact at all with Mtc II. Magnum broad; Mtc II with a narrow magnum facet (20 mm.); Mtc III with a relatively narrow unciform facet (14 mm.) (this facet is broader in *B. robustus*); Mtc IV occupying main portion of unciform; Mtc V articulating chiefly with the outer side.

The linear measurements of the metacarpals are as follows: Mtc II, 155 millimeters; Mtc III, 176; Mtc IV, 174 (?); Mtc V, 137. The proximal phalanges are very broad and large; the median phalanges are short. The distal phalanges are relatively smaller than in *B. robustus*, expanded transversely and of short linear dimensions; the widths are, Ph II, 43 millimeters; Ph III, 45; Ph IV, 46; Ph V, 38.

Pelvis and hind limb.—Massive as the pelvis is, its intermediate character is indicated by the fact that the total length of the innominate bone is 809 millimeters, as compared with the total breadth of 925 millimeters across the two ilia; the posterior opening is correspondingly elongate vertically. The hind limb as compared with the fore limb is long and slender, with the following principal characters: Femur with projecting head, feebly marked third trochanter directly opposite second trochanter, and both well down on the shaft, inner patellar facet much more elevated than outer, patella vertically elongate, inner condyle of the femur much the largest. Tibia relatively elongate and less massive than in *B. robustus*, shaft of fibula much reduced superiorly. Pes as a whole decidedly slender; tarsus having a breadth of 110 millimeters across cuboid and navicular; tuber calcis not placed transversely; astragalus with a relatively long neck; navicular and cuboid relatively deep; metatarsals of medium length and slenderness, surprisingly light in structure; Mts II not abutting against ectocuneiform as in *B. robustus;* Mts III with a very oblique lateral facet for cuboid (differing widely from the broad facet in *B. robustus*); proximal phalanges long and rather narrow; distal phalanges moderately broad.

Brontops robustus Marsh

Type specimen.—Our knowledge of *Brontops robustus* is based on the superb type specimen in the Peabody Museum at Yale University (Yale Mus. 12048) which was discovered and unearthed by Mr. H. C. Clifford in 1875 in the upper *Titanotherium* zone near Chadron, Nebr. It was appropriately made the type of *Brontops robustus* by Marsh, and it is very fully illustrated in Plates XCVI–CIII, CXCV–CCXXIX of this monograph. As noted in detail below, certain of the plates and the very remarkable restoration by Berger under Marsh's direction (Pl. CCXXIX) include bones that were derived from other specimens. In 1916 this skeleton was mounted under the direction of Prof. R. S. Lull, who gives the following measurements: Height at shoulder, 8 feet 2½ inches (=2.502 meters)[45]; length over all, following vertebral column, 15 feet 2½ inches (=4.635 meters); length between perpendiculars to base of tail, 11 feet (=3.353 meters).

Of the presacral vertebrae 26 are preserved—7 cervicals, 17 dorsals, and 2 lumbars—in a continuous series, the third or posterior lumbar being apparently missing.

The characters of the cervicals in lateral view are accurately represented in the restoration forming Plate CCXXIX and in Figure 610, A.

The atlas (Pl. CXCV, figs. 1–5) measures 465 millimeters transversely, 158 vertically, 278 across the axis facets; the neural arch is perforated at the side for the exit of the first cervical nerve, which passes down anteriorly in a deep notch between the junction of the condylar cup with the transverse process (figs. 2, 4); the transverse processes (ribs) are moderately robust, not very widely expanded anteroposteriorly, somewhat truncate or square distally; the neural spine is sessile and slightly grooved but not bifid posteriorly. The axis (Pl. CXCVI) measures 270 millimeters transversely, 290 vertically, the outside measurement of the posterior face of the centrum being transverse 137, vertical 119; the superior border of the spine is acutely convex and slopes obliquely backward, slightly overhanging the centrum posteriorly; the antero-inferior face is abruptly truncate; the odontoid is short; the atlanteal facets are continuous, the median area being transverse, the lateral areas oblique and flaring. In C. 3–7 (Pl. CXCVII) the neural spines increase regularly in height, that in C. 7 being pointed but entirely different in character from the spine of D. 1; the prezygapophyses and postzygapophyses are flattened and face upward and inward, and downward and outward; the laminae of the neural arches increase gradually in width as seen from above in C. 3–C. 7. The cervical transverse processes or ribs (pleurapophyses) in C. 3 exhibit a broad, thin plate; in C. 4 a rugose superior and small flat inferior lamella; in C. 5 rugose and subequal superior and inferior lamellae; in C. 6 a rugose superior lamella and widely expanded, anteroposteriorly flattened inferior lamella; in the imperforate C. 7 the inferior lamella is entirely wanting.

Proportions of presacral centra.—The comparative measurements on page 667 bring out the following characters in the proportions of the centra. The short, deeply opisthocoelous cervical centra (C. 3–7) range from 650 to 700 millimeters in length, from 107 to 114 in width, and from 106 to 113 in height, practically as high as broad. The dorsal centra are less deeply opisthocoelous; they are longer than the cervicals, ranging from 73 to 88 millimeters in length; in the anterior dorsals (Pl. CXCVIII) the vertical exceed the transverse measurements, correlated perhaps with the spines; in the middle and posterior dorsals the vertical are less than the transverse measurements.

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[45] In Professor Lull's judgment this measurement is probably 3 or 4 inches too great—that is, the backbone as mounted is too high.

Comparative measurements of cervicals, dorsals, and lumbars, in millimeters [a]

	Anteroposterior	Transverse	Vertical
C. 1 (atlas)	69	245	--------
C. 2 (axis)	110	267	--------
C. 3	70	108	107
C. 4	65	107	112
C. 5	58+	108	106
C. 6	66	112	111
C. 7	70	114	113
D. 1	73	103	114
D. 2	75	92	[b] 118
D. 3	77	96	117
D. 4	76	98	113
D. 5	76	100	100+
D. 6	77	114	109
D. 7	77	111	103
D. 8	80	108	103
D. 9 [c]	[d] 90	103	[d] 107
D. 10	75	94	90
D. 11	82	[d] 96	[e] 81
D. 12	77	85	84
D. 13	75	90	84
D. 14	84	93	77
D. 15	88	87	77
D. 16	83	96	76
D. 17	77	92	77
L. 1	87	88	89
L. 2	88	[d] 92	90

[a] The longitudinal measurements are taken along the inferior line of the centra from between the edges of the articular facets; the vertical and transverse measurements are taken on the anterior faces of the centra.

[b] Height of spine, 695 millimeters.

[c] The position of this vertebra in the series is somewhat doubtful.

[d] Estimated.

[e] Crushed.

Dorsals.—There are 17 rib-bearing or dorsal vertebrae. The first dorsal (D. 1) marks a very abrupt transition from the cervicals by the sudden elevation of its very broad spine to a height of 590+ millimeters; the laterally flattened upper portion of the spine rests upon the relatively short triangular lower portion. In the succeeding dorsals, D. 2–D. 10 (Pl. CXCIX), the triangular basal portion of the spine, deeply excavated posteriorly (fig. 4), becomes relatively higher until in D. 7 it extends nearly to the top of the spine. The spine of D. 2 (Pl. CXCVIII) appears to have been the stoutest and the most elevated; it is more backwardly directed than that of D. 1. From D. 3 to D. 17, inclusive, the spines gradually diminish in height and become more slender and more backwardly directed. In L. 2 (Pl. CC) the spine is short and obliquely directed backward.

The zygapophyses are characteristic: the postzygapophysis of D. 1 and prezygapophysis of D. 2 are transversely oblique or face respectively outward and inward, whereas in the American Museum skeleton referred to *Brontops* they are subhorizontal. The postzygapophyses of D. 2 face directly downward and backward—that is, in a more nearly horizontal plane. Similarly, the postzygapophysis of D. 2 and the prezygapophyses of D. 3–D. 15 are anteroposteriorly oblique or subhorizontal, facing downward and upward respectively rather than outward and inward. In D. 14 a transition occurs to the outward facing of the postzygapophyses and the inward facing of the prezygapophyses. In D. 17 the articulation is very slightly revolute, convexo-concave. In L. 1 the articulation is not preserved; in L. 2 (Pl. CC) the postzygapophyses are flat and face obliquely outward and downward.

Rib facets.—Throughout the series the capitular facets are the largest on the posterior sides of the centra, attaining a very great size, for the especially large third, fourth, and fifth ribs. In D. 12–D. 17 the capitular facets rise from the base of the neural arches, and even in the posterior dorsals, D. 15–D. 17, the tubercular facets are relatively large and well developed.

Lumbars.—The lumbars are imperfectly preserved, one of these vertebrae being lost entirely. The lumbar exhibits the following distinctive characters: Spine recumbent, zygapophysis facing obliquely outward and inward, not revolute, transverse processes rather feeble, with broadly rugose and sessile inferior keel.

Sacrals.—There are four sacrals (Pls. CCXVIII, CCXIX) rather imperfectly preserved; they rapidly diminish in size, S. 1 being very much larger than the succeeding sacrals.

Caudals.—An unusually perfect series of 16 caudals (Pl. CCI) is preserved in sequence behind the last sacral. The relatively small size of the most anterior caudal (figs. 1–3) is correlated with the small size of the posterior sacral and a small tail. The centra increase in length from C. 1, which measures 43 millimeters, to C. 9, which measures 70, and diminish to C. 16, which measures but 35. Neural spines and rapidly diminishing zygapophyses were present on C. 1–C. 8. C. 3 (figs. 6, 7, 8) exhibits a chevron inclosing the haemal artery; this element may also be preserved in C. 4 (figs. 9, 10) and C. 5 (figs. 11, 12, 13). The transverse processes rapidly diminish behind C. 1 and finally disappear in C. 11. The centra are biconvex. Beginning at C. 8 the centra become laterally compressed, and the posterior centra, C. 12–C. 16, are decidedly compressed laterally.

Ribs.—Nine perfect ribs (Pls. CCII, CCIII) are preserved and fragments of others. On the whole they are more slender and rounded in section than in the skeleton of *Brontops* in the American Museum, described below.

Sternebrae.—Three of the midsternebrae are preserved, measuring collectively 290 millimeters; the anterior (restored in Pl. CCXXIX) and one or more posterior sternebrae are missing. The supposed second sternebra is broadly depressed in section, measuring but 42 millimeters vertically, 123 anteroposteriorly, and 70 transversely; the flattening of the body of this element is partly due to crushing. The supposed third sternebra is deeper, measuring 35 millimeters vertically, and shorter (ap. 95 mm.) and somewhat narrower (tr. 64 mm.). The supposed fourth sternebra, which was largely cartilaginous at the extremities, measures 39 millimeters vertically, 70 anteroposteriorly, and 72 transversely.

Scapulae.—As partly restored, the scapulae of the type measure 690 millimeters vertically and 530 transversely; they are characterized by the narrow rectangular prespinous fossa, the large, broadly triangular postspinous fossa, and the rugose retroverted acrominal spine.

Humerus.—The humerus measures 622 millimeters from the head to the inner condyle. As admirably shown in Plate CCV, it exhibits (1) the deep bicipital groove (fig. 5), (2) the elevated platelike tuberosity (fig. 4) indented on the anterior superior border (fig. 5), (3) the prominent deltoid ridge terminating in the characteristic prominent and somewhat upturned knob (figs. 1, 3), (4) the rugose supinator ridge, (5) the very marked upward extension on the shaft of the internal radial facet (fig. 1).

Radius.—The radius (Pl. CCVI), measuring 495 millimeters, exhibits a transverse diameter of 170 millimeters for the humeral facets (fig. 5) and of 118 for the scaphoid and lunar (fig. 6). The rugose insertion of the brachialis anticus muscle is placed about the middle of the shaft (fig. 1). The shaft is well rounded in midsection (fig. 2a), the transverse diameter being 78 mllimeters.

Ulna.—The ulna (Pl. CCVII), having a total linear measurement of 680 millimeters (olecranon to unciform facet), exhibits the characteristic groove (figs. 2, 3) in the top of the olecranon; a stout trihedral shaft.

Manus.—The right and left manus are both preserved; the unfortunate absence of both lunars renders it difficult to ascertain the exact characters of this important element. The total width of the proximal row of carpals (fig. 1) across the facets is 200 millimeters (estimated), of the distal row 202; the vertical depth through the anterior faces of the scaphoid and magnum is 92; the length of Mtc III is 210; the height from the scaphoid to the extremity of the median metacarpal is 322; this manus, therefore, may be described as moderately broad and short. (See Pl. CCXXVIII.)

The detailed structure of the carpals as figured in Plates CCVIII–CCXI is important. The maximum measurements of the scaphoid (Pl. CCVIII, fig. 5 *r*) are, vertical 65 millimeters, transverse (radial face) 73, anteroposterior 82; the magnum facet (fig. 4) is exceptionally narrow (30), and the scaphoid is therefore relatively narrow transversely, deep vertically, and extended anteroposteriorly. The radial facet of the missing lunar is estimated at 170 millimeters, its magnum facet at 25, the unciform facet at 53; this bone had a relatively narrow, oblique facet on the magnum and a much broader facet on the unciform. The cuneiform (Pl. CCIX, figs. 1–6) is a smaller element, moderately deep (52 mm.) vertically, with a rectangular ulnar facet (fig. 5) which measures 57 millimeters transversely and 48 anteroposteriorly. The pisiform (Pl. CCIX, figs. 7–12) is large, measuring 125 millimeters anteroposteriorly. The trapezoid (Pl. CCX, figs. 1–6) exhibits no evidence of a trapezium facet; it is rather shallow (ap. 37 mm.) with a moderately broad scaphoid facet (fig. 5 *s*), 53 millimeters transversely, 67 anteroposteriorly. The magnum (Pl. CCX, figs. 7–12) measures vertically 40 millimeters and transversely 65 on the anterior face (fig. 7), with a broader scaphoid (fig. 7 *s*) (35) and a narrower (20) lunar facet (fig. 7 *l*). The unciform (Pl. CCXI, figs. 1–6) is a very large element, its maximum breadth being 114 millimeters, height 58, depth of cuneiform facet (ap.) 53 (fig. 1 *p*); superiorly (fig. 5 *l*) it exhibits a broad (55) lunar facet and a slightly broader cuneiform facet (fig. 5 *p*) (60); on the lower surface (fig.6) it has a narrow (12) abutment against the magnum (fig. 6 *m*) and a broader facet for Mtc III (27) (fig. 6 *mc* III).

The metacarpals (Pls. CCXII–CCXV) on the anterior face to the distal facet measure, Mtc II, 220 millimeters; Mtc III, 225; Mtc IV, 210; Mtc V, 180. Their characters are so admirably shown in the figures that they require no further description. The proximal phalanges are figured in Plate CCXVI; the median and distal phalanges and sesamoids are figured in Plate CCXVII. It is noteworthy that the distal phalanges are of moderate size and breadth, very much smaller than in the American Museum skeleton referred to *Brontops*, somewhat broader than in *Menodus*.

Pelvis.—The pelvis is decidedly broad, the entire width across the ilia being 1,220 millimeters (estimated), as compared with 908, the length of the left innominate bone (ilium to ischium). The pelvic outlet measures 373 millimeters vertically (pubic symphysis to sacrum) and 350 transversely. The pubo-ischiadic symphysis measures 357 millimeters longitudinally. The extreme breadth of the iliac plates is 407 millimeters. A more detailed discussion of the characters of the pelvis is continued below.

The association of the fore and hind limbs in this superb specimen is especially important as giving us the proportions.

Femur.—The femur (Pl. CCXX) measures 820 millimeters and the tibia 465. The shaft of the femur is somewhat crushed proximally, the great trochanter extends far (395 mm.) down the outer side, the width across the condyles distally is 187, the patellar trochlea is distinguished by the prominence of the inner facet and by the downward and forward projection of the trochlea. In the distal view (fig. 5) we are struck by the great disproportion between the greatly enlarged inner condyle (fig. 5 *i*) and the much reduced external condyle (fig. 5 *e*). This asymmetry of the end of the femur is naturally correlated with the asymmetry of the proximal faces of the tibia. The patella measures 165 millimeters vertically, 105 transversely, 100 anteroposteriorly; it is very stoutly convex.

Tibia.—The proximal face of the tibia (Pl. CCXXI), exhibits an elongate internal facet for the inner condyle of the femur (fig. 5 *c*) and a shorter external facet for the outer condyle (fig. 5 *e*). The facets converging into the wide and distinctly paired intercondylar spines—that is, the internal and external facets—are entirely separate; the cnemial crest is obtusely rugose (fig. 1). The shaft (fig. 1 *a*) is trihedral in midsection, the transverse diameter being 81 millimeters and the anteroposterior diameter the same. Distally there is a shallow trochlea for the astragalus (fig. 6).

Fibula.—The fibula (Pl. CCXXII), articulating by a flat proximal extremity (fig. 8) to the outer face of the tibia, extends into a rounded or subtrihedral shaft to form the external malleolus with facets (fig. 7 *t′*, *a*, *c*, and fig. 5 *a*) for the tibia, astragalus, and calcaneum.

Pes.—The left pes (Pl. CCXXVIII, fig. 2) is perfectly preserved except the phalanges. The maximum width of the astragalus and calcaneum combined is 144 millimeters, the depth from the top of the astragalus to the extremity of Mts III 320, to the extremity of the phalanx of D. 3 420 (estimated). The calcaneum (Pl. CCXXIV) is distinguished by moderate length (230 mm.), marked width (85 mm.) of the shaft of the tuber calcis (figs. 1–3), the long axis of which is obliquely transverse. The anterior or astragalar face (fig. 1) exhibits tibial (t), fibular (f) (32 mm.), ectal (a) (78 mm.), sustentacular (a′) (55 mm.), and inferior (a″) (32 mm.) facets, the last being strikingly reduced; distally (fig. 5) the cuboidal facet is divided into two parts, a larger anterior and a very much smaller posterior part; it also shows the ectal (a′) and sustentacular (a″) calcaneal facets. The astragalus (Pl. CCXXIII) is distinguished by the small astragalo-calcaneal inferior facet, the very broad (44 mm.) cuboidal facet (fig. 3 *c″*), the moderate elongation of the neck (fig. 1); the total width of the proximal trochlea (fig. 5) is 112 millimeters. The cuboid (Pl. CCXXV, figs. 7–12) is distinguished especially by its broad abutment (fig. 12, mt III; 35 mm.) for Mts III; superiorly the cuboido-calcaneal facet (fig. 11; 35 mm.) is double (c, c″) and somewhat narrower than the cuboido-astragalar facet (fig. 11 *a*; 36 mm.); it unites with the ectocuneiform (fig. 8, *ec*) by two separate facets, the posterior of which is not represented in the drawing; its maximum vertical depth (fig. 7) is 46 millimeters. The navicular (Pl. CCXXV, figs. 1–6) is shallow (fig. 1; 35 mm.), presenting inferiorly (fig. 6) a broader (42 mm.) ectocuneiform (*ec*) and a narrower (30 mm.) mesocuneiform (*m*) facet. The distinctive feature of the ectocuneiform (Pl. CCXXVI, figs. 7–12) is its anterior depth (fig. 7; 27 mm.) and double, internal lateral abutment facets (fig. 8, mt. II; fig. 12, mt. II, mt. II′) for Mts II; the mesocuneiform (Pl. CCXXVI, figs. 1–6) is consequently shallower (fig 2) vertically (20 mm.), measuring superiorly (fig. 5) 35 millimeters (tr.) by 48 (ap.). Mts II (Pl. CCXXVIII), measuring vertically 180 millimeters, abuts laterally above, against the ectocuneiform, a primitive feature; the shaft with a sharply convex ridge in front is deeply concave behind. Mts III (Pl. CCXXVIII), measuring 208 millimeters vertically, is distinguished by its moderately broad (42 mm.) ectocuneiform, an unusually broad cuboidal (35 mm.) facet; the shaft is broadly convex anteriorly and hollow posteriorly. Mts IV (Pl. CCXXVII, figs. 1–7), measuring 170 millimeters vertically, exhibits a shaft subrectangular in section superiorly and flattened and rounded in its middle portion (fig. 7), with a rugose line for muscular attachment, extending obliquely downward and inward across the anterior face (fig. 1); the distal face (fig. 6) exhibits the large share taken by the sesamoids (*ss*) and the limited share taken by the phalanges (*ph*).

Mounted skeleton in the American Museum of Natural History provisionally referred to Brontops

A mounted skeleton and skull (No. 518) in the American Museum of Natural History is now provisionally referred to the genus *Brontops*. It exhibits many specific if not generic distinctions from the type skeleton of *B. robustus* just described. Yet the characters of the skull and teeth relate it to *Brontops* and clearly separate it from either *Menodus* or *Brontotherium*.

The skeleton is a composite. Its anterior part as far back as the ilium belongs to one individual (Am. Mus. 518) which was discovered by the American Museum expedition of 1892, sent out under the direction of Dr. J. L. Wortman, who was assisted by Mr. O. A. Peterson. It was found near the head of Corral Draw in the Big Badlands of South Dakota. According to N. H. Darton, who in 1901 determined the level of this specimen, it was found 32 feet below the 3-foot siliceous limestone layer at the top of the *Titanotherium* zone (level Chadron C). Expeditions in two subsequent years, aided by the Princeton expedition, resulted in the discovery of the remains of other animals of similar proportions, which were used in the mounted skeleton—namely, the pelvis (Am. Mus. 1065), the left tibia (Am. Mus. 1075), fibula (Am. Mus. 1071), pes (Am. Mus. 1073, 1076), two femora (Am. Mus. 1442, 1443). A few parts in the feet are restored in plaster. The collocation of these hinder parts with the leading specimen is probably not certainly correct.

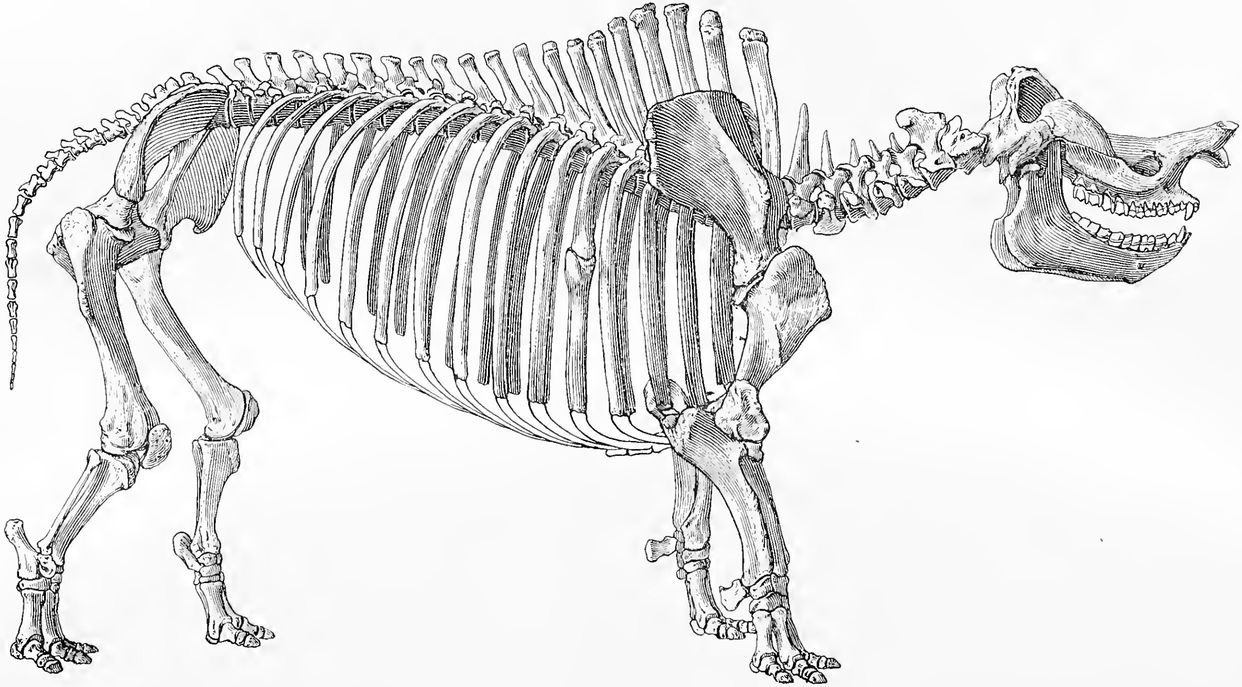

FIGURE 606.—Mounted skeleton of *Brontops robustus*, female

Based chiefly on Am. Mus. 518; Corral Draw, Big Badlands, S. Dak., upper *Titanotherium* zone. The skull, fore limbs, and thorax belong to one individual (Am. Mus. 518); the pelvis, hind limbs, and postdorsal vertebrae were supplied from other individuals, as listed in the text. In the drawing the scapula and fore limb are placed higher up on the side of the thorax than in the skeleton as mounted. One-nineteenth natural size.

