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To Mr. Gilmore
With the author's greetings

MEMOIRS

OF THE

AMERICAN MUSEUM OF NATURAL HISTORY

NEW SERIES, VOLUME III, PART II

ON THE STRUCTURE AND RELATIONS OF *NOTHARCTUS*, AN AMERICAN EOCENE PRIMATE

BY W. K. GREGORY

SEPTEMBER, 1920

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THE AMERICAN MUSEUM OF NATURAL HISTORY

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PART II.—ON THE STRUCTURE AND RELATIONS OF *NOTHARCTUS*, AN AMERICAN EOCENE PRIMATE

STUDIES ON THE EVOLUTION OF THE PRIMATES, PART III[1]

BY W. K. GREGORY

PLATES XXIII–LIX

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[1] For Parts I and II, see Bull. Amer. Mus. Nat. Hist., XXXV, pp. 239–355.

PREFACE

Important skeletal remains of Eocene Primates of the genus *Notharctus* Leidy, including skulls, teeth, and incomplete skeletons, were obtained in Middle Eocene strata of the Bridger Basin, Wyoming, by American Museum expeditions under Mr. Walter Granger in 1903 and 1904. This delicate material was freed from the matrix and prepared for study and exhibition chiefly by Mr. Albert Thomson. It was generously assigned by Professor Osborn and Dr. Matthew to the writer to be described and compared with the earlier collections of Eocene Primates in this Museum. These collections have already been studied and described, as to their diagnostic generic and specific characters, in several papers in the Bulletin of this Museum by Osborn (1902), Matthew (1915), and Granger and Gregory (1917), so that the following pages deal chiefly with the morphology and evolution of the genus *Notharctus* and with the relationships of the Notharctinæ with other groups of primates. Preliminary reports on this subject were made by the present writer in 1913, 1915, and 1916 in the papers cited in the bibliography.

The auditory region and ossicles of *Notharctus osborni* were very skilfully freed from the matrix by Mr. Abram E. Anderson, who also prepared many other specimens and all the photographic illustrations for this work. The line drawings, unless otherwise noted, were drawn under the writer's direction by Mrs. Elizabeth M. Fulda.

A few words of explanation may be offered as to the illustrations which are reproduced from the works of other investigators. If, according to a conventional method, one had given drawings or photographs only of the *Notharctus* material itself, that would have been a sufficient record for the few investigators who, in the course of future decades, would read the text with care and make their own detailed comparisons after having duly assembled the literature of the subject and with their own specimens for comparison in hand. But if (as the important nature of the material seems to warrant) it is desirable to make the whole subject available also to a wider circle of scientists — specialists in other fields who have neither the inclination nor the facilities for a first hand study of this material,— then it is necessary to supply abundant comparative illustrations in order to show at a glance what are the resemblances and differences between these Eocene Primates and other members of the same order. Accordingly the writer has reproduced for comparison many of the excellent figures of the Eocene Primates of Europe published by Dr. Stehlin in his Critical Catalogue of the Swiss Eocene mammals, and a few of the remarkable engravings of the osteology and myology of recent indrisine lemurs in the memoir by Milne Edwards on the Anatomy of the Lemurs of Madagascar. Cuvier's and Laurillard's "Planches de Myologie" have yielded several useful illustrations, and the same is true of other sources which are acknowledged in the legends of the text figures. Some of the photographs of primate skulls which were made by Mr. Anderson for the late Dr. Elliot's Monograph on the Primates have been carefully retouched and reproduced for comparison with figures of the skull of *Notharctus osborni*.

INTRODUCTION

The present series of studies on the Evolution of the Primates is addressed not only to palæontologists but to anatomists and anthropologists, to students of the dentition of mammals, and to all who are concerned with the origin, evolution, and functions of the human skeleton. The main objects of the series are, first, to state and illustrate the anatomical facts without bias or prejudice, and, second, to determine as far as possible the main evolutionary stages through which the observed anatomical conditions have been attained and towards which they may point.

Naturally, such evolutionary conclusions and evaluations as are adopted in this work result from a comparison of the observed conditions with a general background or concept of evidence, which in many cases could not be fully exposed without lengthy discursions from the immediate topic. For example, the conception of the successive stages of the evolution of the limbs of primates outlined at the end of this work rests upon the following classes of evidence.