As mounted with great skill by Mr. Adam Hermann, the skeleton is about 14 feet long, 8 feet high, and 4 feet broad. The sex can not be positively determined, as the canine teeth were wanting and are restored in plaster. The teeth are well worn, the protocones of m^2, m^3 being slightly abraded. The animal was therefore in the tenth stage of growth, as defined below, a fairly old adult.

An interesting feature of the skeleton, which may bear upon the question of the sex, is the exostosis and false joint in the center of the seventh rib on the right side (fig. 606); this was undoubtedly an after repair of a fracture, which may have been incurred in fighting. This would support the idea that the skeleton is that of a male, although it is known that the bulls of larger quadrupeds sometimes charge upon females which refuse their advances. As the cranial characters are decidedly those of a female the latter supposition is more probably the correct one.

The generic and specific determination of this skeleton is extremely difficult. It was originally referred by Osborn to *Titanotherium* (*Brontops*) *robustum*, but later he referred it to *Brontotherium gigas*, ♀, chiefly because the carpus (Am. Mus. 518) differs in important characters from that of Marsh's type of *Brontops robustus*.

Unfortunately the specimen lacks all the front teeth, as far back as p^3 and p_2. The upper premolars have the tetartocones retarded and well constricted, as in *Brontops*, and very different from the progressive circular tetartocones of male brontotheres. A supposed female of *Brontotherium gigas* (Am. Mus. 1006) also has the tetartocones much constricted, but the reference of this specimen is very doubtful. The external cingulum of the upper premolars and molars is absent, as it is in both *Brontops robustus* and *Brontotherium*, so this character is not decisive. The external cingulum of the lower premolars is reduced. On the whole the molar-premolar dentition appears closer to that of *B. robustus* than to that of *Brontotherium*.

The lower jaw as a whole presents no close resemblance to the jaws of brontotheres; from the type of *Brontops robustus* it differs in minor characters; perhaps its nearest resemblance is to the type of *Diploclonus tyleri*. The significant measurements of the skull and dentition, though few, are nearer to those of the type and referred *Brontops robustus* (especially Am. Mus. 1069) than to those of large male brontotheres. The skull is relatively larger than those of the supposed female brontotheres of *Brontotherium curtum* and *B. gigas* and differs from them in many characters.

The sections and contours of the horns and nasals are certainly different from those of the supposed female brontotheres and still more from those of the male brontotheres. The cranial sections are, in fact, closer to those of *Diploclonus tyleri* and *Brontops robustus* (especially Am. Mus. 1083).

The manus has the magnum much broader, more angulate than that of *B. robustus* as figured by Marsh. The lunar and magnum are also wider and more angulate than in the supposed *Brontotherium gigas* manus in the National Museum (No. 4262).

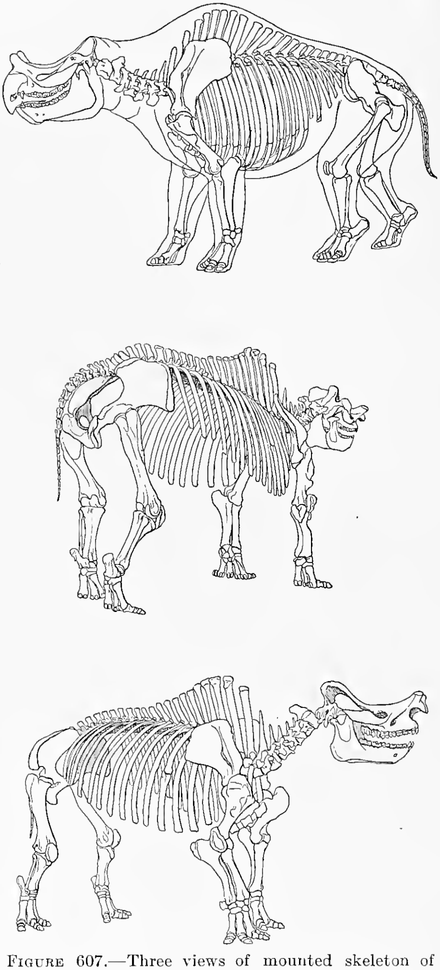

FIGURE 607.—Three views of mounted skeleton of *Brontops robustus*, female

Chiefly Am. Mus. 518. After Osborn and Wortman (1895.105). The skull and whole anterior part of the skeleton as far back as the pelvis belong to one individual. The pelvis and hind limbs are supplied from other specimens. (See fig. 606.)

As the hind limbs mounted with this skeleton belong to other individuals they do not assist in the determination of the principal specimen.

On the whole, the evidence indicates that the mounted skeleton is not that of a female brontothere but is a member of the brontopine group, probably a phase in the evolution of *Brontops*.

The vertebral formula is cervicals 7, dorsals 17, lumbars 3(?), sacrals 4, caudals 20+. In detail the vertebrae resemble those of *B. robustus* more than those of *Menodus giganteus*, but they are clearly distinguished in many characters from both species.

Adaptive provision for the insertion of. a powerful ligamentum nuchae correlated with the heavy skull is seen in the great rise of the four anterior dorsal spines, which are subequal in length, with their very rugose superior extremities and triangular basal portions fitted to resist the strain of the neck muscles. The neck is short but moderately flexible; the back is short, the tail greatly reduced.

The detailed characters of the presacral vertebrae are best illustrated in Plates CXCV–CC, which were drawn with such accuracy that most of the measurements can be taken from them. In the following description comparison is made throughout with the type of *Brontops robustus*.

The massive atlas measures 440 millimeters across the pleurapophyses, which are prominently convex (unlike the type of *B. robustus*) at the extremities; inferiorly the vertebrarterial canal traverses a broad (54 mm.) bridge; the hypapophysis is tuberous; the neural spine is prominent and bifid. The axis exhibits atlanteal facets 235 millimeters in width; the vertebrarterial canal traverses the central portion of the platelike pleurapophysis (the lower portion in *B. robustus*); the superior border of the spine is somewhat indented anteriorly and broadly tuberous posteriorly. In cervicals 3–7 the pre- and postzygapophyses face obliquely inward and outward, respectively, as in *B. robustus;* the superior and inferior laminae of the transverse processes differ considerably in detail from those of *B. robustus*, as seen by comparison of Figure 618 and Plate CCXXIX. In the ribless C. 7 the spine suddenly increases in height to about the same proportions as that of *B. robustus*. The cervical centra are deeply opisthocoelous, the transverse and vertical diameters being about equal.

The first dorsal is distinguished from that of the type of *B. robustus* by the fact that the postzygapophyses are subhorizontal as in the succeeding dorsals, whereas in *B. robustus* the postzygapophyses of D. 1 and the prezygapophyses of D. 2 are transversely oblique, resembling those of the cervicals. The neural spines of dorsals 1–17 are characteristic; the spine in D. 1 is greatly elevated and transversely compressed; the spines of D. 2, D. 3, D. 4 are subequal in height, gradually expanding into broad rugosities at the tips; the triangular basal portion of the spine, with its posterior groove, rises rapidly from D. 1 to D. 4; at the same time the spines diminish rapidly in anteroposterior diameter, and this diminution proceeds as far back as the spine of D. 14, behind which the spines increase again in anteroposterior diameter into the lumbar region. The zygapophyses, beginning with the postzygapophyses of D. 1, lie in subhorizontal planes as far back as D. 11, thence shift to transversely oblique planes D. 12–D. 14, and into nearly vertical planes, D. 15–D. 16. The zygapophysial facets of D. 17 and L. 1 are distinguished from all others by being concavo-convex but not revolute as in *Palaeosyops*. The diapophyses, or attachment of the tubercles of the ribs, pass from broadly expanded plates in D. 1 backward into tuberosities of diminishing size in D. 11, and above these tuberosities they rise in D. 12–D. 17 into distinct vertical processes. The capitular facets are borne largely on the posterior faces of the centra and in a less degree on the anterior faces, throughout as in *B. robustus*, rising gradually to the upper sides of the centra.

Three lumbars, although somewhat crushed laterally, afford all the principal characters. They exhibit stouter spines and transverse processes than in *B. robustus*. The postzygapophyses of L. 1 and the prezygapophyses of L. 2, although vertically placed, have a convexo-concave articulation like that between D. 17 and L. 1; in L. 2 and L. 3 the zygapophysial facets are flattened or plane and placed in oblique planes.

The caudals are added from another individual, and neither the specific determination nor the enumeration is certain. C. 2 is represented with a chevron, and this, as Hatcher has pointed out, may be an error; the first chevron may occur below C. 3, as in *B. robustus*. The centra are typically biconvex, increasing in length from 40 millimeters in C. 1 to 60 in C. 8. The bifid spines and the vestigial zygapophyses persist in C. 1–C. 9; the transverse processes subside in the same vertebrae.

The ribs are admirably preserved in a continuous series on both sides. The general characters are as follows: Ribs 1–5 progressively increase in length and width of section anteroposteriorly; ribs 5–8 are of approximately equal length but slightly decrease in anteroposterior measurement; ribs 9–17 decrease in length, also in anteroposterior diameter or width; they increase in the convexity of the outer surface, passing from a more flattened to a more convex, lenticular section. The measurements may readily be taken from the restoration except those of R. 1 (445 mm.), R. 2 (555 mm.), and R. 3 (625 mm.).

As compared with the Eocene titanothere *Palaeosyops* the tubercles are less widely separated from the heads, this being correlated with the less extreme transverse extension of the diapophyses. The large size of the ribs, the persistence of tubercles posteriorly, the abbreviation of the lumbar region all indicate an enormously capacious chest and abdominal cavity.

Two of the mid-sternebrae are preserved. They are laterally compressed, with flaring articular surfaces, concave superior and convex inferior surfaces; the most anterior, which may represent the second sternal, measures 94 millimeters anteroposteriorly and 65 transversely; the succeeding sternal measures 85 millimeters anteroposteriorly and 48 transversely.

The scapula is perfectly preserved on both sides. (The scapulae are placed too low on the side of the thorax; cf. corrected placing in fig. 606.) It exhibits a vertical diameter of 657 millimeters, as compared with 690 millimeters in *B. robustus* (type). Its maximum horizontal diameter is 572 millimeters. The postspinous fossa is much more expanded than the prespinous fossa, the posterior border presenting a concave backward and upward surface to the thickened rugose suprascapular border, which rises with a convex arch to a point in front of the spine, at the same time thinning gradually; the anterior border is extremely thin in the midsection, forming a deep rectangle, passing below into the coracoid process; the diameter of the glenoid border is 160 millimeters. The tuberous elevated apex of the spine is considerably below the center of the scapula, in contrast with that in *Palaeosyops major*, which is above the center; the spine is still more elevated at this point than in *B. robustus*.

The proportions of the bones of the fore limb are indicated by the relative lengths of the humerus (550 mm.), radius (460), and lunar to tip of middle digit (365).

The humerus is 50 millimeters shorter than that of Marsh's type of *B. robustus*. Its greater tuberosity and deltoid crest are substantially similar to those in the type of *B. robustus* (Pl. CCV); its lesser tuberosity is much more prominent than in that type. These tuberosities, together with the great supinator crest, indicate an enormous development of the supraspinatus, infraspinatus pectoral, subscapularis, deltoid, and other muscles. The anterior trochlea of the humerus, as in that of *B. robustus*, presents a decided upward extension of the internal face, correlated with the elevation of the internal half of the radius. This is a distinctive character of the titanothere forearm.

FIGURE 608.—Scapulae of Oligocene titanotheres

A, *Brontops robustus*, Yale Mus. 12048 (type); B, *Brontops*, Am. Mus. 518; C, *Allops crassicornis*, British Mus. 5743 M; D, *Menodus trigonoceras*, Munich Museum. One-eighth natural size.

The proportions of the radius may be judged from the total length (460 mm.) as compared with the total proximal breadth (165 mm.) and the distal breadth (162 mm.), figures which should be contrasted with those of the radius of *Menodus giganteus*. The principal characters are the elevation of the inner side of the proximal humeral facet; the presence of a prominent rugosity for the insertion of the brachialis anticus near the middle of the shaft; a deep median groove 180 millimeters below this rugosity for the common extensor tendon; and a larger transverse diameter of midshaft (72 mm.) as compared with the anteroposterior diameter (65 mm.).

The ulna is highly characteristic, measuring 600 millimeters over all. It is distinguished by the bifid, prominent and deeply cleft olecranon; the concave anterior surface of the shaft with very rugose internal and external borders; and the reduced inferior extremity.

The manus (fig. 609) is highly characteristic of this specimen and may be readily recognized by its breadth and massive proportions; the peculiar, irregular form of the magnum, which is unlike that of either *Menodus* or *Brontops robustus* (type); the comparatively broad and distally spreading terminal phalanges; and the secondary carpal displacement, as shown in the very broad lunar-magnum facet and the relatively small size of the lunar-unciform facet. The proportions are shown by the following measurements: Width of proximal carpals (across facets), 207 millimeters; height of Mtc III, 218. These measurements indicate that the manus is relatively broader, or has less vertical depth, than that of the type of *Brontops robustus*.

The carpus, considered in detail and compared especially with the carpus of *Brontops robustus* (Pl. CCXXVIII), shows these principal features: The scaphoid has a broader displacement on the magnum; its width is 89 millimeters, its vertical anterior measurement 54. The lunar is broad and depressed, with a much broader magnum facet than in *B. robustus;* its width is 90 millimeters, vertical depth (anterior) 59; it also rests widely upon the unciform. The cuneiform is characterized by a broad external tuberosity for muscular attachment. Width 64 millimeters, vertical height 47. The trapezoid measures, scaphoid facet, anteroposterior 74 millimeters, vertical 33. The magnum (tr. 76, vert. 47) is the most highly characteristic element, being readily distinguished from that of either *Menodus* or *Brontops robustus* (type) by (1) its vertical wedgelike extension upward between the scaphoid and lunar, (2) its exceptionally large size and breadth, and (3) its narrow contact with the unciform correlated with the marked spreading of the proximal end of Mtc III. The unciform has a less transverse extent as seen from in front than in either *Menodus* or *Brontops robustus*, correlated with the less extreme displacement of the proximal carpals.

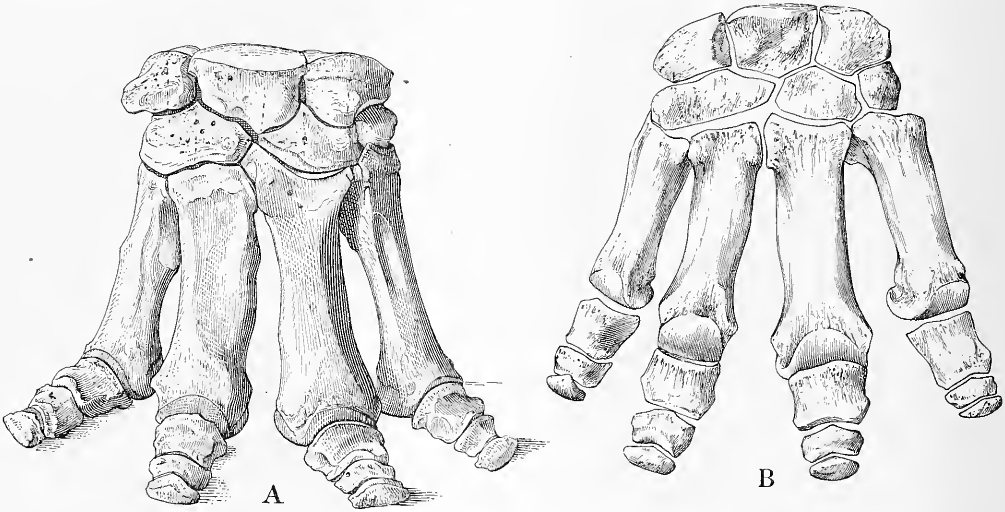

FIGURE 609.—Manus of *Brontops?* sp. and *Brontops dispar?*

A, Am. Mus. 518, a mounted skeleton referred to *Brontops?;* B, Carnegie Mus. 92, a mounted skeleton referred to *Brontops dispar?*. The carpals of this specimen are somewhat distorted by crushing. One-fourth natural size.

The metacarpals exhibit the following linear measurements: Mtc II, 212 millimeters; Mtc III, 218; Mtc IV, 204. They are larger and somewhat more massive throughout than in *Brontops robustus.* A striking feature is the great proximal width of Mtc III and its elongate upward extension against the unciform between the magnum and Mtc IV; this process is much longer than in *Menodus* or in *Brontops robustus* type.

The terminal phalanges are highly distinctive, being double the size of those of *Menodus* and much larger than those of *Brontops robustus;* they are rugose and expand distally, especially on D. 2–4, somewhat as in the rhinoceros. The terminal phalanx of D. 3 measures 55 millimeters transversely.

As the pelvis and hind limb of this mounted skeleton are not associated with the leading specimen and not certainly determinable as to genus and species a detailed description of these parts may be omitted. These specimens bear the following American Museum numbers: Pelvis, 1065; left femur, 1443; right femur, 1442; left tibia, 1075; right tibia and fibula, 493; left fibula, 1071; pes, 1073 and 1076.

Mounted skeleton of Brontops brachycephalus? in the Victoria Memorial Museum, Ottawa

The author has had no opportunity of studying this specimen, but a figure of it has been supplied through the courtesy of Mr. Harlan I. Smith and Mr. Charles M. Sternberg, of the Victoria Memorial Museum. (See figs. 610, 611.)

Manus provisionally referred to Brontops robustus?

A large manus in the American Museum (No. 1046[46]) is provisionally referred to this genus and species. As compared with the manus of the mounted skeleton already described (Am. Mus. 518) its measurements are as follows:

Comparative measurements of manus referred to Brontops robustus, in millimeters

	Am. Mus. 518	Am Mus. 1046 (right)	Am. Mus. 1046 (left)
Breadth	207	205	[a]194
Vertical	100	100	[a]104
Scaphoid, transverse	89	83	[a]70
Scaphoid, vertical	54	52	55
Lunar, transverse	90	89	--------
Lunar, vertical	59	[a]55	--------
Cuneiform, transverse	64	58	69
Cuneiform, vertical	47	[a]45	50
Trapezoid, anteroposterior	74	76	67
Trapezoid, vertical	33	39	37
Magnum, vertical	47	41	40
Magnum, transverse	76	[a]70	65
Unciform, vertical	68	56	--------
Unciform, transverse	92	105	--------
Mtc II, vertical	212	--------	--------
Mtc II, transverse	56	56	--------
Mtc III, vertical	218	--------	--------
Mtc III, transverse	58	57	--------

[a] Estimated.

Diploclonus Marsh

Skeleton of Diploclonus tyleri Lull

In the Amherst College Museum is an important though incomplete skeleton (No. 327), the type of *Diploclonus tyleri* Lull, which was found in Spring Draw Basin, about 10 miles from the mouth of Bear Creek, a tributary of Cheyenne River, S. Dak. The specimen was found lying 35 feet above the base of some 200 feet of *Titanotherium*-bearing beds. The skull and dentition are described on page 503.

The material includes a skull and lower jaw, the atlas and axis, two cervical vertebrae, nine dorsals, thirteen ribs, and the greater part of the fore and hind limbs. Lull's description (Lull, 1905.1, pp. 448–456) of the vertebrae and limb bones is as follows:

> *The atlas.*—The atlas is a broad, heavy bone, with wide articular facets and expanded transverse processes. The spine is extremely low, and the short truncated hypapophysis extends backward. Of the foramina, only that for the dorsal root of the first cervical nerve is present, the ventral one, well shown in *Palaeosyops*,[47] being here represented by a deep notch as in the rhinoceros, which our specimen also resembles in the lack of a vertebrarterial canal and in the relative widths of the anterior and posterior facets.
>
> The dimensions of the atlas are:
>
> | | Millimeters |
> |---|---|
> | Total width | 320 |
> | Width across atlar-occipital facets | 204 |
> | Width across atlar-axis facets | 255 |
>
> *The axis.*—The axis is a massive bone with a high neural arch, the spine being an equilateral triangle in midsection. On its posterior face a shallow groove arises between the zygapophyses which fades out about two-thirds of the way to the summit. The prezygapophyses overhang the atlas in front but present no articular facets. The odontoid process is a truncated cone and is not so prominent relatively as in *Palaeosyops*, being about one-third the length of the centrum measured along its inferior face. The latter exhibits a low longitudinal ridge below but is not deeply excavated on either side, as in *Paloeosyops*. The transverse processes of the specimen are broken away, but the bases of its two supports are seen, indicating the position of the vertebrarterial canal, which is placed rather high on the centrum, though not on a line with its upper surface, as is *Palaeosyops*.
>
> The postzygapophyses look downward and outward; their horizontal axes, if continued, would intersect at an angle of 90°. Altogether both atlas and axis resemble those of a rhinoceros much more than those of *Palaeosyops*.
>
> The measurements of the axis are as follows:
>
> | | Millimeters |
> |---|---|
> | Total height to summit of spine | 295 |
> | Greatest breadth | 241 |
> | Length of centrum including odontoid | 133 |
>
> The remaining cervicals are distinctly opisthocoelous, with zygapophyses which widely overlap one another. With the exception of the sixth, they are quite poorly preserved, and the sixth is so badly crushed as to make measurements very unreliable.
>
> Of the dorsals, nine only are referable to the type specimen, though three others are added in the mount. The opisthocoelous centra are preserved, but the spines and transverse processes are lacking.
>
> *The ribs.*—Portions of thirteen ribs from both sides of the body are preserved. In general form they are quite rhinoceros-like, being somewhat widely expanded in the shaft. The capitulum is nearly spherical in most of the ribs preserved, and the two facets are separated from each other by a deep groove. In an anterior rib, the second or third, the tubercular facet, while mainly on the posterior side, arches over so as to lie in part on the anterior face. The other ribs have the tubercular facet entirely on the posterior face. The resemblances again are with the rhinoceros rather than with *Palaeosyops*.

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[46] Parts of two individuals were included under the number 1046, there being one right and two left manus.

[47] Earle, Charles, Acad. Nat. Sci. Philadelphia Jour., 2d ser., vol. 9, p. 294, 1892

The appendicular skeleton

Fore limb.—While both scapulae are incomplete, they supplement each other so that our knowledge of them is fairly perfect. The proximal half of the left with its spine is well preserved, while of the right nearly the entire distal border is present.

The glenoid is deeply concave anteroposteriorly and is broadly elliptical in outline. The coracoid process is conical, somewhat downwardly curved at the tip, separated by a deep notch from the glenoid border, and not arising directly from it, as in *Palaeosyops*, but separated by an interval of 38 millimeters. The spine is high in the middle, with a broad roughened border. It lowers insensibly into the general level of the scapular face above and below, with no indication of an acromion. The tuberosity is not very pronounced, and the distal border is nearly straight.

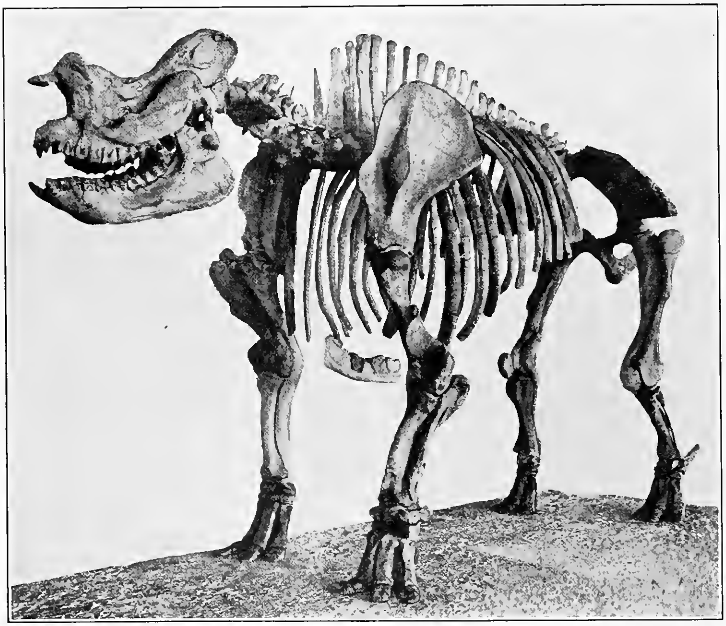

FIGURE 610.—Mounted skeleton of *Brontops brachycephalus?*

In the Victoria Memorial Museum, Ottawa, Canada. Collected on Sage Creek, Niobrara County, Wyo., probably from the lower *Titanotherium* zone (Chadron A). One complete individual except the left femur, right radius and ulna, and a few foot bones. Maximum height 6 feet 6 inches. Courtesy of Charles M. Sternberg. Less than one-twentieth natural size.

The dimensions of the scapula are:

	Millimeters
Total length (estimated)	690
Width of superior border (estimated)	405
Fore-and-aft diameter of glenoid fossa	133
Height of spine	95

The humerus.—The distal portions of both humeri are preserved, but of the proximal portions that of the right only, and as there is a portion of the shaft missing, the length can not be measured. The distal end is broad and heavy, the external condyle being especially prominent and roughened for muscular attachment. The inner trochlear is much the larger and is higher than the outer one, thus indicating an outward flexing of the elbow joint. The aconeal fossa is large and deep, but there is no foramen. The breadth of the extremity measured at right angles to the axis of the shaft is 210 millimeters.

	Millimeters
Breadth of shaft	85
Fore-and-aft diameter of shaft	77

The radius.—That of the left side is well preserved, except that its distal end is somewhat weathered. It is not notably heavy and has a well-rounded shaft, but slightly compressed fore-and-aft at the distal end. The radioscaphoid facet is prolonged upward on the posterior face, indicating a considerable range of flexion of the wrist.

The principal dimensions of the radius are:

	Millimeters
Length	490
Anteroposterior diameter of mid shaft	60
Lateral diameter of mid shaft	65
Lateral diameter of lower end	110

The ulna.—The entire left and fragments of the right are preserved, except for the distal end of the former, which is badly weathered. The ulna is notable for its huge compressed olecranon, which widens out distally into a heavy roughened tubercle.

The ulna measurements are as follows:

	Millimeters
Length (estimated)	620
Anteroposterior diameter of olecranon from the humeral facet	170
Lateral diameter of olecranon tubercle	140
Fore-and-aft diameter of mid shaft	80
Lateral diameter of mid shaft	80

The manus (Pl. IV, figs. 1–3).—The general proportions, well shown in the figure, are somewhat broad rather than slender and in direct correlation with the proportions of the skull.

As has often been stated, the manus shows some distinctly artiodactyl features, the most notable being the retention of four digits with the main axis between digits 3 and 4, rather than lying in the third itself. Another remarkable feature is the extreme flexibility of the carpus, especially in the development of a true ginglymoid joint between the proximal and distal row of carpals. * * * All of the elements are present in the carpus, with the exception of the trapezium, of which the last vestige has disappeared. The proximal facets are shown in Figure 1 of Plate IV, though the limits of the radial and ulnar areas are not with certainty definable.

The scaphoid articulates with the lunar by two facets separated from each other by a roughened trough. The superior scapholunar facet is long and narrow, its short axis vertical and straight, while its longer axis sweeps to the rear in a gentle convexity. It has the same anteroposterior extent as the scaphoradial facet above. The inferior scapholunar facet is much smaller, having but half the fore-and-aft extent of the superior. Distally the scaphoid articulates with the trapezoid and the magnum and together with the lunar forms the deep groove into which the pulley-like pivot of the magnum fits.

The lunar is a somewhat larger bone than the scaphoid, articulating distally both with the magnum and the unciform. The articulation between the lunar and cuneiform is again double, the two facets being separated by a well-defined channel, which runs backward and slightly upward. The two lunar-cuneiform facets are about equal in area. One can form a very good idea of the distal lunar facets by the study of their complementary facets figured in Plate IV, Figure 2.

The cuneiform is about half the bulk of the lunar and presents two facets on its inner face in every way the complements of the lunar-cuneiform. On the proximal face there is a large, saddle-shaped facet for the ulna, and a smaller, semicircular cuneiform-pisiform facet in the rear, set almost at right angles with the plane of the first. Distally there is a large cuneiform-unciform facet, having the general form of an equilateral triangle with rounded angles. It is again saddle-shaped, concave in its fore-and-aft axis.

The pisiform is lacking from the right manus, but that of the left is present and well preserved. It is much compressed laterally, with a deep vertical expansion of the distal end, which is decidedly rugose. The bone presents a gentle, sweeping curve through an arc of nearly 90°. Proximally it bears two well-defined contiguous facets for articulation with the cuneiform and ulna respectively.

Of the distal row of carpals the trapezoid is absent, having been replaced in the mount by that from another individual. It is not a precise fit, there being some variation between its facets and those of the original bone.

The articular faces are well shown in the figure, and it will be noted that lateral movement is impossible, while a remarkable range of flexion is indicated.

The magnum has on its lower face facets for the articulation of metacarpals 2 and 3, that for 2 being rectangular, about four times as long as wide. The pivot of the magnum is high and prominent, as indicated in the figure.

The unciform is the largest bone in the carpus, with the possible exception of the lunar. Distally it bears two facets for metacarpals 4 and 5, while on the radial side there is one which articulates both with the magnum and with metacarpal 3, the limits of the two articulations not being discernible.

A study of the distal carpal facets and the proximal metacarpal ones gives evidence again of more or less fore-and-aft movement, but in the case of the median metacarpal no lateral movement at all. The lateral metacarpals, on the contrary, were capable of lateral as well as fore-and-aft movement, so that, while the foot would spread somewhat when the creature's weight was borne upon it, it was all in the lateral bones. This would seem to be still further evidence that the true axis of the foot was between digits 3 and 4, as in the artiodactyls.

The principal dimensions of the manus are:

	Millimeters
Width of proximal facets	170
Width of distal carpals	170
Depth, lunar to summit of metacarpal 3	80
Length of metacarpal 3	250

The hind limb

The entire limb is figured in Plate IV, Figure 4. There was no trace of the pelvis found associated with No. 327, though the limbs are in excellent preservation and give but little evidence of distortion by crushing.

The femur.—This is a fine bone, notable for its extreme flatness, which indicates the pillar-like posture of the bone, as in the elephant, as the shaft would not have been sufficiently rigid to withstand springing had the thigh been flexed. Another interesting feature is the absence of a third trochanter—a character given by Marsh in his definition of the genus *Megacerops*. There is a ridge on the outer side of the femur continuous above with the great trochanter, which probably represents the vestige of the third. The measurements are:


FIGURE 611.—Mounted skeleton of *Brontops brachycephalus?*

Oblique front view. In Victoria Memorial Museum, Ottawa (shown also in fig. 610). About one thirty-fifth natural size.

	Millimeters
Length	785
Width of proximal end	236
Width of distal end	204
Width of mid shaft	117
Depth of mid shaft	60

The tibia.—The general form of this bone is well shown in the figure and calls for no special comment. The measurements of the tibia are:

	Millimeters
Length	446
Width of proximal end	200
Depth of proximal end	132
Width of mid shaft	80
Depth of mid shaft	77

The fibula is quite slender with expanded articular extremities; length, 395 millimeters.

The pes.—The general proportions are in keeping with those of the manus. All of the tarsal elements are represented, with the exception of the entocuneiform, which is entirely lacking.

The calcaneum.—The tuberosity is rather long and very rugous at its distal end, and with a much flattened shaft which is about one-half as wide as long. The calcaneum bears facets for articulation with the cuboid, the astragalus, and on its upper outer face a small one for the articulation with the fibula.

The calcaneo-astragalar facet is somewhat saddle-shaped, its fore-and-aft axis being a reversed curve, first concave, then convex. The sustentacular facet, however, is deeply concave, the transverse axis curving through an arc of 90°, while the fore-and-aft axis is straight. Below there is but one facet, the calcaneo-cuboid, somewhat semilunar in shape, extending about half the width of the bone. Except for the articulation with the fibula, there is little evidence of movement between the calcaneum and the adjoining bones.

The astragalus presents a beautiful hourglass-shaped astragalotibial facet, bearing on its outer face a clearly defined fibula facet. The range of flexion and extension in the tibiotarsal joint is considerable. Distally two facets are indicated, that for the navicular being by far the larger and somewhat flattened, and with a small, prominent, downwardly projecting process, which effectually limits any fore-and-aft motion. A prominent ridge divides the two facets, that for the cuboid being an elongated triangle, first convex and then concave from before backward.

The navicular is very flat and presents two distal facets, that for the ectocuneiform being the larger and somewhat triangular in shape, while that of the mesocuneiform is semilunar, the line of demarcation between the two being almost straight.

The cuboid has a thickness equal to that of the navicular and ectocuneiform combined and exhibits proximally two contiguous facets, the lesser for the calcaneum and the greater for the astragalus. Distally there are two facets, the external, the area of which is about four times the greater, being for metatarsal 4. This is somewhat saddle-shaped, while the other, that of metatarsal 3, is nearly flat.

The ectocuneiform is absent in the right pes, though present in the left, being replaced in the former by that of another individual. It articulates distally with metatarsals 3 and 2, though the latter articulation almost fades out anteriorly, broadening as one goes to the rear. This is markedly different from most titanothere feet which the author has seen, in which a wide line of contact is indicated on the face of the tarsus. There is, however, no possibility of contact between the mesocuneiform and metatarsal 3, as the former articulate distally with metatarsal 2 only.

The whole pes is remarkably rigid when compared with the manus, as there is little indication of any intertarsal movement, none between the tarsus and the median metatarsal, and no lateral and but little fore-and-aft play between the tarsus and the lateral metatarsals.

The principal dimensions of the pes are:

	Millimeters
Width of astragalar facet	105
Length of calcaneum	208
Width of the distal row of tarsals	140
Height, astragalus to proximal end of the third metatarsal	108
Length of the third metatarsal	205

Conclusion

The general proportions of the skeleton would indicate a huge animal, 7 feet 4 inches in height to the withers and something over 12 feet in length, somewhat rhinoceros-like in aspect, but with more massive, pillar-like limbs, which, as Professor Osborn has shown, are correlated with great weight. The extreme flexibility of the carpus seems to indicate an elephant-like habit of kneeling on the wrists when rising and lying down. The creature was hardly adult, as indicated by the unossified vertebral epiphyses, though probably of full stature, and it indicated a form in the middle stage of evolution.

The numerous resemblances in both the skull and the skeleton of *Diploclonus tyleri* to *Brontops robustus* strengthen the conclusion that the *Diploclonus* phylum is an offshoot of the *Brontops* phylum. The resemblances extend to the principal measurements of the skull and skeleton in the end members of the two genera. The chief differences are seen in the wider and more specialized manus of *Brontops robustus* and in its longer femur. (Gregory.)

SUBFAMILY MENODONTINAE

Allops Marsh

Two very incomplete skeletons are associated with skulls of the genus *Allops*, one in the Field Museum at Chicago referred to *Allops marshi*, the other in the British Museum (Natural History) referred to *Allops crassicornis?*. This meager material has so far yielded but few clear generic characters of the postcranial skeleton; it merely indicates that the smaller species of *Allops* have short limbs as compared with both *Brontops robustus* and *Menodus trigonoceras*.

Allops marshi

An incomplete skeleton in the Field Museum (No. P6900) comprises six dorsal vertebrae, 21 caudals, part of the pelvis, and much of the limbs. The skull of this specimen is described on page 514. This skeleton as mounted in the Field Museum, under the direction of Dr. E. S. Riggs, is figured below.

Vertebrae.—The dorsals are strongly opisthocoelous. The centra measure from 48 to 50 millimeters on the midventral line. The 21 caudals measure 111 millimeters in length, the tail being relatively long. The midcaudals increase in length; the posterior caudals diminish, as shown by the following measurements:

	Millimeters		Millimeters		Millimeters
1	40	8	67	15	53
2	40	9	64	16	51
3	41	10	65	17	46
4	50	11	63	18	41
5	60	12	63	19	36
6	63	13	61	20	31
7	65	14	59	21	25

Fore limb.—The height of the fore limb at the shoulder is estimated at 1,285 millimeters.

The right scapula is nearly complete, except at the top. Its height is estimated at 500 millimeters, as compared with 690 in *Brontops robustus* and 640 in *Menodus trigonoceras*.

The humerus measures 425 millimeters from the head to the distal trochlea as compared with 615 in *Brontops robustus* (type) and 557 in *Menodus trigonoceras*. The crest of the great tuberosity is moderately developed, much lower than in *B. robustus;* it is continued antero-internally into the usual incurved hooklike process for the insertion of the supraspinatus muscle; this process is much less expanded than in *B. robustus*. The deltoid tuberosity, on the lower outer part of the deltopectoral crest, is also less developed than in *B. robustus*. The circumference of the humerus at the narrowest part of the shaft is 230 millimeters. The middle of the shaft is rather slender, but the proximal end is wide. The rugosity for the brachialis anticus, on the anterior face, is prominent.

The radius is only 360 millimeters in length, as compared with 495 in *Brontops robustus* (type) and 525 in *Menodus trigonoceras*. The ratio of the length of the radius to the basilar length of the skull, in per cent, is as follows: *Allops marshi*, 53; *Brontops robustus* (type), 64.8; *Menodus trigonoceras*, 75.

The ulna also is short, 475 millimeters in length, as compared with 680 in *Brontops robustus* (type) and 595 in *Menodus trigonoceras*. The olecranon is long and less expanded than in *B. robustus* (type).

The manus is small, measuring only 142 millimeters across the proximal carpals as compared with 200 in *Brontops robustus* (type). At the same time it is relatively wider than that of *Menodus trigonoceras*, which has about the same absolute width (149 mm.) but a far longer median metacarpal. The carpals present nothing remarkable. The combined transverse width of the scaphoid and lunar is 95 millimeters; that of the cuneiform 49. The depth of the carpus from the top of the lunar to the summit of Mtc III is 63 millimeters. The median metacarpal (Mtc III) is relatively and absolutely short and wide, 155 millimeters in length as compared with 225 in *Brontops robustus* (type) and 233 in *Menodus trigonoceras*.

Hind limb.—The hind limb is quite short, the length of the limb from the head of the femur to the ground being only 1,150 millimeters (estimated), even with the limb fully extended.

The crest of the ilium is relatively narrow, measuring 530 millimeters in width.

The femur (length 590 mm.) is relatively shorter than in *Brontops robustus* (type), the ratio of the length of the femur to the basilar length of the skull, in per cent, being as follows: *Allops marshi*, 90; *Brontops robustus* (type), 107; *Menodus trigonoceras*, 100.4. The circumference of the shaft of the femur is 210 millimeters.

The tibia is short (length 350 mm.), the comparative ratios of the length of the tibia to the basilar length of the skull, in per cent, being as follows: *Allops marshi*, 53; *Brontops robustus* (type), 56; *Menodus trigonoceras*, 60.

The pes is small, the length of the calcaneum being only 147 millimeters as compared with 230 in *Brontops robustus*. The width of the tarsus across the navicular and cuboid is 90 millimeters, the width of the astragalus 70, and that of the cuboid 42. The tuber calcis is oval in section. The facet for the fibula on the calcaneum is prominent.

Allops crassicornis (referred)

An incomplete skeleton in the British Museum (5743 M) belongs with the skull described in Chapter VI. The postcranial skeleton is represented by the atlas, axis, two cervicals, two dorsals (all more or less crushed or imperfect), the right humerus, radius, and manus (lacking cuneiform and two distal rows of phalanges), the left femur, tibia, and astragalus, the right pes (lacking meso- and entocuneiform and all the smaller phalanges), the right and left patellae.

Vertebrae.—As compared with *B. robustus* the transverse processes of the atlas were proportionately smaller, projecting less, rounded instead of truncate distally; the facets for the occipital condyles were less oval in shape and tapering more at the bottom; in top view the atlas lacks the median groove in the neural arch seen in *B. robustus*. In the inferior view there is a decided median process from the posterior haemal surface.

Measurements of the atlas

	Millimeters
Extreme width	275
Neural arch, maximum anteroposterior	87
Width across cotyli	180

In comparison with *B. robustus* (type) the vertebrarterial foramen of the atlas is larger, the dorsal expansion of the neural arch is lighter, the odontoid less spout-shaped, the condyles for the atlas more vertical, narrower transversely and deeper vertically; on the inferior surface the haemal ridge seems more pronounced.

Measurements of the axis

	Millimeters
Width across condyles (estimated)	180
Odontoid to posterior border of centrum	93

Fore limb.—The scapula is well preserved, 570 millimeters in length and 290 in width, less expanded laterally than in *B. robustus*. The humerus (length 450 mm.) is slightly longer than that of the Field Museum specimen of *A. marshi* (425). The circumference of the shaft measures 225 millimeters. The radius is similar to that of *A. marshi*, its length being 350 millimeters, circumference of shaft 160, breadth of distal end 120, of proximal end 117, least width of shaft 48. The manus is noteworthy for the wide displacement of the scaphoid on the magnum, of the lunar on the unciform, so that there is only a very narrow lunar-magnum facet. Perhaps in correlation with this character the median metacarpal (Mtc III) appears to be relatively somewhat wider than in typical Oligocene titanotheres.

FIGURE 612.—Parts of skeleton of *Allops crassicornis?*

British Mus. 5743 M, consisting of parts of skeleton, including skull and lower jaw. A_1, Atlas, front view; A_2, atlas, top view; B_1, axis, side view; B_2, axis, front view; C, scapula; D_1, right humerus, outer side view; D_2, right humerus, front view; E, right manus; F. left femur, front view; G, left tibia, front view. One-sixth natural size.

Measurements of manus

	Millimeters
Manus, lunar to D. III, phalanx 3	240
Transverse, across carpals	150
Scaphoid, breadth	65
Scaphoid, height	45
Lunar, breadth	50
Lunar, height	40
Trapezoid, breadth	40
Trapezoid, height	29
Magnum, breadth	48
Magnum, height	31
Unciform, breadth	77
Unciform, height (maximum)	41

Hind limb.—The total height of the hind limb from the femur to the bottom of Mts III is estimated as 1,170 millimeters. The femur is short, length 560 millimeters, circumference of shaft 230. The tibia also is very short (345 mm.).

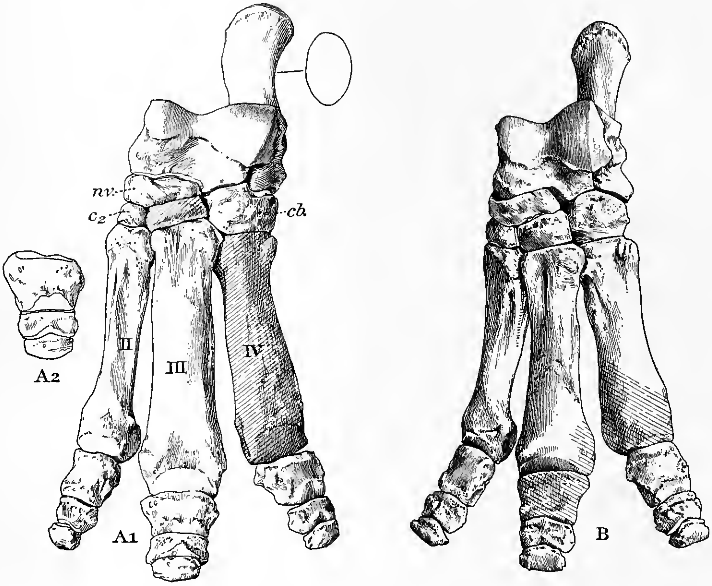

FIGURE 613.—Pes of *Menodus trigonoceras*, referred, and *M. heloceras*

A1, Front view of pes of *M. trigonoceras* (Am. Mus. 1079), with ectocuneiform and Mts IV restored. (This pes was associated with the manus shown in fig. 614, A.) A2, The same, phalanges of D. III, front view. B, Front view of pes of *M. heloceras* (Am. Mus. 1080, reversed). One-fourth natural size.

Measurements of the pes

	Millimeters
Total length, os calcis to D. III, phalanx 3	320
Width across astragalus and calcaneum	100
Calcaneum, length	140
Calcaneum, greatest breadth	93
Astragalus, length (vertical) midline	60
Astragalus, breadth	82
Cuboid, vertical height, midline	27
Cuboid, breadth	60
Navicular, vertical height	20
Navicular, breadth	63
Mts III, height	155

Menodus

Lower Oligocene titanotheres of dolichopodal (relatively narrow-footed) and swift-limbed type.

Menodus heloceras? (Cope)

The specific reference of the finely preserved pes of *Menodus* in the American Museum (No. 1080) is somewhat doubtful, but there can be no question that it belongs to one of the small and primitive species of that genus (*M. heloceras* or *M. proutii*).

The family characters are well marked—namely, (1) large fibulocalcaneal facet; (2) large tibio-calcaneo-astragalar facet; (3) widely separated "sustentacular," "ectal," and "inferior" astragalocalcaneal facets; (4) displacement of Mts III against cuboid and of Mts IV against ectocuneiform, displacements that are very slight and that indicate the primitive character of this pes.

The generic characters of *Menodus* are equally well marked—namely, (1) pes relatively long and narrow, or elevated, in all its elements; (2) long axis of tuber calcis extended obliquely anteroposteriorly, not transversely as in *Brontops*, the tuber terminating in a rounded suboval head; (3) sustentaculum of calcaneum slender and downwardly directed; (4) cuboid relatively narrow, vertically extended, with slight lateral abutment against Mts III; (5) mesocuneiform distally shorter than ectocuneiform; (6) enlargement of Mts IV and reduction of Mts II indicating that the main weight is carried upon the third and fourth digits (D. 3 and D. 4), the second digit (D. II) being relatively reduced; (7) corresponding reduction of Mts II and sharply convex ridge on its anterior face, as in *Brontops robustus* (type); (8) striking narrowness or reduction of terminal phalanges, which are even narrower than the middle phalanges.

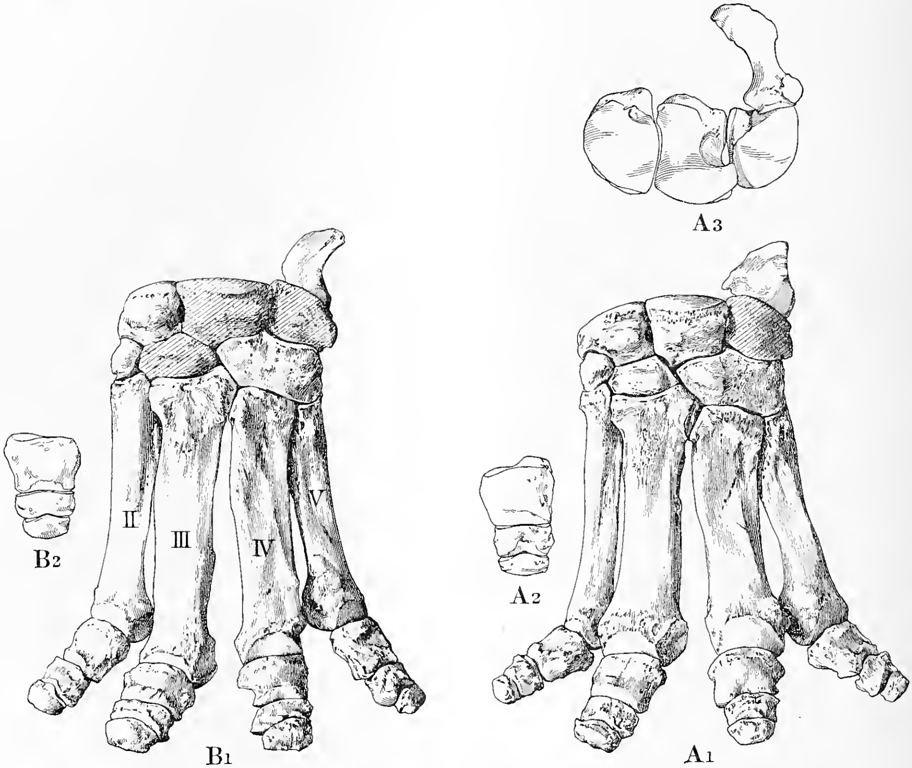

Figure 614.—Manus of *Menodus trigonoceras?*

A, Am. Mus. 1079 (compare fig. 613): A_1, Front view, cuneiform restored; A_2, phalanges of digit III; A_3, top view of carpus. B, Am. Mus. 515: B_1, Manus, front view (lunar and magnum incorrectly restored); B_2, phalanges of digit III. One-fourth natural size.