(1) Evidence concerning the origin of mammals from Permo-Triassic therapsid reptiles. It would be presumptuous for the writer to take anything for granted with regard to this topic or even to touch it at all, if he had not always endeavored to make good the opportunity (afforded by the resources of this Museum and by his friendship with Professor Williston, Dr. Broom, Dr. D. M. S. Watson and others) of acquiring "autoptic knowledge" of the Palæozoic Tetrapoda, and especially of the Permian and Triassic mammal-like reptiles, a considerable collection of the latter being under his care and frequently studied by himself and colleagues.

The problem of the origin of the mammals has, of course, an immediate bearing upon the origin of the primates, including man, and thus has at least a potential value and interest to anatomists, anthropologists, and others, as well as to palæontologists. But if there be anatomists who still uphold the view that mammals have been derived from amphibians rather than from late Palæozoic reptiles, or if there be others who regard such problems as still in the purely speculative stage, the writer can only refer, in this work, to the growing literature[1] of the subject, or suggest a re-examination of all the evidence in the light of modern comparative anatomy.

(2) A second class of evidence, which is largely taken for granted in the discussion of the evolution of the limbs of primates, relates to the following questions. What primitive characters of the limbs and axial skeleton should be ascribed to the very little-known Cretaceous ancestors of the various orders of placental mammals? Was there ever a single group of primitive placental mammals? Or are the placental orders polyphyletic derivatives of different orders of pre-placentals? And did a central stock give rise by adaptive radiation to the already differentiated placental orders and families of the Paleocene? Answers to such questions have long been sought by investigators in this Museum through a study of the representatives of many orders and families of Paleocene and Lower Eocene placental mammals, and of the clearly demonstrable divergent trends of evolution exhibited in many of these phyla

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[1] Cited and reviewed especially in the following papers:

Watson, D. M. S. 1911. The Skull of *Diademodon*, with Notes on those of some other Cynodonts. Ann. Mag. Nat. Hist., (8) VIII, pp. 293–330. [Resemblances of Therapsids to Mammals, pp. 325–326.]

Gregory, W. K. 1913. Critique of Recent Work on the Morphology of the Vertebrate Skull, Especially in Relation to the Origin of Mammals. Journ. Morph., XXIV, No. 1, March.

Broom, R. 1914. Croonian Lecture On the Origin of Mammals. Philos. Trans. Roy. Soc. London, (B) CCVI, pp. 1–48.

Gregory, W. K., and Camp, C. L. 1918. A Reconstruction of the Skeleton of *Cynognathus*. Bull. Amer. Mus. Nat. Hist., XXXVIII, pp. 447–563.

during Paleocene and subsequent times. Cope and Wortman, the great pioneer collectors and students of Paleocene mammals, pointed the way for the systematic series of explorations of the early Tertiary horizons of the West which has been sent out year after year by this Museum under the direction of Professor Osborn and in charge of Mr. Walter Granger. The many thousands of specimens collected from these early horizons have been accurately recorded as to geological level, and have been or are being described in the faunistic and systematic studies of Osborn, Matthew, Granger, and others as noted below in the bibliography. This is the material upon which are based many statements in this paper as to what are here regarded as primitive placental characters.

A related class of evidence referred to in other parts of this work deals with the origin and evolution of the dentition of placental mammals. This has been so often discussed in previous works by Professor Osborn[1] and the writer[2] that it may be dismissed here with a brief statement of the writer's concept of the dentition of the primitive placental mammals perhaps in a Mid-Cretaceous stage of development: dental formula of adults $\frac{3,1,4,3}{3,1,4,3}$ of deciduous dentition $\frac{3,1,4}{3,1,4}$; dentition on the whole more or less like that of an opossum. Opposite upper incisors arranged in convergent series, overhanging lower incisors, canines caniniform, the tip of the lower canine received in a pit in the maxilla, in front of the upper canine; first three premolars simple, but gradually becoming more like $p\frac{4}{4}$; p^4 bicuspid with a metastyle shear, p_4 submolariform with low talonid; upper molars acutely triangular in form, extended transversely, lower molar trigonids fitting into spaces between upper molars, hence protoconid-paraconid shears of lower molars shearing past metacone-metastyle shear of uppers; talonids of lower molars overlapping on crowns of uppers, narrow transversely, their hypoconids fitting between the barely separated para- and metacones.