The specific characters of this pes (those of *M. proutii* or *M. heloceras*) are (1) simple, oval shaft of the tuber calcis, the entire length of the calcaneum being 158 millimeters; (2) relatively narrow (22 mm.) displacement of the astragalus upon the cuboid; (3) total width of 191 millimeters of the combined distal facets of the calcaneum and astragalus; (4) navicular relatively deep, measuring 22 millimeters vertically, 58 transversely, with broad (35) ectocuneiform and relatively narrow (19) mesocuneiform facets; (5) cuboid relatively deep (vert. 35, tr. 45) with broader calcaneal than cuboidal facets proximally, an extremely large facet (tr. 37, ap. 47) for the enlarged Mts IV, and a relatively small, ill-defined facet for Mts III, the displacement being rather incipient; (6) similarly ectocuneiform deepened (vert. 23, tr. 35), with a characteristic pair of ectal facets for the cuboid and a double pair of ental facets for the mesocuneiform and Mts II, respectively; (7) mesocuneiform correspondingly shallow (vert. 16, tr. 23, ap. 36) for the support of the reduced Mts II; (8) the shaft of Mts IV considerably exceeds that of Mts III in stoutness and greatly exceeds that of Mts II; (9) Mts III (length 175 mm.) is distinguished by a deep antero-internal groove in the superior portion of the shaft, and Mts II (length 156) has a subtriangular section, owing to the anterior ridge and grooving and flattening of the outer side facing toward Mts III.

Among the chief primitive and specific characters of this pes are, therefore, the relatively narrow displacement of the astragalus and cuboid and of Mts II and Mts III against the cuboid and ectocuneiform respectively.

The proximal phalanges of D. 2 and D. 4 are relatively elongate and are laterally compressed, a striking feature of this region being that the middle phalanges are carried on the plantar side of the proximal, there being apparently a sharp flexure between them. The distal phalanges are very narrow and but slightly expanded at the extremities, the transverse measurements being, II, 30 millimeters; III, 30+; IV, 28.

Menodus trigonoceras

Referred manus and pes

The reference of the pes of *Menodus trigonoceras?* (Am. Mus. 1079) to the genus *Menodus* is confirmed by the presence of all the generic characters already enumerated, as found in the pes referred to *M. heloceras* or *M. proutii*—namely, the slender, rounded shaft of the tuber calcis, the narrow, obliquely directed sustentaculum, the reduced cuneiform, the relatively slender Mts II with the sharp ridging and grooving of the superior portion of its shaft, the small size of the terminal phalanges, the laterally compressed cuboidal facet. We note, however, several important progressive characters in this pes, which remove it from the more primitive stage of *M. heloceras* and relate it to the more progressive stage which we suppose to be that of *M. trigonoceras*. All the dimensions of the pes are larger, and the bones of the tarsus are decidedly broader and flatter; the summit of the tuber calcis is of more flattened or elongate oval section; the cuboid is relatively broadened and flattened, and Mts III is broadly articulated with it by displacement, and the proximal phalanges, especially those of D. 3 and D. 4, are shorter.

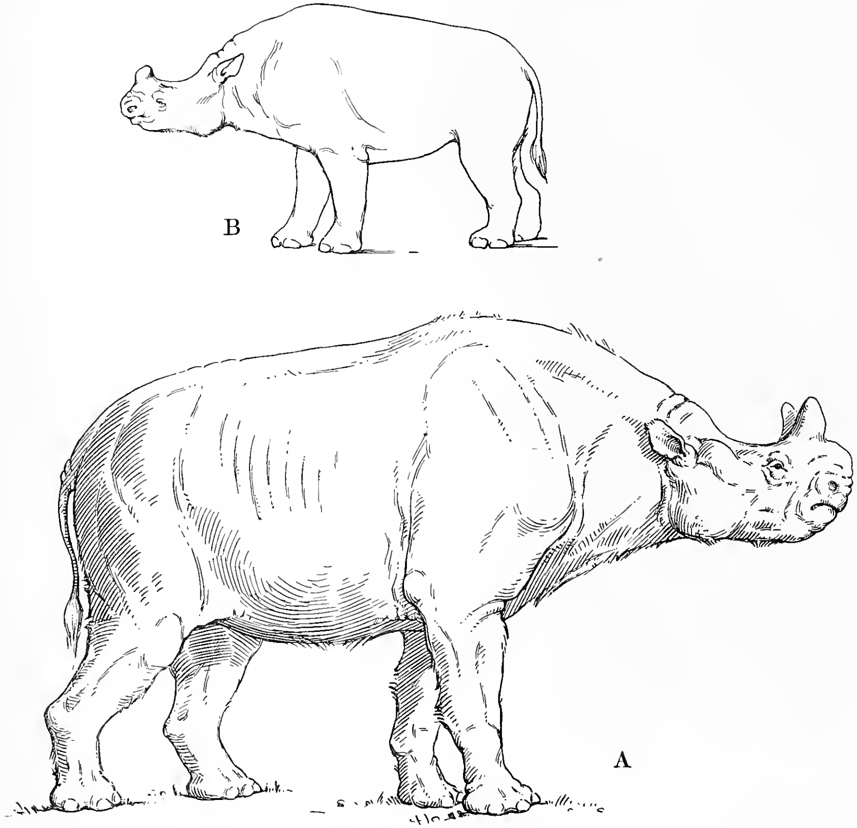

FIGURE 615.—Restorations of *Menodus trigonoceras* (A) and *Allops marshi* (B)

Not drawn to scale. A is based on the mounted skeleton in the Munich Museum and is about one twenty-second natural size (6 feet 5 inches).

The calcaneum measures 155 millimeters vertically; the combined distal astragalar and calcaneal facets measure 105 millimeters transversely; the navicular is decidedly more flattened (vert. 22, tr. 53); the cuboid also is more flattened (vert. 36, tr. 57), but it still exhibits a narrower astragalar (27) than calcaneal (42) facet; the mesocuneiform is distinctively small (tr. 23, ap. 43). Mts II is readily distinguished by its anterior median ridge bordered ectally by a groove; it measures 173 millimeters vertically; it exhibits a narrow, proximal ectocuneiform facet. Mts III, a large and elongate bone, measures 200 millimeters vertically and exhibits ar elatively broad (20 mm.) proximal abutment against the cuboid.

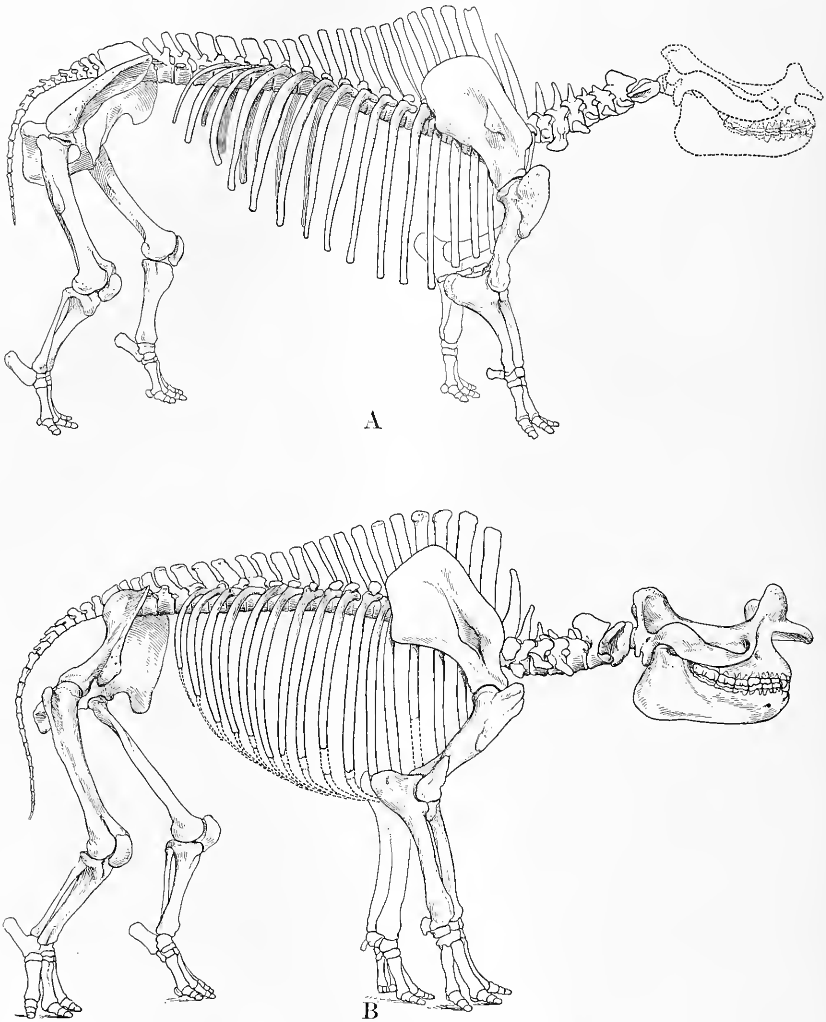

Figure 616.—Mounted skeletons of *Brontops dispor?* and *Menodus trigonoceras*

A, *B. dispar?*, supposed female, Carnegie Mus. 92; Warbonnet Creek, Sioux County, Nebr.; lower *Titanotherium* zone, perhaps 30 feet above the Pierre shale (Hatcher). Adapted from a photograph published by Hatcher. The scapula and fore limb are here placed higher up on the thorax than in the skeleton as mounted. The skull, destroyed by weathering, is here restored in outline from supposed females of *B. dispar*. B, Skeleton of *M. trigonoceras* in the Munich Museum; Hat Creek badlands, Sioux County, Nebr. (compare fig. 615, A). In the mounted skeleton the thorax is placed too high in relation to the scapula, but this error is corrected in the drawing. Both figures one twenty-second natural size.

As shown in Figure 613, in the relatively small D. 2 the proximal phalanx is more primitive—that is, narrow and elongate; the distal phalanx is small; on D. 3 and D. 4 the proximal and median phalanges as compared with those of *M. heloceras* are broad and strong; the terminal phalanges are broader than in *M. heloceras* but still retain the small dimensions characteristic of this genus; the marked expansion of the phalanges on D. 2, D. 3 is in keeping with the tendency prophesied in *M. heloceras* or *M. proutii* toward the support of the greater weight of the limb on the third and fourth digits.

The manus of *Menodus* (Am. Mus. 1079, fig. 614), fortunately associated with the pes above described, is no less readily distinguished in all its parts from the type of *Brontops robustus*. Its most striking distinctions lie (1) in the high, narrow proportions of the manus as a whole, but especially of the carpus; (2) in the extreme displacement illustrated especially in the broad abutment of the lunar on the unciform with the correspondingly reduced narrow oblique lunar magnum facet; and (3) in the small simple form of the magnum which readily distinguishes it from that of *Brontops*. The proportions are shown in the following measurements: Proximal breadth of carpus, 155 millimeters, as compared with length from lunar to extremity of D. 3, 340 millimeters; thus the carpus is relatively narrower from side to side and deeper anteroposteriorly in proportion to its length than that of *Brontops*.

The extreme displacement of the carpus is first noticed in the relatively wide extension of the scaphoid on the magnum, in the correspondingly small weight the lunar transmits to the magnum, as compared with its broad surface resting on the unciform. The anteroposterior measurement of the radial face of the lunar (73 mm.) decidedly exceeds its transverse measurement (59 mm.), whereas in *Brontops robustus* (type) the anteroposterior and transverse measurements of the radial facet of the lunar are subequal. The radial face of the scaphoid measures 55 millimeters transversely by 59 anteroposteriorly. The cuneiform is wanting in this specimen. The trapezoid, which exhibits no face for a trapezium facet, measures 28 millimeters vertically, 38 transversely, 48 anteroposteriorly. The magnum measures 25 millimeters vertically by 54 transversely; it is of simpler and more quadrate form than in *Brontops* owing to the oblique ectal facet for the lunar above and the unciform below. The unciform is decidedly broad, constituting one of the most characteristic features of the *Menodus* carpus with its broad abutment against Mtc III, measuring transversely 82 millimeters. The metacarpals are elongate but not extremely so, the vertical measurements through the middle of the shaft being, Mtc II, 196 millimeters; III, 199; IV, 188; V, 172. The shafts are relatively much more slender than in *Brontops robustus*. Mtc III exhibits a short, broad process abutting against the unciform, like that seen in *Brontops*.

Mounted skeleton in the State paleontologic collection at Munich

This specimen (fig. 616, B) from the Hat Creek badlands of Nebraska comprises the greater part of the skeleton. It was presented to the Museum by Commerzienrath Th. Stützel in 1897. The skull is a typical *Menodus trigonoceras*. (See p. 528.) The limbs are notably slender and elongate, in comparison with those of *Brontops*, *Allops*, and *Brontotherium*, the apparent slenderness of the limbs having been increased by crushing. The following description is based on the observations of the author and of Dr. Ernst Stromer von Reichenbach.

Mounting.—The skeleton as mounted has the scapulae placed too low on the sides of the thorax, the curvature of the backbone is not quite correct, the intervertebral spaces are not wide enough, so that the backbone is somewhat too short. Certain parts of the skeleton are more or less restored in plaster, especially the symphysis of the lower jaw, the outer side of the first three right upper premolars, the middle of the upper border of the occiput, both wings of the atlas, the spinous process of the atlas, the posterior half of the tail, the greater part of the left ilium, both hind feet (except the upper and lower ankle bones and the second right metatarsus).

Dimensions.—The total length of the skeleton from the tip of the nasals to the drop of the tail is estimated at 3 meters. The height at the withers, to the tip of the second dorsal spine, is 2.28 meters.

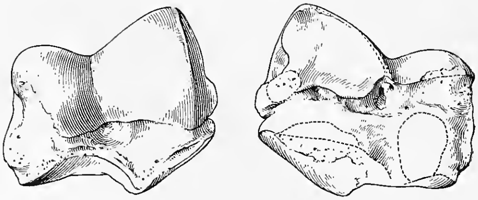

FIGURE 617.—Left astragalus of *Menodus giganteus*

Am. Mus. 505, Chadron. Front and rear views. One-third natural size.

Vertebrae.—The vertebral formula of the specimen as mounted is cervicals 7, dorsals 17, lumbars 3, sacrals 4(?), caudals 21 (restored).

As compared with *Brontops robustus* (type) the spine of the atlas is higher and its lateral process thicker, the spine of the axis is longer and lower, the centra of the cervical vertebrae are longer and their spines lower, except the spine of C. 7, which is higher; the spines of the first two dorsals are subequal in height and of fairly uniform diameter from base to summit; the spines of the dorsals D. 4 and D. 5 are straight, less concave anteriorly; the parapophyses appear to be lower. The spine of the third dorsal (D. 3) is the highest; behind that the spines decrease gradually in height to the caudals; all appear thin transversely and relatively high as compared with those of *B. robustus*. The spines of D. 1–D. 4 are remarkably thin and lack the deep posterior grooves, except at the base. The articular facets of the prezygapophyses in the third cervical vertebra present upward and somewhat inward; in the succeeding vertebrae they gradually turn more strongly inward, especially in the midthoracic vertebrae. On the last dorsal and first lumbar the articular processes are weaker than usual. The last dorsal bears a shallow facet for the tubercle of the rib. The lumbar vertebrae bear flattened diapophyses just above the base of the neural arches. In D. 1 and D. 2 the posterior zygapophyses are nearly horizontal.

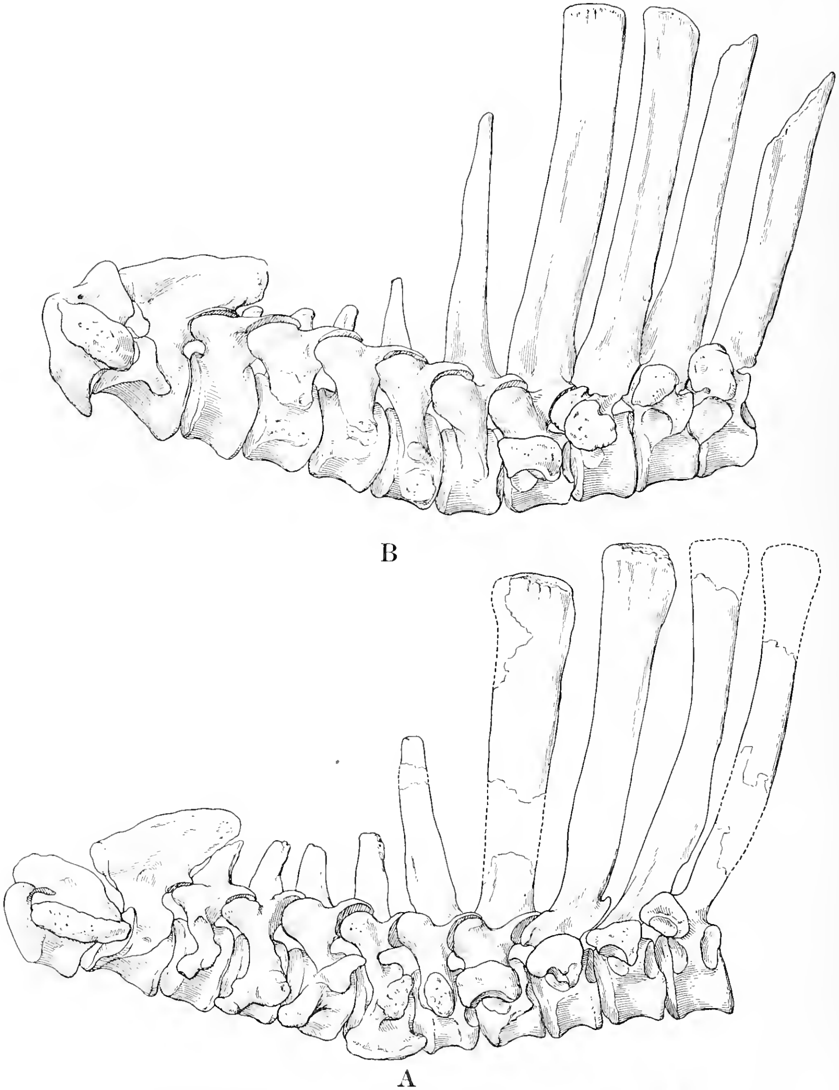

FIGURE 618.—Cervical and first four dorsal vertebrae of *Brontops robustus* and *Menodus giganteus*

A, *B. robustus*, vertebrae of type (Yale Mus. 12048); B, *M. giganteus*, vertebrae associated with skull in the Field Museum (P 5927). Both one-eighth natural size.

Longitudinal axial measurements of vertebrae

	Millimeters
7 cervicals, as mounted, anteroposterior	600
17 dorsals, as mounted, anteroposterior	1, 270
3 lumbars, anteroposterior	230
Sacrals (crushed), anteroposterior	150
21 caudals, anteroposterior	1, 000
Atlas, ventral arch, anteroposterior	65
Axis, length (ventral, omitting the odontoid tip)	110
Sixth cervical, ventral length of centrum	86
First dorsal, height of spine	43

Ribs.—The ribs are long and slender, and the chest was probably narrow. The sixth rib is the longest. The estimated length of some of the ribs on the right side is as follows:

	Millimeters		Millimeters
R 1	445	R 6	890
R 2	530	R 8	870
R 5	795	R 17	515

Fore limb.—As mounted the height from the top of the scapula to the ground is 2,400 millimeters, the lengths of the successive segments being, scapula 640, humerus 557, radius 525, manus 350. The scapula is very distinctive in type, being long and narrow anteroposteriorly. The glenoid is narrow, and so is the coracoid process. The spine is but little expanded, and the postscapular fossa is not greatly extended posteriorly. The humerus, although considerably crushed, is profoundly different in proportional characters from that of *Brontops robustus*, being long and slender, with a small crest on the great tuberosity and less developed deltoid and supinator crests. The radius and ulna also are long and slender; the olecranon is very deep, laterally compressed, and with a deep terminal groove. The manus is high and narrow with long metacarpals and a narrow carpus. The scaphoid is narrow, with a deep concave facet for the trapezoid, which was vertically high. The lunar is narrow, with a fair-sized facet for the magnum. The magnum also is rather narrow. The unciform is deeply extended downward on the outer side, for Mtc V. The terminal phalanges are narrow.

Measurements of fore limb

	Millimeters
Scapula, height (middle of glenoid to dorsal border)	640
Scapula, width (at right angles to preceding measurement)	460
Humerus, length (head to capitellum)	557
Humerus, right, extreme length	620
Radius, right, midlength	525
Radius, width of head	145
Radius, width of distal end	125
Ulna, length	660
Manus, length	350
Width across distal end of radius and ulna	170
Carpus, width	149
Carpus, height, lunar to summit of Mtc IV	80
Scaphoid, width	52
Scaphoid, height	47
Lunar, width	65
Lunar, height	72
Trapezoid, anteroposterior	47
Mtc II, height	214
Mtc III, height	233
Mtc IV, height	225
Mtc V, height (estimated)	191
Terminal phalanx of D. II, right, width	34
Terminal phalanx of D. III, right, width	43
Terminal phalanx of D. IV, right, width	38
Terminal phalanx of D. V, right, width	29

Pelvis and hind limb.—The hind limb also is long and slender, the total height of the hind limb as mounted being 1,430 millimeters; the height from the top of the ilium to the ground 1,900. The pelvis is elongate and narrow (partly increased by pressure), the total length being 820 millimeters, and the breadth as mounted 830. The length of the outer part of the crest of the ilium is 580, of the inner part 290. The femur is extraordinarily long and slender. The hind feet are poorly preserved and do not give much character.

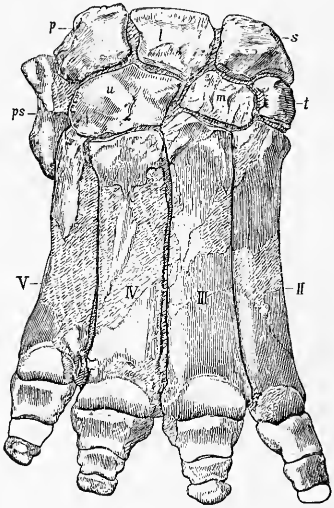

FIGURE 619.—Manus referred to *Menodus giganteus*

Yale Mus. 12012. Figure prepared by Berger under direction of Marsh. Observe the small terminal phalanges and the relatively high, narrow lunar. Slightly less than one-fifth natural size.

Measurements of hind limb

	Millimeters
Femur, midlength	703
Femur, least width of shaft	85
Tibia, length	430
Astragalus to Mts III	302

Menodus giganteus

The postcranial skeleton of this species is positively known chiefly from a scapula and a series of vertebrae in the Field Museum (No. 5927), which is associated with a superbly preserved skull. (See p. 535.) An astragalus associated with the fine skull Am. Mus.

505 is shown in Figure 617. Referred material of *M. giganteus* comprises a manus in the Yale Museum (No. 12012, fig. 619), a radius and ulna in the Carnegie Museum (No. 120), and a pelvis with both hind limbs in the University of Nebraska Museum (No. 3296).

Cervical and dorsal vertebrae in the Field Museum

The vertebrae in the Field Museum (No. 5927) include the seven cervicals and the first five dorsals. The centra of all the vertebrae are relatively elongate, and the first two dorsals have very long and broad spines. (See fig. 618.)

Measurements of vertebrae

	Millimeters
Length of six cervicals (without atlas)	575
Length of seven cervicals (with atlas) (estimated)	660
Axis, length of centrum (excluding odontoid process)	150
Cervical 3, length of centrum	83
Cervical 4, length of centrum	80
Cervical 5, length of centrum	78
Cervical 7, length of centrum	76
Cervical 7, total height	585
Dorsal 1, total height	730
Dorsal 4, length of centrum	78

Radius and ulna in the Carnegie Museum

The radius (Carnegie Mus. 120) is very long and slender.

	Millimeters
Radius, length	475
Radius, width at top	123
Ulna, length	595

Pelvis and hind limbs in the Nebraska Musuem

A pelvis with both hind limbs in the Museum of the University of Nebraska at Lincoln (No. 3296) is referable either to *M. trigonoceras* or to *M. giganteus*. All the elements are relatively long and narrow.

	Millimeters
Pelvis, length	902
Pelvis, width (crushed)	952
Femur, length	762
Tibia, length	432

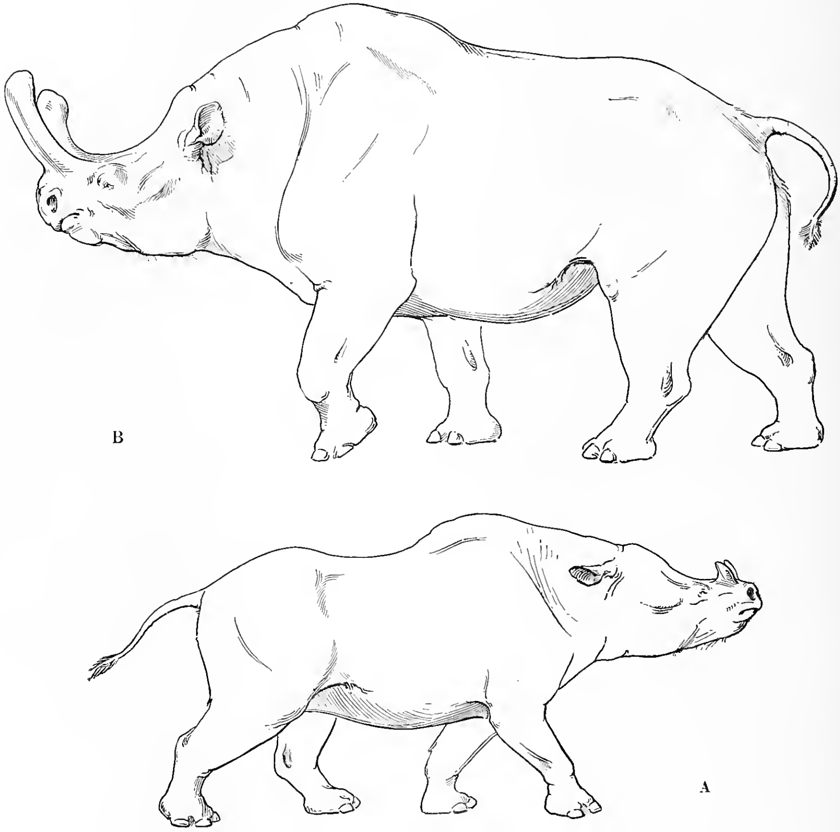

FIGURE 620.—Restorations of *Brontotherium leidyi* (A) and *B. platyceras* (B)

About one-thirtieth natural size.

Manus in the Yale Museum

A manus in the Peabody Museum of Natural History at Yale University (No. 12012) may pertain to *Menodus giganteus;* there is no proof of association with Marsh's type of *Brontotherium ingens* (= *Menodus giganteus*), as the manus was received at the Museum in 1874, whereas the skull was received in 1873, although both came from the same general region and from the same collector (Devendorf).[48]

The manus (fig. 619) is of the high, narrow type seen in *Menodus.* The phalanges are bent back in the rock so as to lie against the back of the hand. In the figure they are represented a little too small and appear to taper too suddenly.

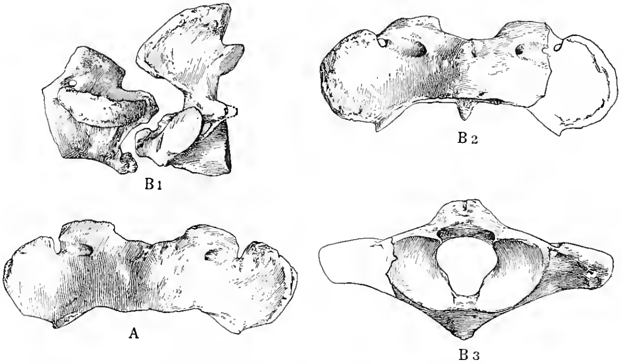

FIGURE 621.—Atlas and axis of *Brontotherium leidyi*

A, Carnegie Mus. 93; atlas, top view. B, Carnegie Mus. 114; atlas and axis provisionally referred to *B. leidyi.* B₁, Atlas and axis, side view; B₂, atlas, top view; B₃, front view. One-eighth natural size.

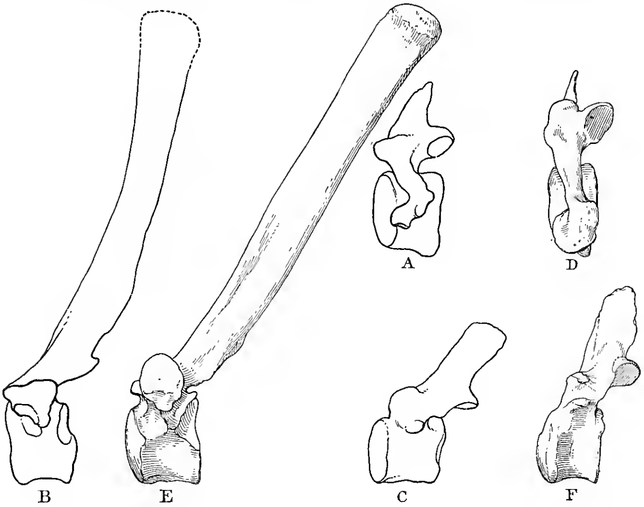

FIGURE 622.—Vertebrae of *Brontops robustus* (A, B, C), Yale Mus. 12048 (type), compared with those of *Brontotherium gigas* (D, E, F), Am. Mus. 492

A, D, Third cervical vertebra; B, E, third dorsal vertebra; C, F, second (?) lumbar vertebra. The third cervical vertebra of *Brontops* has a much longer centrum and a stouter neural arch. (The neck of *Brontotherium* was shorter.) The third dorsal vertebra of *Brontops* has the spine curved anteroposteriorly and the lateral process less elevated. The second (?) lumbar vertebra of *Brontops* has a longer centrum and more recumbent neural arch. One-eighth natural size.

SUBFAMILY BRONTOTHERIINAE

The Brontotheriinae include lower Oligocene titanotheres, extremely graviportal and brachypodal, especially in the pes.

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[48] Information kindly supplied by Prof. R. S. Lull.

Brontotherium Marsh

In the genus *Brontotherium* the only postcranial elements that are certainly associated with identified skulls are the following:

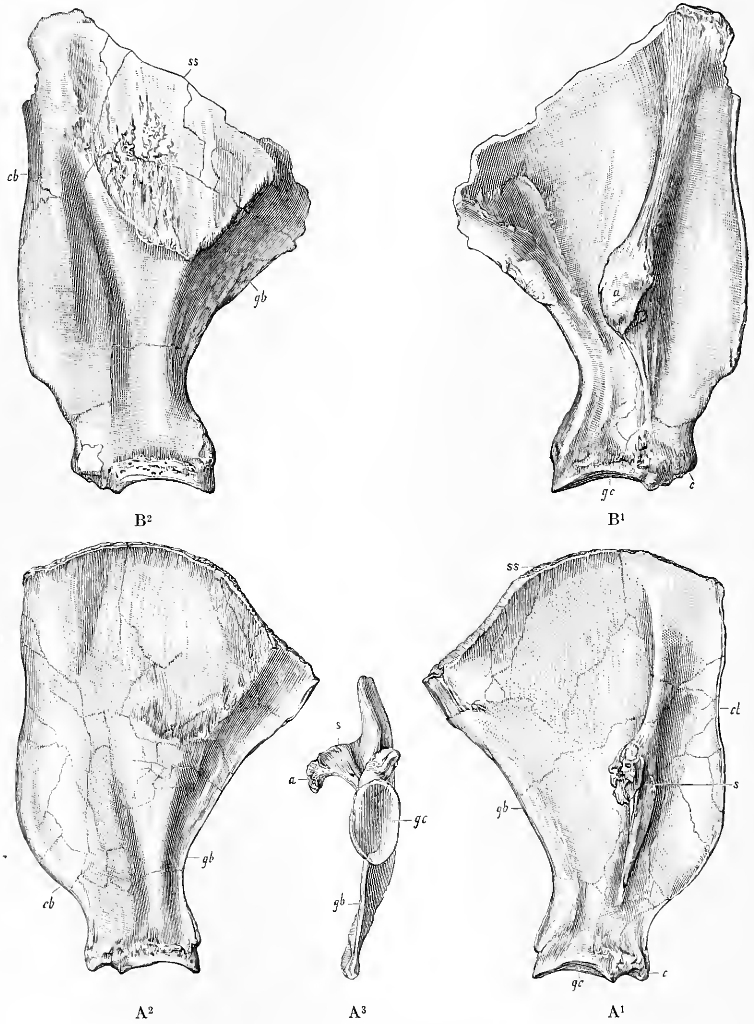

Figure 623.—Scapulae of Oligocene titanotheres

Figures prepared by Berger under the direction of Marsh. A, *Brontotherium gigas hatcheri*, Nat. Mus. 4262: A^1, Outer side; A^2, inner side; A^3, distal view. B, *Brontops?*: B^1, Outer side, B^2, inner side. One-eighth natural size.

Brontotherium leidyi, Carnegie Mus. 93, skull, lower jaw, atlas, scapula, humerus, radius and ulna, femur, tibia.

Brontotherium gigas, Am. Mus. 492, skull, pelvis and sacrum, second dorsal vertebra with ribs, ulna, lunar.

Brontotherium gigas hatcheri, Nat. Mus. 4262, skull, lower jaw, the greater part of both fore limbs and feet, parts of both hind limbs and feet, and probably the pelvis. Parts of two other individuals were mixed with this skeleton but have been separated by J. W. Gidley.

Brontotherium? sp., Am. Mus. 1443, manus; Am. Mus. 1047, manus and pes (specific reference doubtful).

This material may now be described as a whole, the several parts being compared with those of *Brontops robustus* (type).

Vertebrae referred to Brontotherium leidyi, Carnegie Museum

[Figs. 621, 622]

The atlas of *B. leidyi* (Carnegie Mus. 93) is comparatively small, measuring only 305 millimeters in greatest transverse diameter. It differs from that of *Brontops robustus* (type) in being proportionately higher, less extended transversely, with less expanded lateral processes and with a higher neural protuberance; the posterior ventral process is produced sharply backward. The axis of *B. leidyi* (Carnegie Mus. 114), apart from its much smaller size, differs from that of *B. robustus* chiefly in the far less backward prolongation of the neural spine, in the more vertical position of the posterior zygapophysial facet and the less transverse position of the anterior condylar facets for the atlas.

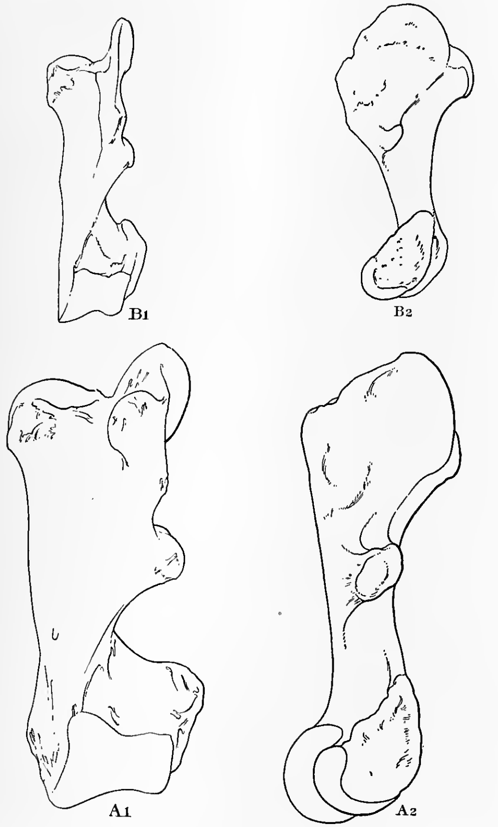

FIGURE 624.—Humeri of *Brontops robustus* and *Brontotherium leidyi*

A, *Brontops robustus*, Yale Mus. 12048 (type). B, *Brontotherium leidyi*, Carnegie Mus. 93, associated with skull. A_1, B_1, Left humerus, front view; A_2, B_2, left humerus, outer side view. In *Brontotherium leidyi* the crest of the great tuberosity is relatively larger and more widely expanded and the deltoid process is relatively smaller. One-eighth natural size.

Vertebrae referred to Brontotherium gigas, American Museum

This material is associated with a skull (see p. 570) and a pelvis (see p. 692).

The third (?) cervical vertebra (*B. gigas*, Am. Mus. 492) has the centrum much shorter anteroposteriorly (55 mm.) than in *B. robustus* (type); its neural arch is very small and slender; the lateral transverse process is more broadly expanded distally; and the zygapophysial facets, both anterior and posterior, appear to face more vertically than in *B. robustus*. Accordingly the neck of *B. gigas* appears to have been shorter and deeper than that of *B. robustus*.

The third dorsal vertebra (*B. gigas*, Am. Mus. 492) is much stouter than that of *Brontops robustus* (type). Its centrum is larger and deeper, the neural arch longer, straighter, and wider. The swelling above the facet for the tubercle of the rib is much larger.

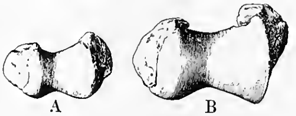

FIGURE 625.—Humeri of *Megacerops? acer?* and *Brontotherium gigas?*

A, *M.? acer?*, Am. Mus. 6351; B, *B. gigas*, Am. Mus. 1062. Distal views. One-eighth natural size.

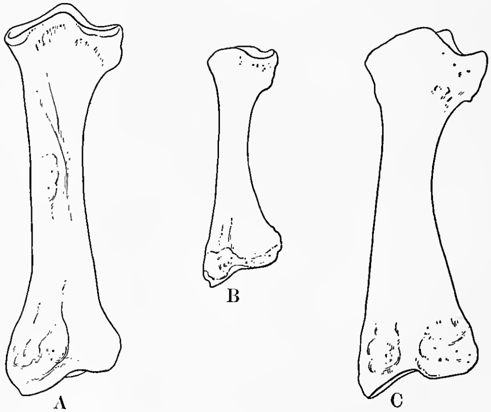

FIGURE 626.—Radii of *Brontops robustus*, *Brontotherium leidyi*, and *Brontotherium gigas*

A, *Brontops robustus*, part of type skeleton, Yale Mus. 12048; B, *Brontotherium leidyi*, Carnegie Mus. 93, associated with skull; C, *Brontotherium gigas*, Am. Mus. 492, associated with skull. The two ends of the radius in *Brontotherium* appear to be wider, and the external contour more deeply concave; the styloid process is more acute. One-eighth natural size.

The second(?) lumbar vertebra (*B. gigas*, Am. Mus. 492) has a less elongate centrum (ap. 87 mm.) than that of *Brontops robustus* (type) (96 mm.); the neural spine is apparently longer and more vertical and the postzygapophysial facet more oblique; the anterior face of the centrum is more convex.

Fore limb referred to Brontotherium leidyi, Carnegie Museum

This fore limb is from the Chadron A levels in which the species *B. leidyi* occurs.

The scapula of *B. leidyi* (Carnegie Mus. 93) is less expanded transversely than that of *B. gigas* (Nat. Mus. 4262). The generic differences from the scapula of *Brontops robustus* are not yet apparent. The humerus (*B. leidyi,* Carnegie Mus. 93) is a relatively very small bone (mid-length 380 mm.) with an enormously expanded crest of the great tuberosity.

FIGURE 627.—Radius and ulna of *Brontotherium*

A, *B. leidyi,* Carnegie Mus. 93, outer side view of radius and ulna; B, *B. gigos,* Am. Mus. 492. One-eighth natural size.

Its distal end is relatively narrower and higher than in *Brontops robustus* (type). The radius (*B. leidyi,* Carnegie Mus. 93) is likewise very short (mid-length 305 mm.). Even in *B. gigas* (Am. Mus. 492, mid-length 460 mm.) the radius is relatively shorter than in *Brontops robustus* (type) (mid-length 500). In both species the whole contour of the radius in front view is markedly different from that of *B. robustus* (type); the styloid process is produced farther downward; the external contour is more sharply concave; the internal contour is straighter; the middle of the head is less angulate. The ulna both in *B. leidyi* (Carnegie Mus. 93, length 410 mm.) and in *B. gigas* (Am. Mus. 492, length 642 mm.) has the sigmoid notch much less deeply concave in side view than in *Brontops robustus;* the shaft of the ulna appears to be more slender, especially at the lower end. In *B. gigas* the tuberosity of the olecranon (for the main mass of the triceps) is widely expanded transversely.

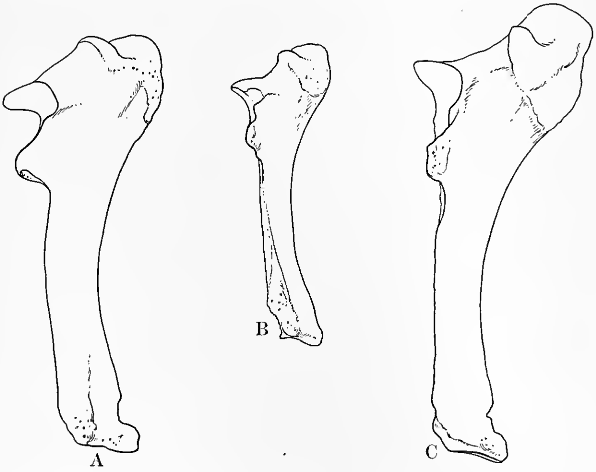

FIGURE 628.—Ulnae of *Brontops robustus, Brontotherium leidyi,* and *Brontotherium gigas*

A, *Brontops robustus,* Yale Mus. 12048 (type); B, *Brontotherium leidyi,* Carnegie Mus. 93; C, *Brontotherium gigas,* Am. Mus. 492. The proximal part of the ulna of *Brontops* is wider and the olecranon is perhaps shorter than in *Brontotherium.* One-eighth natural size.

Manus of Brontotherium, U. S. National Museum

The manus of *Brontotherium* is known from the lunar of *B. gigas* (Am. Mus. 492) and from a mixed lot of specimens in the National Museum (No. 4262; see p. 690).

This manus (fig. 631), which probably belongs with the skull of *B. gigas* (Nat. Mus. 4262), is much smaller than that referred to *B. gigas* (Am. Mus. 492), but it agrees in measurements and in characters with another manus (Am. Mus. 1047) which is assigned provisionally to *B. hatcheri.* Hence it seems probable that the manus shown in Figure 631 represents a female of either *B. hatcheri* or *B. gigas.* The differences between the manus of *Brontotherium* and that of *Brontops robustus* are exhibited in Figure 630. In general the manus appears to be more compact and less spreading, especially at the lower end, than that of *Brontops robustus;* the magnum is wider and the lunar magnum articulation more extended; there are also detailed differences in the other carpal elements, but at present it is not known whether any of these are constant or how far they may be individual rather than generic differences.

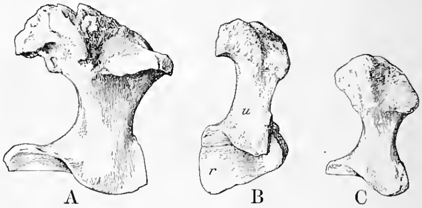

FIGURE 629.—Olecrana of *Brontotherium* and *Megacerops?*

End view. A, *B. gigas,* Am. Mus. 492; B, *B. leidyi,* Carnegie Mus. 93; C, *Megacerops?* sp., Am. Mus. 351 (6351?). The olecranon of the largest animal is greatly swollen. One-eighth natural size.

Pelves and hind limbs referred to B. gigas

Pelvis.—The pelvis of *Brontotherium* is known from three specimens—a well-preserved pelvis of *B. gigas* (Am. Mus. 492), associated with a skull and some

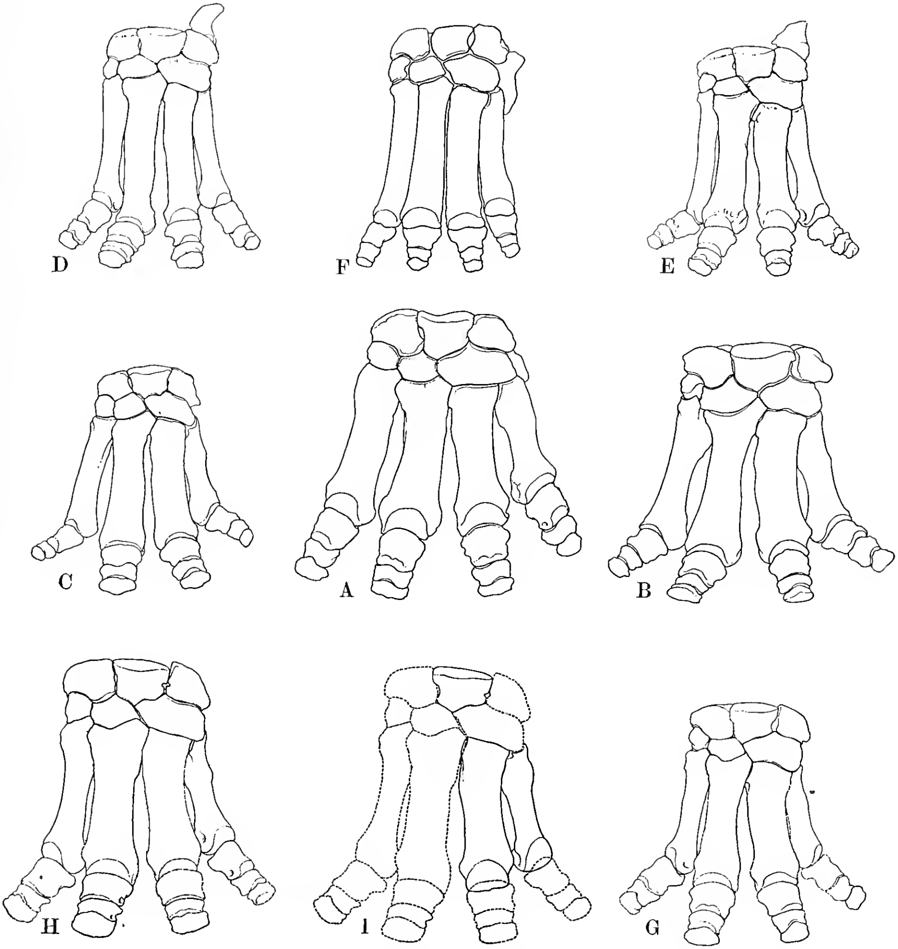

FIGURE 630.—Manus of Oligocene titanotheres

A, *Brontops robustus,* Yale Mus. 12048 (type); B, *Brontops robustus?,* Am. Mus. 518; C, *Diploclonus tyleri,* Amherst Mus. 327 (type); D, *Menodus trigonoceras,* Am. Mus. 515; E, *Menodus trigonoceras,* Am. Mus. 1079; F, *Menodus giganteus,* Yale Mus., after Marsh; G, *Brontotherium hatcheri,* Am. Mus. 1047 (two middle digits restored); H, *Brontotherium gigas?,* Am. Mus. 1443 (two middle digits restored); I, *Brontotherium gigas,* Am. Mus. 492 (digits I, II restored). All one-eighth natural size. In general the manus of *Menodus* is high and narrow and has small distal phalanges; that of *Brontotherium* is short and wide and has wide distal phalanges. The manus of *Brontops* appears to be of intermediate type.

other parts of the skeleton; a well-preserved pelvis referred by Marsh to *B. gigas* and figured in Plate CCXXXI (Nat. Mus., no number); and a pelvis in the National Museum (No. 4262) probably associated with skull and limbs referred to *B. gigas*.

The pelvis of *B. gigas* differs from that of *Brontops robustus* in its greater relative width and in having the outer iliac crest produced more downward and less directly outward.

Measurements of pelvis in Brontotherium gigas and Brontops robustus, in millimeters

	B. gigas, Am. Mus. 492	Brontops robustus Yale Mus. 12048 (type)
Width	1, 170	1, 220
Length iliac crest to ischial tuberosity	820	900
Pelvic index, $\frac{\text{width}}{\text{length}} \times 100$	142	134

Femur.—The femur of *B. leidyi* (Carnegie Mus. 93) lacks the proximal end, but the bone appears to be relatively broader than in *Brontops robustus* (type). The characters of the bone in *B. gigas* are not known.

Tibia.—The tibia of *B. leidyi* (Carnegie Mus. 93) is relatively wider at the proximal end than that of *B. robustus*.

Pes.—The pes of *Brontotherium* is supposed to be represented by three metatarsals (Pl. CCXXXII) and some phalanges (Pl. CCXXXV), which Marsh referred to *B. gigas;* by an incomplete pes (Am. Mus. 1047); and by a partial pes which may be associated with the skeleton of *B. gigas* (Nat. Mus. 4262). The pes, as a whole, is extremely short and wide, the third metatarsal measuring 160 millimeters in length and 76 in maximum width near the distal end, as compared with 225 in length and 88 in width in *B. robustus* (type). The index of the third metatarsal is thus 47 in *B. gigas* and 40 in *B. robustus*

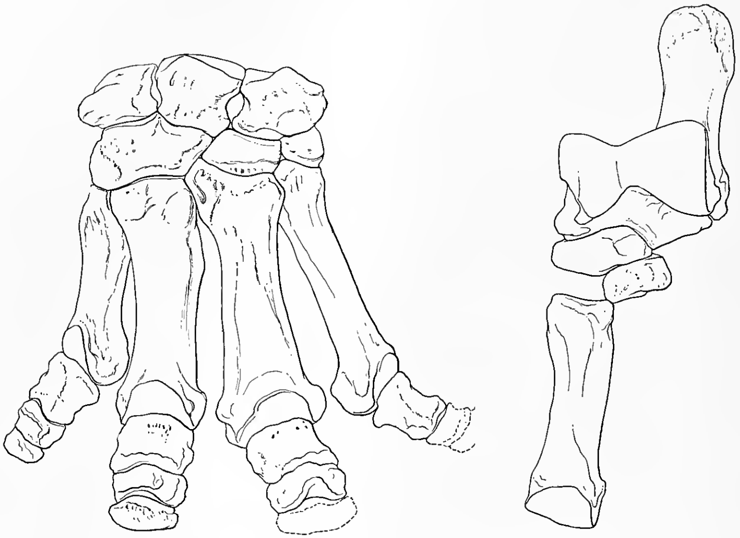

FIGURE 631.—Manus and pes referred to *Brontotherium gigas hatcheri*

Nat. Mus. 4262. One-fourth natural size.

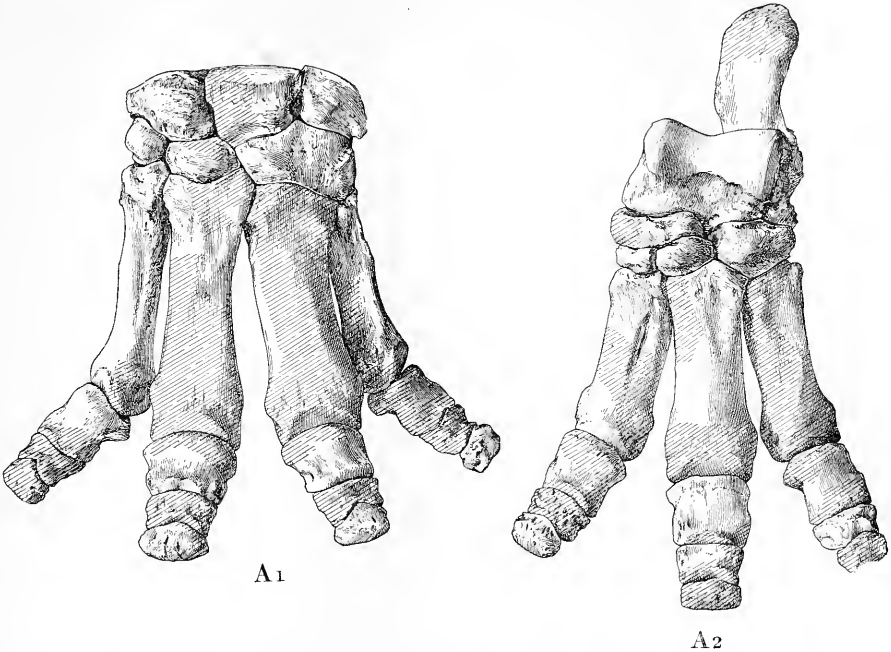

FIGURE 632.—Manus and pes referred to *Brontotherium hatcheri*

Am. Mus. 1047. A_1, Manus, as restored. Most of digits III and IV and part of the lunar are restored. A_2, Pes, as restored. Much of the digits and a part of the navicular are restored. One-fourth natural size.

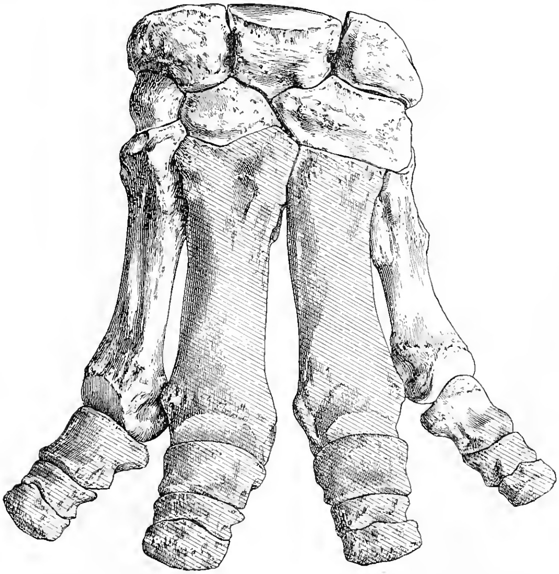

FIGURE 633.—Manus referred to *Brontotherium gigas*, as restored

Am. Mus. 1443, reversed. Digits III and IV and the phalanges of digits II and V restored. One-fourth natural size.

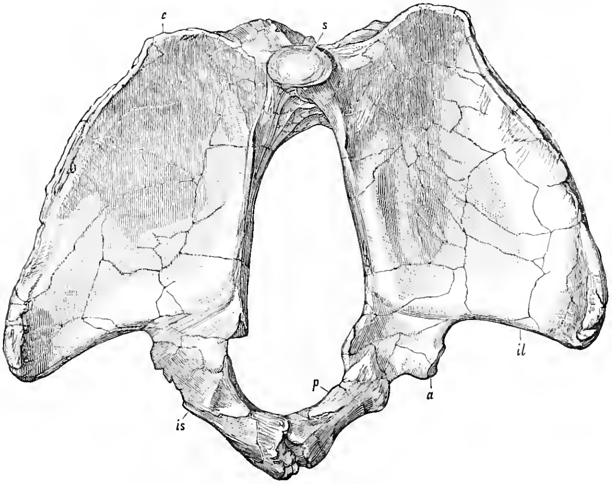

FIGURE 634.—Pelvis of *Brontotherium gigas hatcheri*

Nat. Mus. 4262. Associated with skull and limbs. After Marsh. About one-eleventh natural size

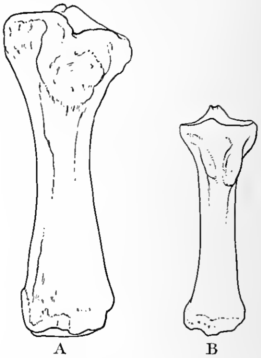

FIGURE 636.—Tibiae of *Brontops robustus* and *Brontotherium leidyi*

A, *Brontops robustus*, Yale Mus. 12048 (type); B, *Brontotherium leidyi*, Carnegie Mus. 93. One-eighth natural size.

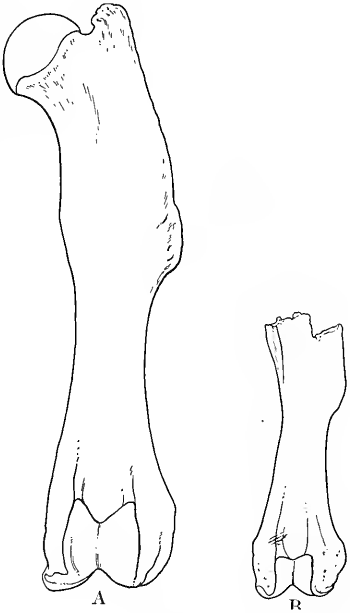

FIGURE 635.—Femora of *Brontops robustus* and *Brontotherium leidyi*

A, *Brontops robustus*, Yale Mus. 12048 (type); B, *Brontotherium leidyi*, Carnegie Mus. 93. One-eighth natural size. The *Brontotherium* femur appears to be wider in proportion to its length.

FIGURE 637.—Tibia and fibula of *Brontotherium leidyi*

A, Carnegie Mus. 93, outer side view or right tibia. B, Carnegie Mus. 114, inner side view of left fibula. One-eighth natural size.

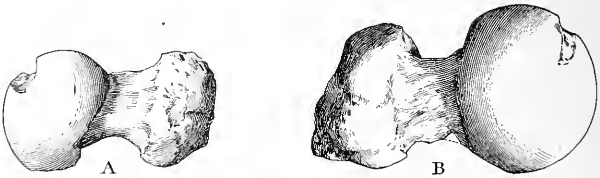

FIGURE 638.—Femora of *Megacerops?* and *Brontotherium?*

A, *Megacerops? acer?*, Am. Mus. 6351. B, *Brontotherium?* sp., Am. Mus. 6347. Proximal view. One-fourth natural size.

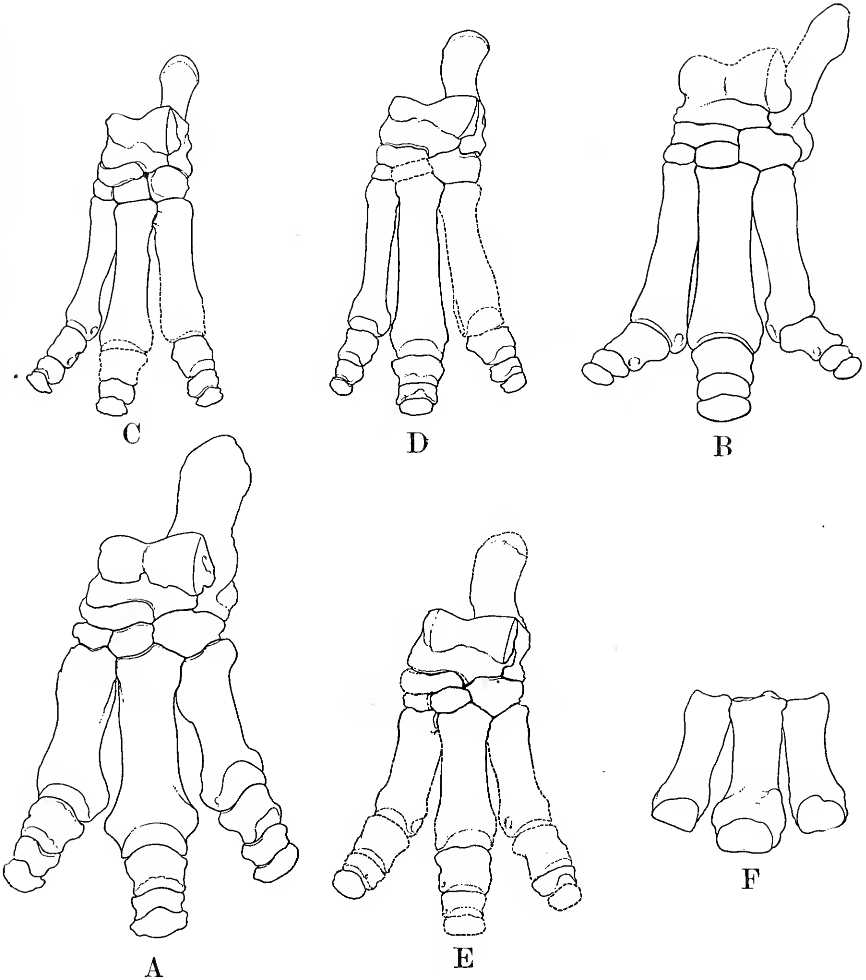

FIGURE 639.—Pes of Oligocene titanotheres

A, *Brontops robustus*, Yale Mus. 12048 (type); B, *Diploclonus tyleri*, Amherst Mus. 327 (type); C, *Menodus? heloceras*, Am. Mus. 1080; D, *Menodus trigonoceras*, Am. Mus. 1079; E, *Brontotherium hatcheri?*, Am. Mus. 1047; F, *Brontotherium? gigas*, Yale Mus., after Marsh. One-eighth natural size. The pes of *Menodus* is very narrow, that of *Brontotherium* is very short and broad; the others are of intermediate type.

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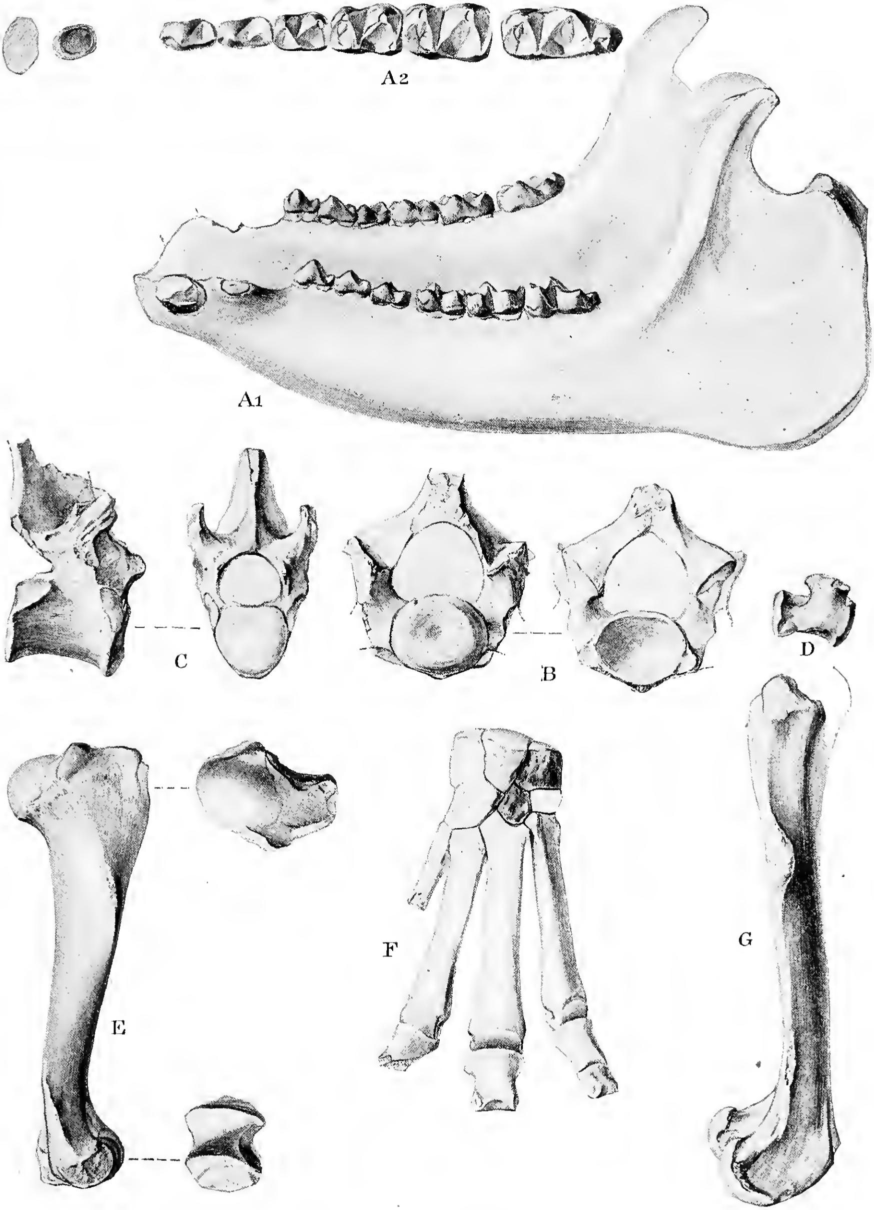
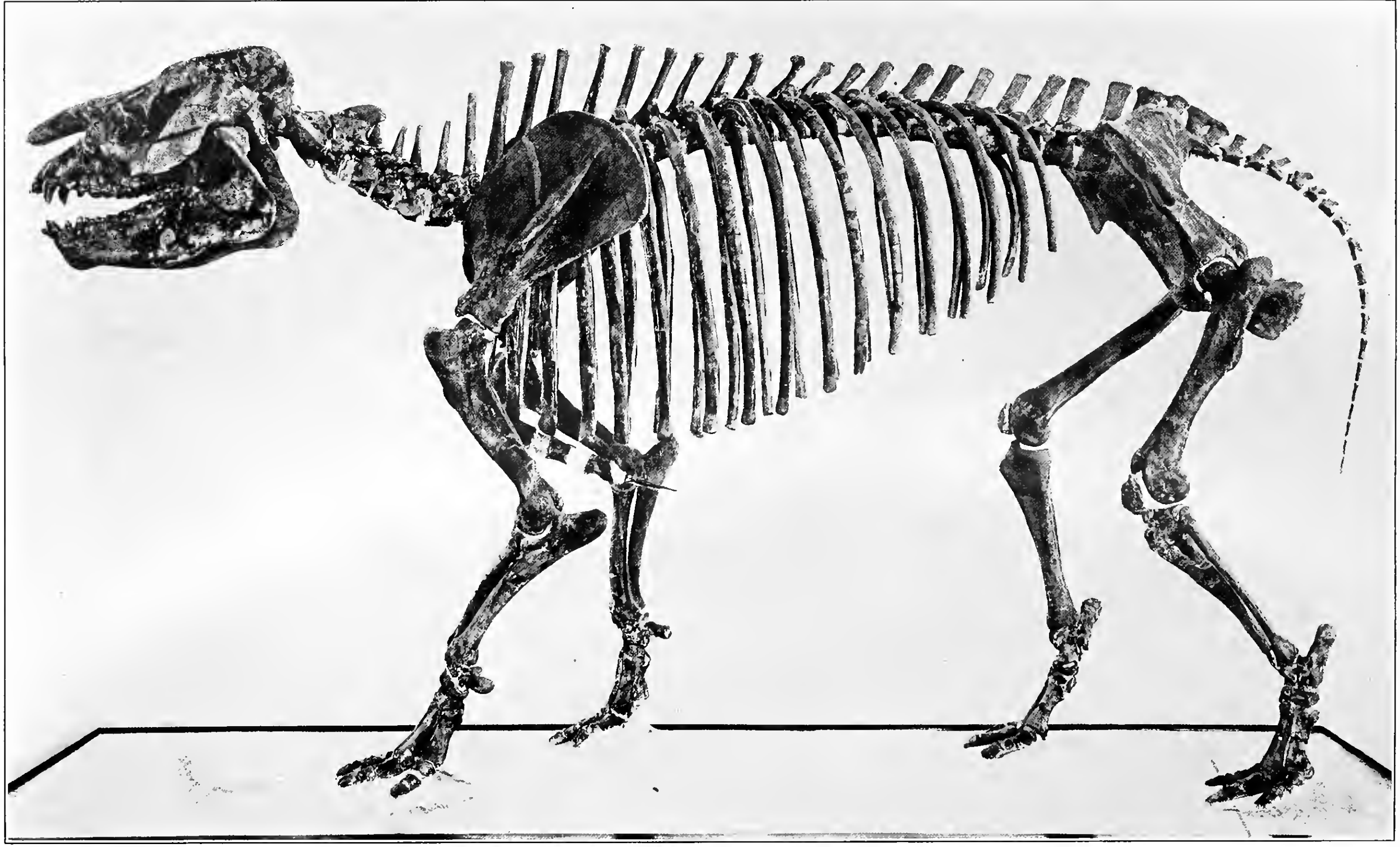


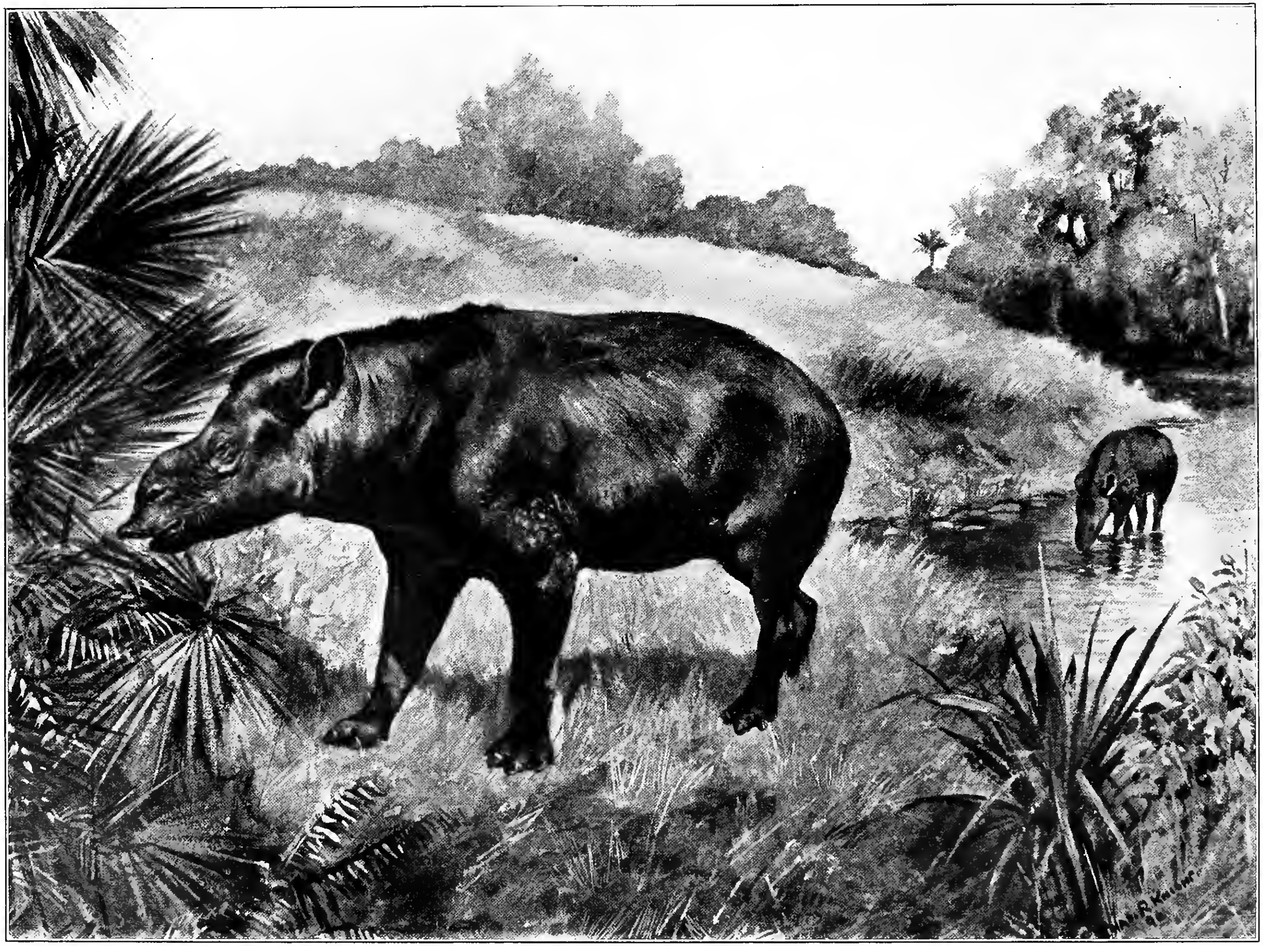
TYPE SKELETON OF EOTITANOPS PRINCEPS

Am. Mus. 296; Wind River formation, Wind River Basin. A_1, Lower jaw and dentition, one-half natural size; A_2, left lower teeth, three-fourths natural size; B, cervical, C, dorsal, and D, caudal vertebrae, all three-fourths natural size; E, right humerus, three-eighths natural size; F, right manus, one-half natural size; G, right femur, three-eighths natural size



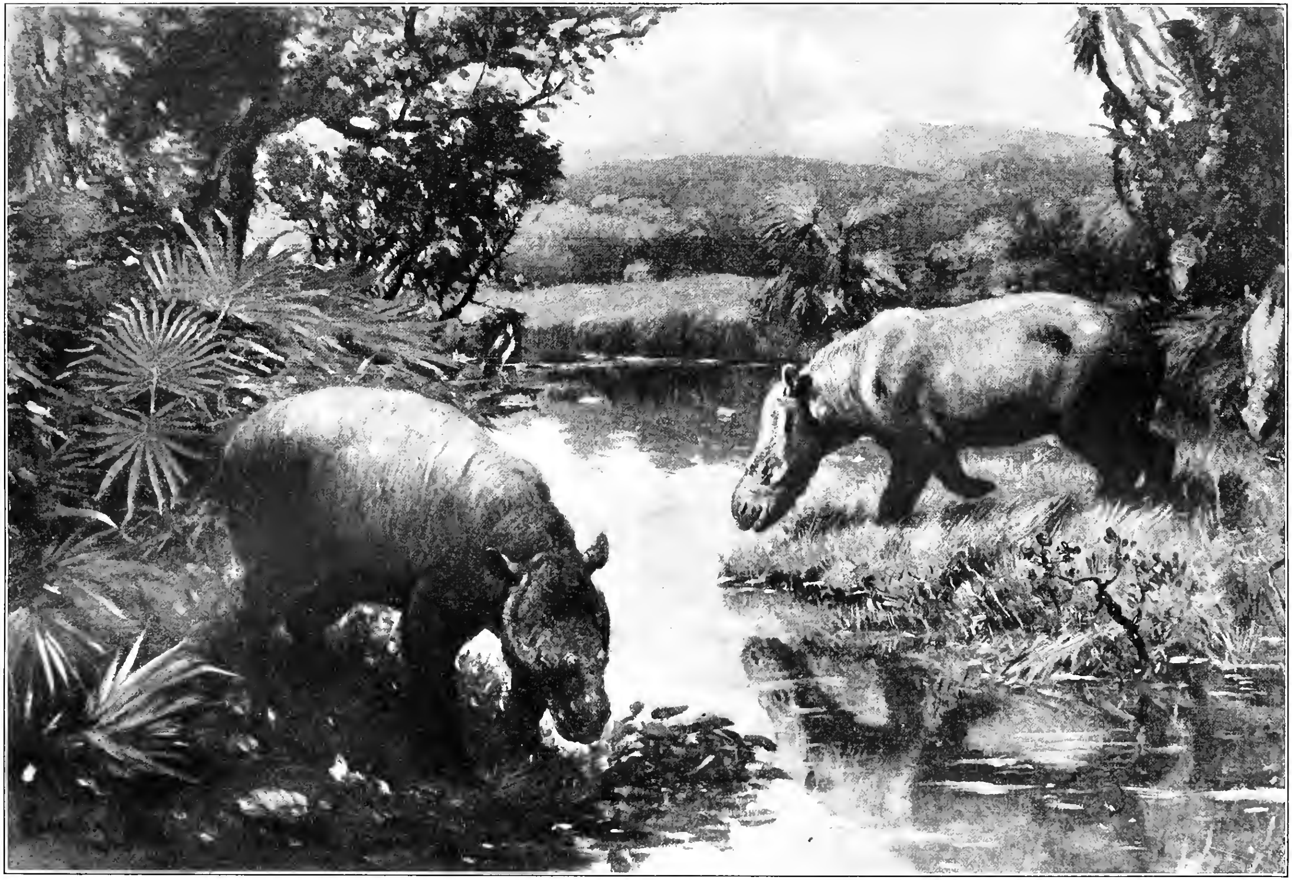
COMPOSITE MOUNTED SKELETON OF PALAEOSYOPS LEIDYI IN THE AMERICAN MUSEUM OF NATURAL HISTORY

Parts of several individuals are included in this skeleton (see p. 620), chiefly from the type specimens (Am. Mus. 1554). One-eighth natural size



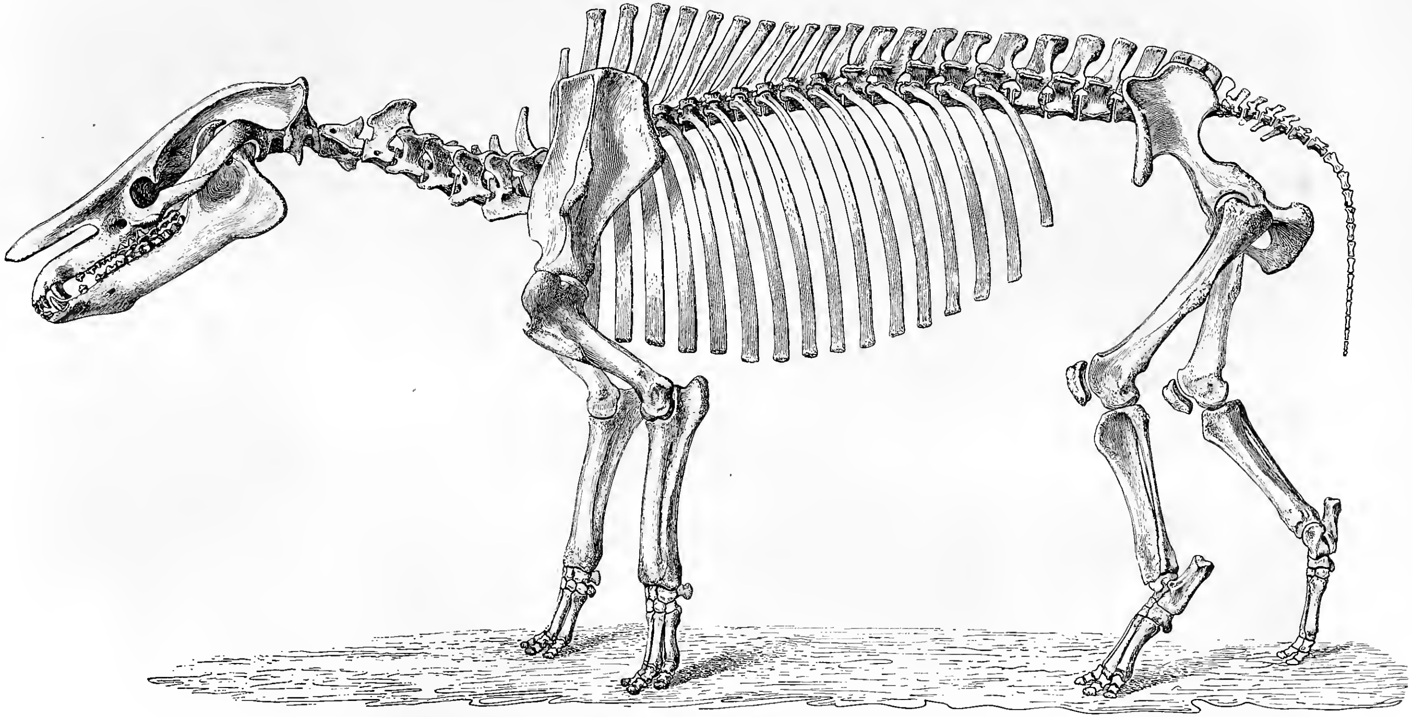
RESTORATION OF PALAEOSYOPS OF THE BRIDGER BASIN, WYO.

Painted by Charles R. Knight in 1902 under the direction of the author



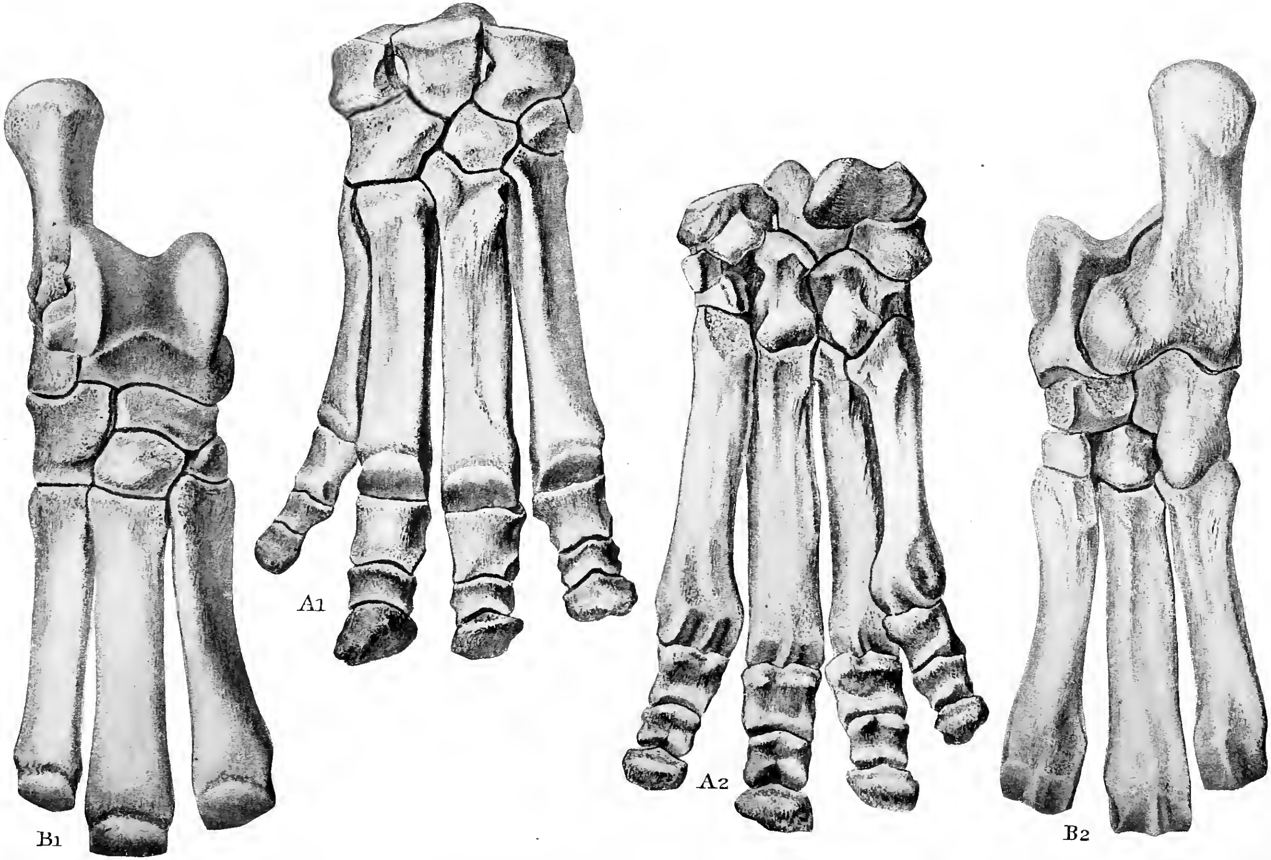
RESTORATION OF MANTEOCERAS (LEFT) AND DOLICHORHINUS (RIGHT) OF THE UINTA BASIN, UTAH

Painted by Charles R. Knight in 1906 under the direction of the author



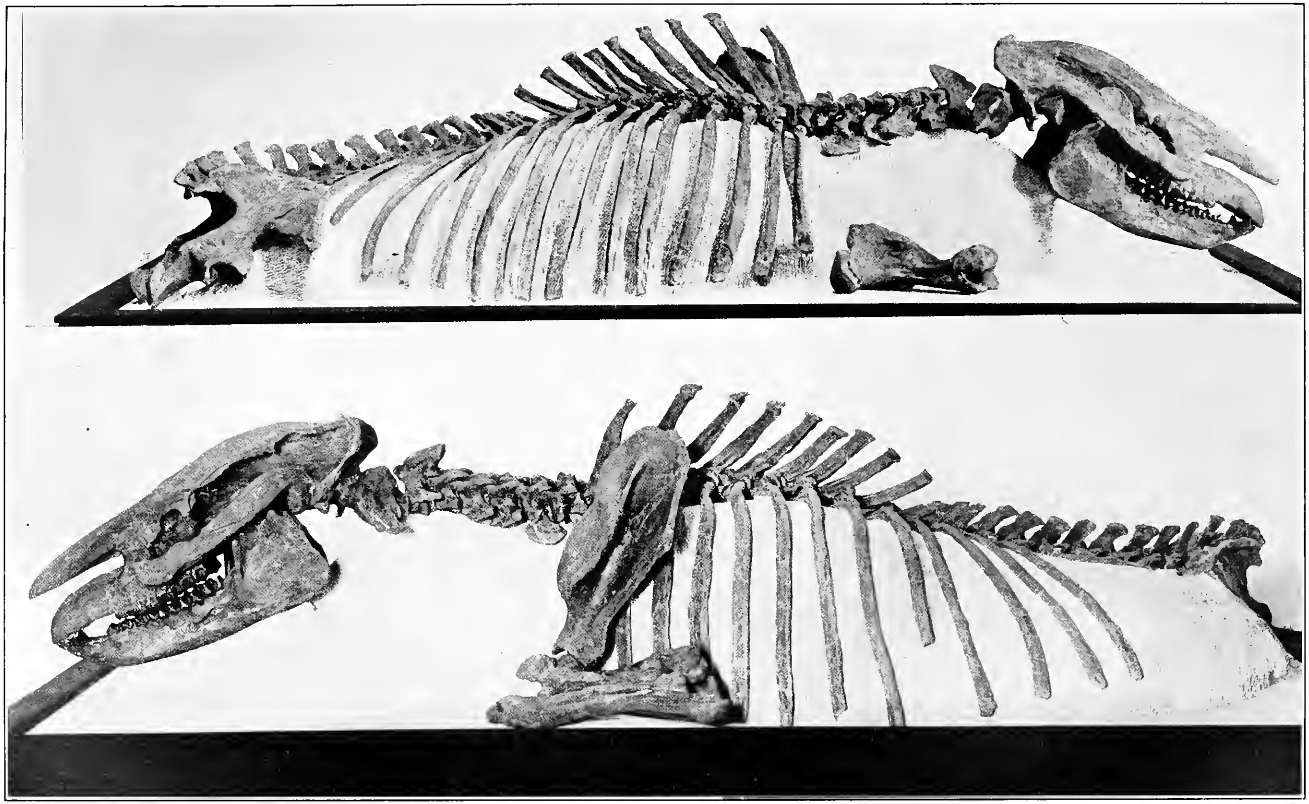
RESTORATION OF THE SKELETON OF DOLICHORHINUS LONGICEPS

Drawn by Sidney Prentice under the direction of Dr. W. J. Holland and O. A. Peterson and based on remains of several individuals in the Carnegie Museum. (After Holland.) One-tenth natural size



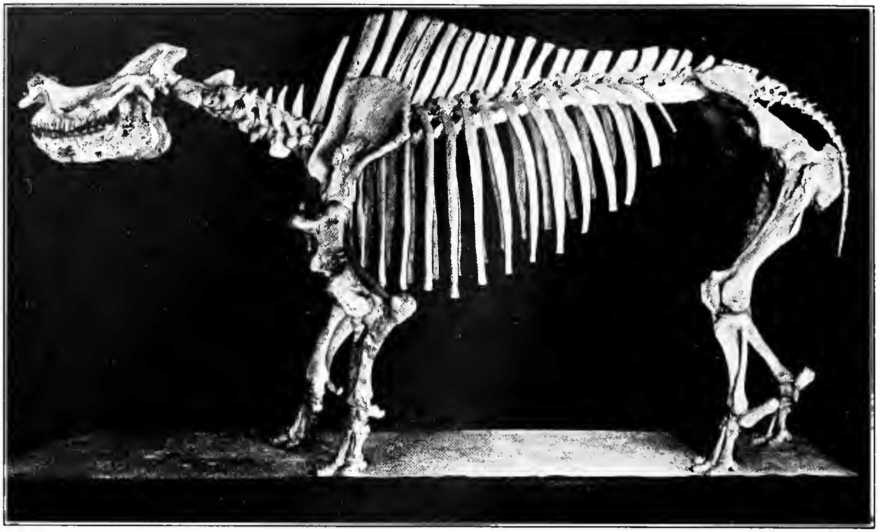
MANUS AND PES OF DOLICHORHINUS LONGICEPS

(After Peterson.) One-half natural size, A_1, Dorsal view of manus; A_2, palmar view of manus :B_1, dorsal view of pes; B_2, plantar view of pes



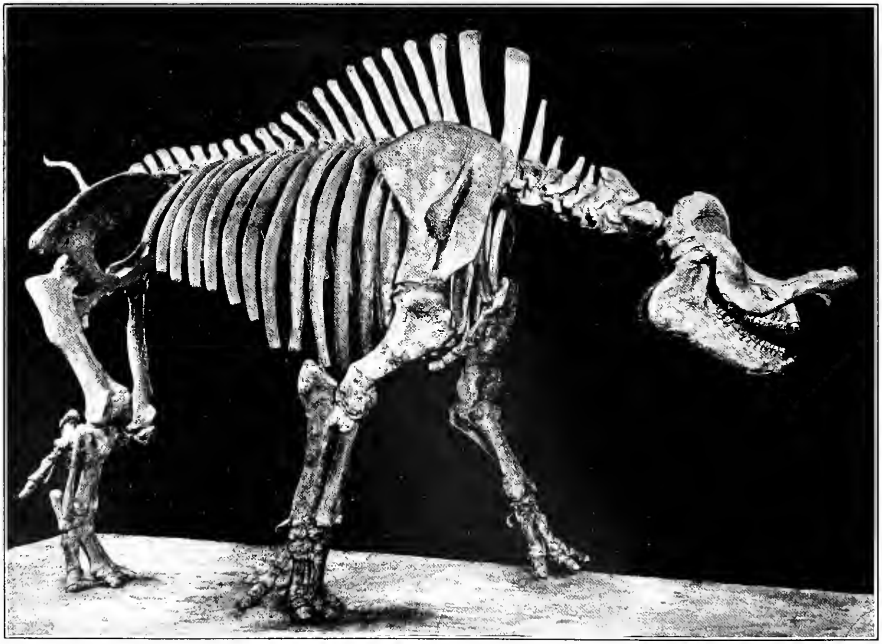
SKELETON OF DOLICHORHINUS LONGICEPS

Field Mus. 12200



A. BRONTOPS DISPAR, FEMALE

In Carnegie Museum. The skull belongs to another individual. Slightly more than one-twentieth natural size. Courtesy of Dr. W. J. Holland

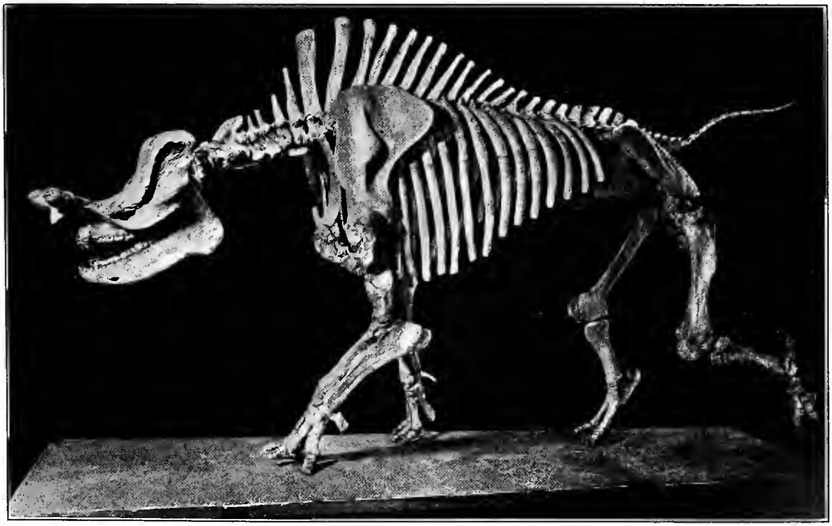


B. BRONTOPS ROBUSTUS, TYPE

Yale Mus. 12048. Oblique side view. About one twenty-fourth natural size. Maximum height 8 feet 2½ inches to top of dorsal spine. Courtesy of Prof. R. S. Lull. (Compare Pl. XXXIV)

MOUNTED SKELETONS OF BRONTOPS

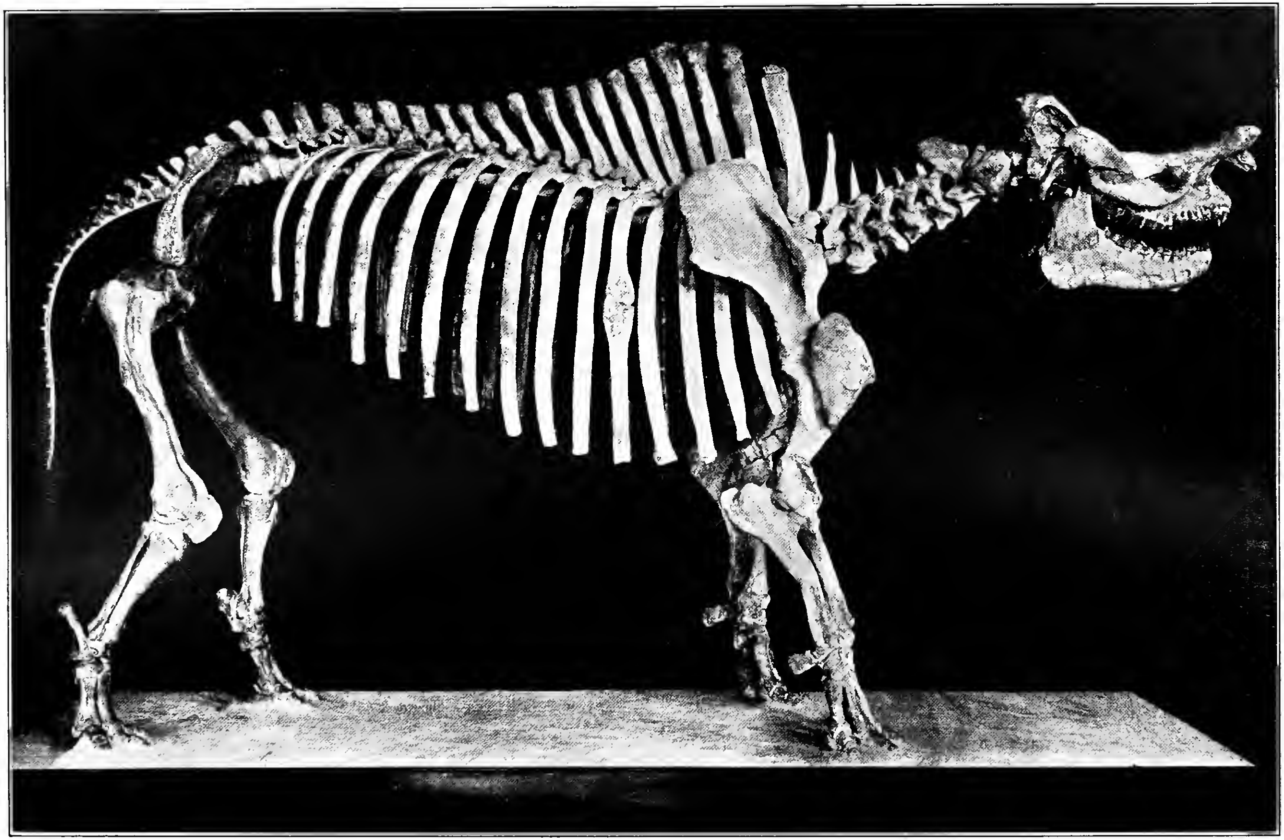
A



B

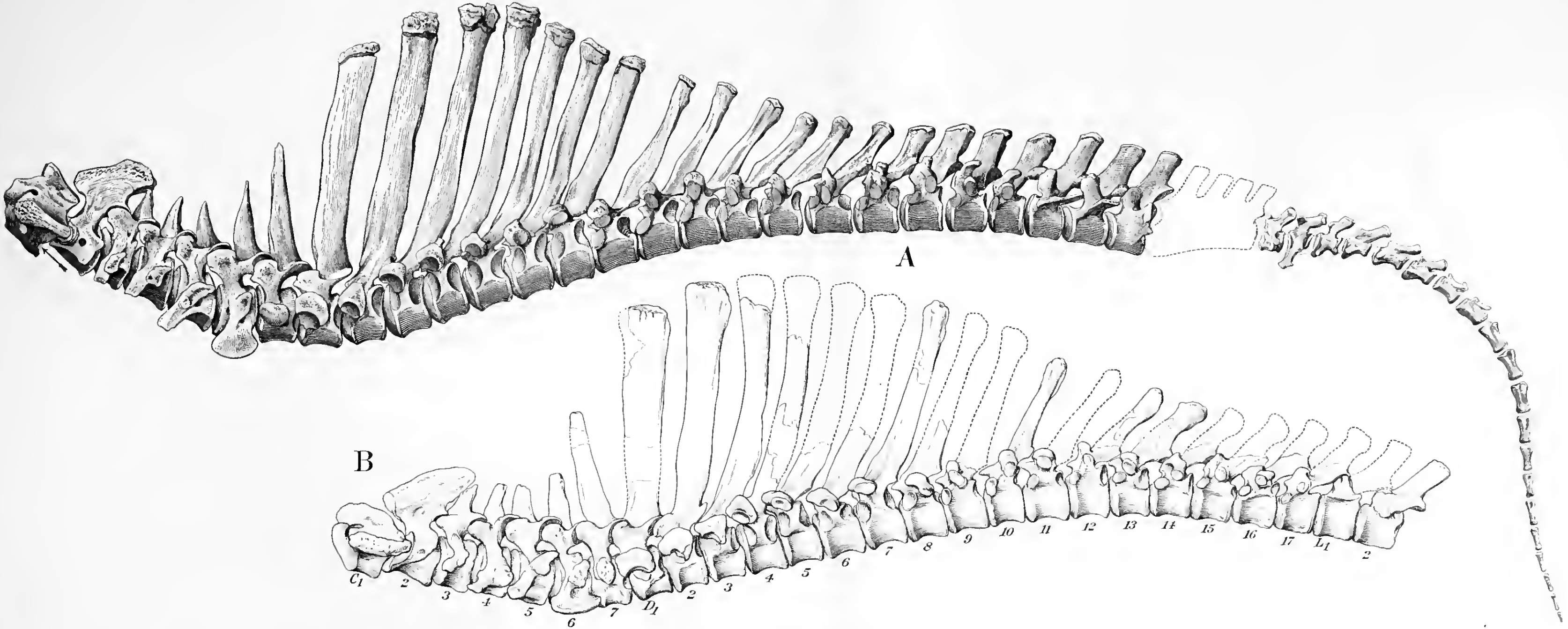
MOUNTED SKELETON OF BRONTOPS ROBUSTUS, TYPE

Yale Mus. 12048. Courtesy of Prof. R. S. Lull. A, Oblique front view; B, side view. (Compare Pl. XXXIII, B)



MOUNTED SKELETON REFERRED TO BRONTOPS ROBUSTUS?

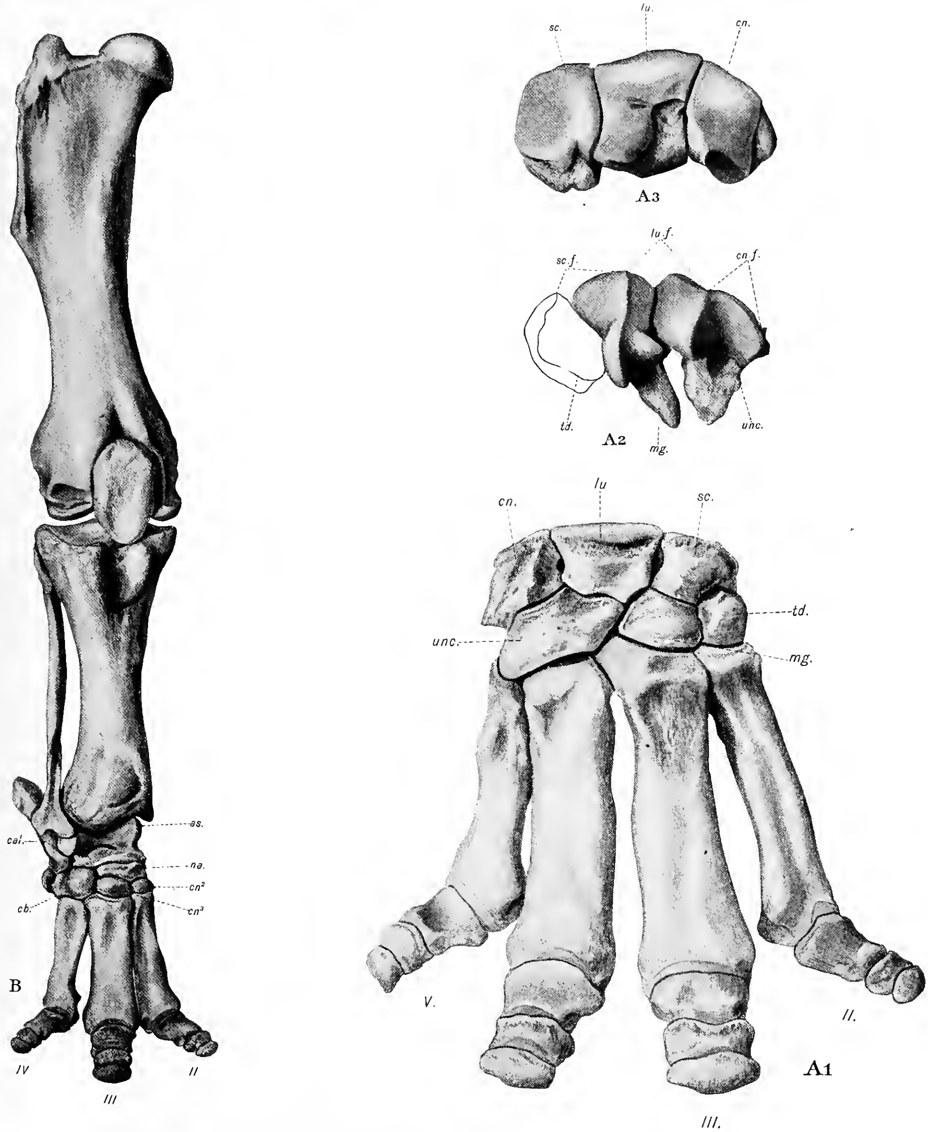
Am. Mus. 518. One-nineteenth natural size



VERTEBRAL COLUMN OF BRONTOPS

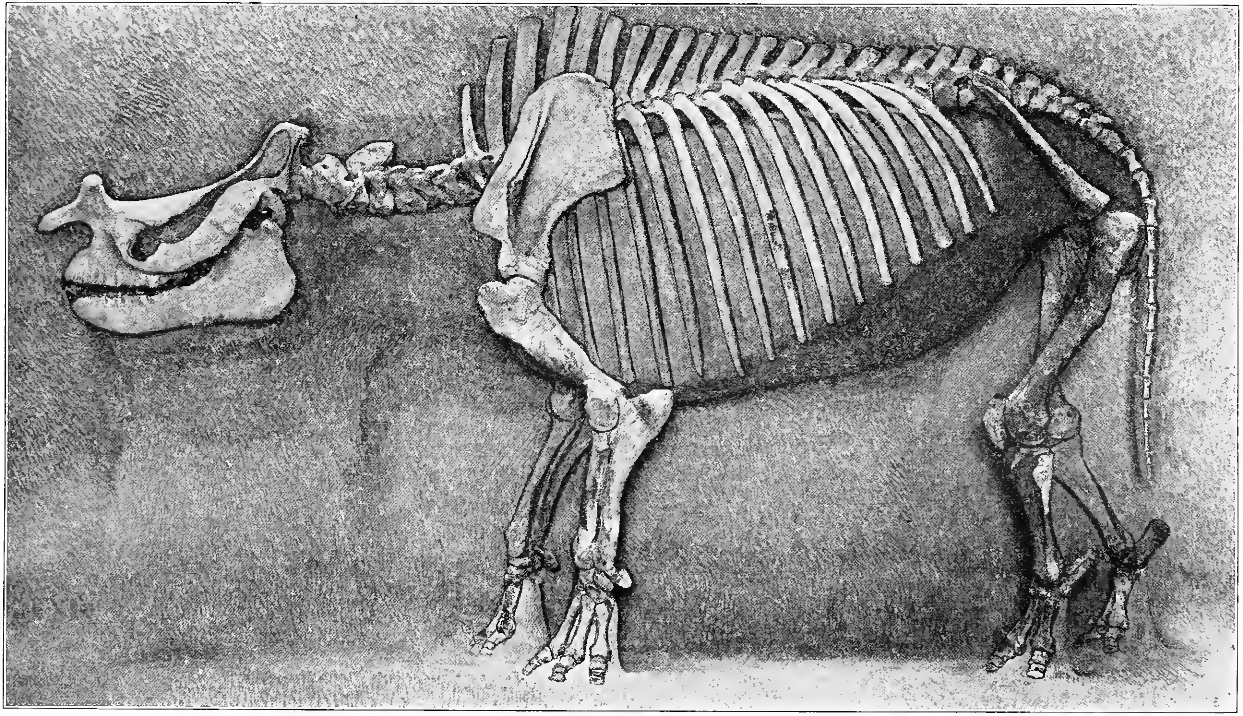
A, *Brontops robuſtus*? (Am. Mus. 518). The cervical and dorsal vertebrae belong to one individual. The lumbar, sacral, and caudal vertebrae are supplied from other individuals of uncertain reference. B, *Brontops robuſtus*, type (Yale Mus. 12048), presacral vertebrae. This figure was obtained by copying the carefully executed figures of the separate vertebrae made by F. C. Berger under the direction of Professor Marsh and then placing the new drawings in sequence to represent the vertebrae as if they were in articulation

(101959—29)



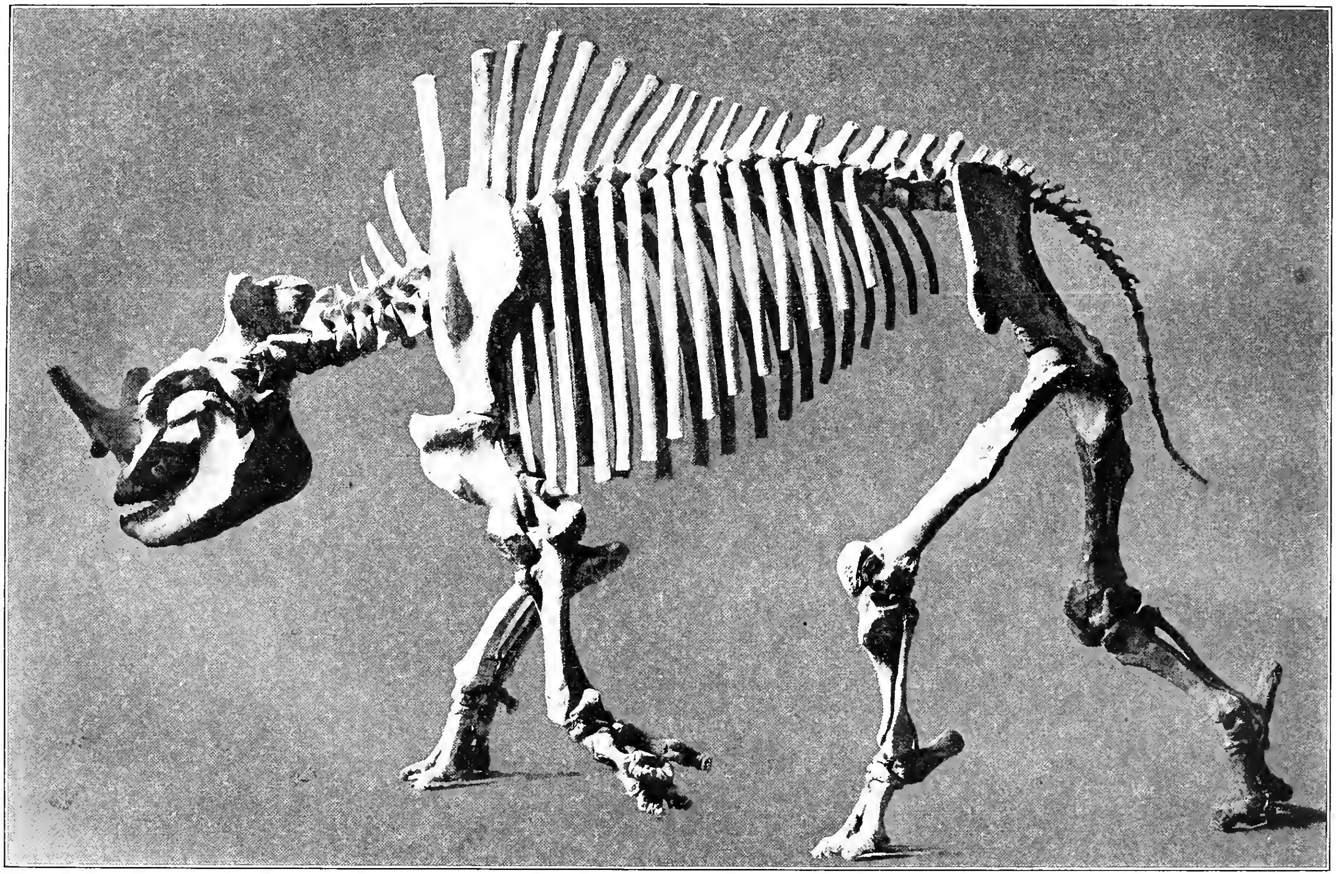
MANUS AND HIND LIMB OF DIPLOCLONUS TYLERI LULL

Amherst Mus. 327, type. (After Lull.) A_1, Right manus; A_2, proximal aspect of distal carpals; A_3, proximal aspect of proximal carpals; all one-fourth natural size. B, Right hind limb, one-eighth natural size



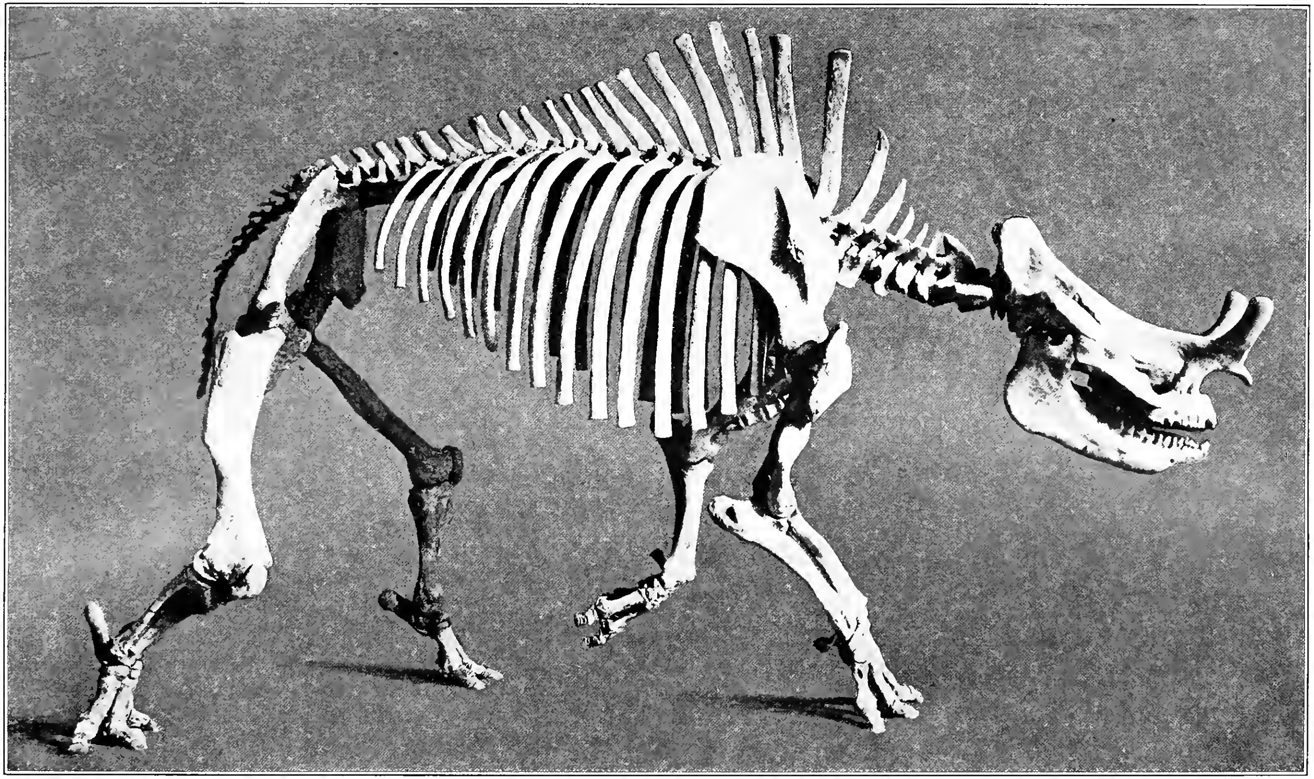
MOUNTED SKELETON OF ALLOPS MARSHI

Field Mus. 6900. Slightly over one-thirteenth natural size. Courtesy of Dr. E. S. Riggs



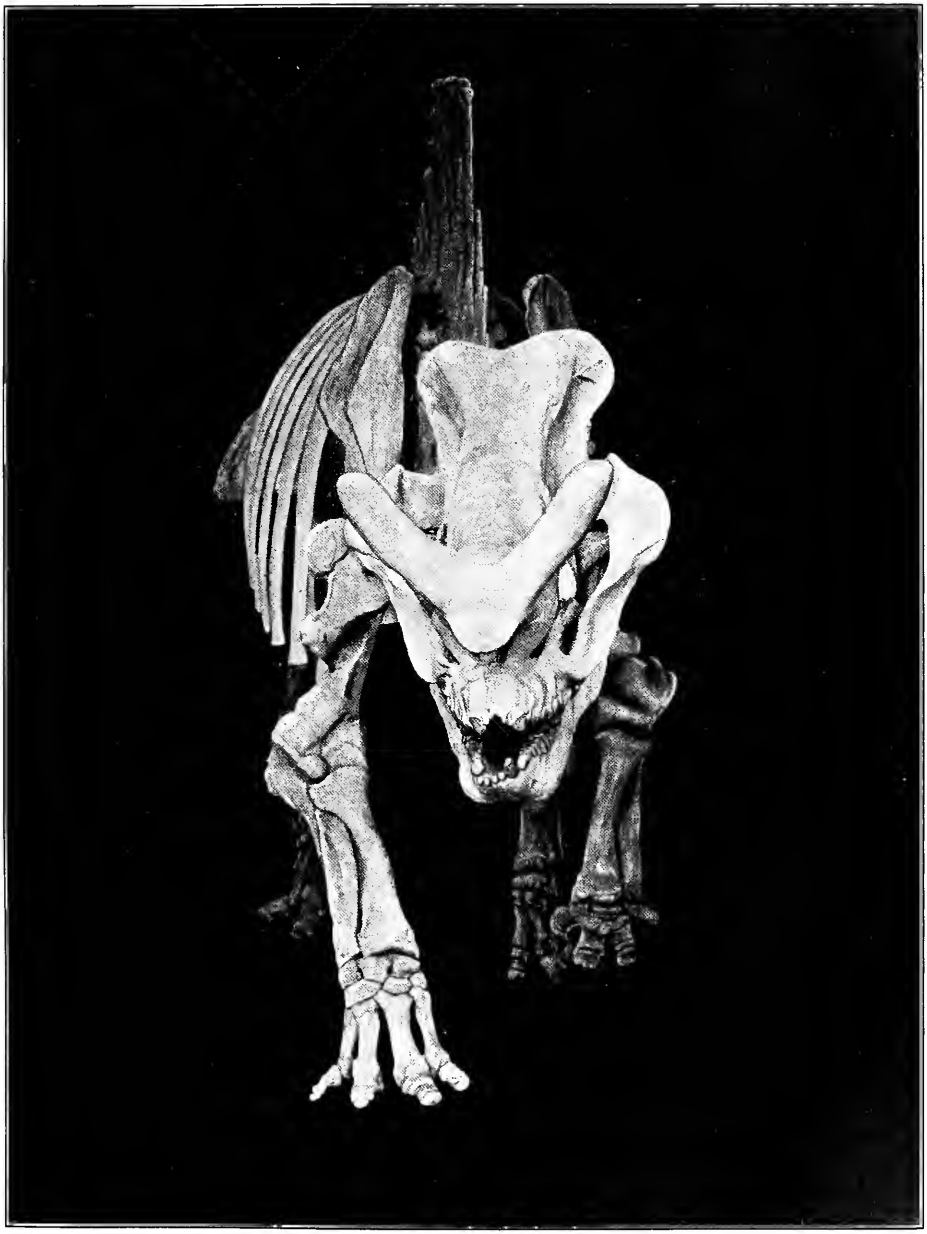
MOUNTED SKELETON OF BRONTOTHERIUM HATCHERI, LEFT SIDE VIEW

Nat. Mus. 4262. About one-fifteenth natural size. (Compare Pls. XL, XLI, and XLII)



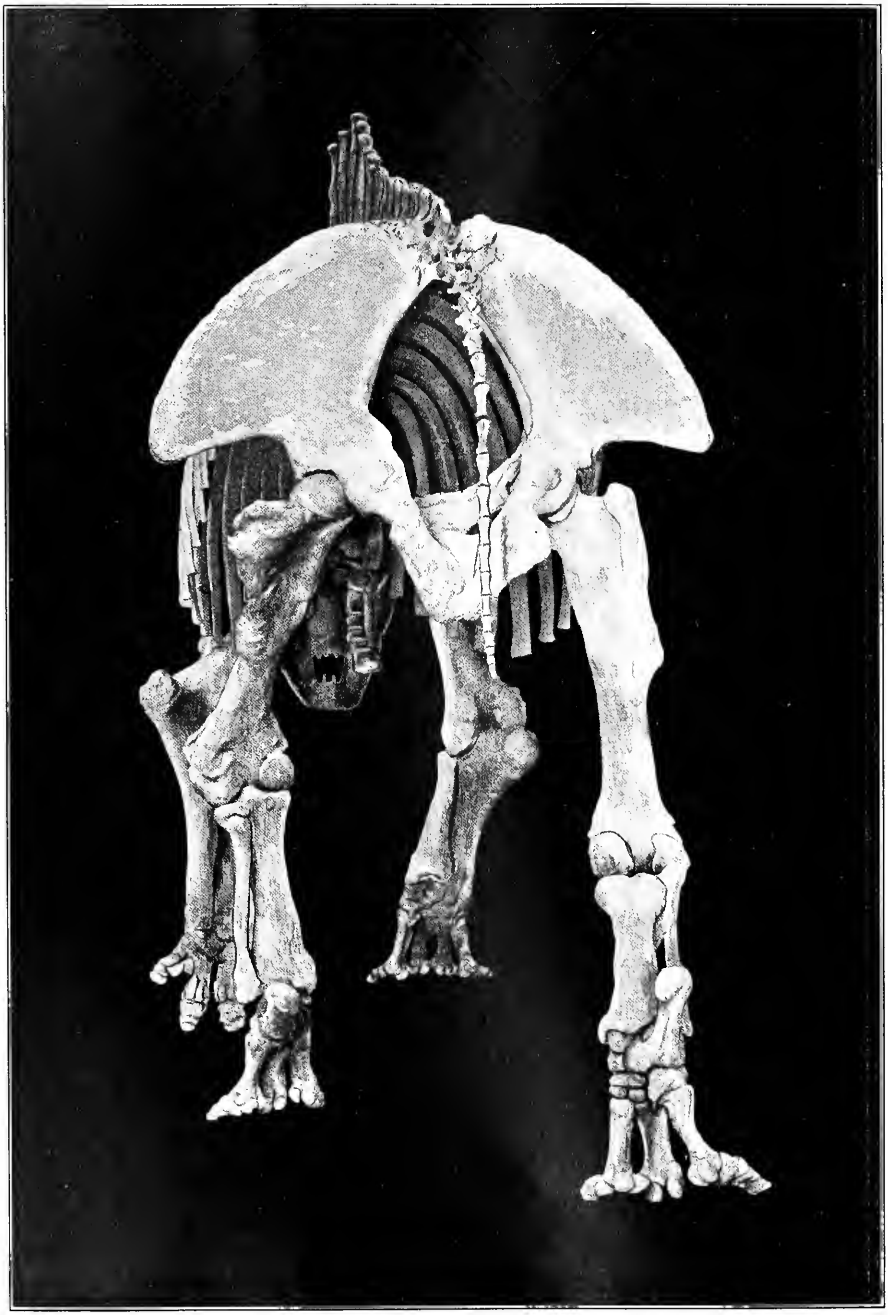
MOUNTED SKELETON OF BRONTOTHERIUM HATCHERI, RIGHT SIDE VIEW

Nat. Mus. 4262. Somewhat less than one-seventeenth natural size. (Compare Pls. XXXIX, XLI, and XLII)



MOUNTED SKELETON OF BRONTOTHERIUM HATCHERI, FRONT VIEW

Nat. Mus. 4262. (Compare Pls. XXXIX, XL, and XLII)



MOUNTED SKELETON OF BRONTOTHERIUM HATCHERI, BACK VIEW

Nat. Mus. 4262. (Compare Pls. XXXIX, XL, and XLI)