Such forms and relations of the upper and lower teeth are more or less completely retained in the most primitive known members of many phyla of Eocene carnivores, insectivores, and primates. They were originally associated with orthal[3] jaw movement, stout zygomatic arches, a long face with rather small orbits, and very narrow brain-case surmounted by a sagittal crest. The primates very early lost one pair of incisors in each jaw, shortened the face, and enlarged the orbits and brain-case; but *Notharctus* and its predecessors had not yet gone far along this line of advance since they retained a comparatively small brain-case and very many primitive characters of the dentition.

A vast field of evidence afforded by comparative anatomy, taxonomy, and palæontology quite clearly indicates, in the writer's opinion, that the general stages in the evolution of the vertebrates from the most primitive gnathostomes of the Ordovicic to man, with their approximate geological horizons, were as follows:

Stage 1. ? Ordovicic. Primitive gnathostomes with gill-arch jaws and cartilaginous endoskeleton.
Stage 2. ? Siluric. Primitive rhipidistian fishes.
Stage 3. Devonic. Protetrapoda.[4]
Stage 4. Carbonic. Proreptilia.

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[1] Osborn, H. F. 1907. Evolution of Mammalian Molar Teeth, To and From the Triangular Type. Edited by W. K. Gregory, New York: The Macmillan Co.

[2] Gregory, W. K. 1916. The Cope-Osborn "Theory of Trituberculy" and the Ancestral Molar Patterns of the Primates. Bull. Amer. Mus. Nat. Hist., XXV, pp. 239–257.

Gregory, W. K. 1918. The Evolution of Orthodonty. The Dental Cosmos, May, 1918.

[3] This word is here used as defined by Cope (1887, Amer. Naturalist, p. 991), noting the movement of the jaws in a vertical plane as in the carnivorous mammals. Some authors use orthal as if it meant movement in an anteroposterior direction.

[4] See Gregory, W. K. 1915. Present Status of the Problem of the Origin of the Tetrapoda, with Special Reference to the Skull and Paired Limbs. Ann. N. Y. Acad. Sci., XXVI, pp. 317–383.

Stage 5. Permian. Therapsida.
Stage 6. Triassic. Prototheria.
Stage 7. Jurassic. Pre-placentals.
Stage 8. Cretaceous. Pre-lemuroids.
Stage 9. Eocene. Pre-anthropoids.
Stage 10. Miocene. Pre-hominids.
Stage 11. Pliocene. Primitive Hominidæ.
Stage 12. Pleistocene. Modernized races of man.

From this point of view *Notharctus* and its allies represent the comparatively little-changed survivors of the primitive lemuroid stock which gave rise to all the higher lines of primates. In the other direction these Eocene lemuroids tend to connect the primates with the long series of stages leading back to the beginning of the gnathostome vertebrates.

PREVIOUS DISCOVERIES AND INVESTIGATIONS[1]

The history of the discovery of Eocene primates in Europe is given by Stehlin (1912, p. 1165), who states that as far back as 1822 G. Cuvier (*op. cit.*, p. 265) described a certain small and imperfect fossil skull from the Paris Basin; he regarded it as a small pachyderm related perhaps to *Anoplotherium*, with which he compared it, and so gave it the name *Adapis* "nom employé quelquefois pour le Daman."

In 1873 Delfortrie described a similar skull from the French Phosphorites, under the generic name *Palæolemur*. Gaudry (in an appendix to Delforties's paper) confirmed the lemurine affinities of this genus and showed that it was very probably the same animal as Cuvier's *Adapis;* but the idea that *Adapis* was related to the "Pachyderms" long persisted in France.

Subsequent contributions to knowledge of the structure and relations of *Adapis* and allied forms were made by Gervais, Filhol, Gaudry, Flower, Lydekker, Schlosser, Zittel, Winge, Leche, Forsyth Major, and Grandidier. In 1883 (pp. 43–47) Filhol confirmed the generic distinction of *Adapis* from *Notharctus* and other North American "lémuriens." He demonstrated the resemblances to and the differences from the existing lemurs, and refers to an earlier work in which he had proposed the name Pachylémuriens to distinguish the *Adapis* group from recent lemurs.

Forsyth Major (1901, p. 135) concluded that "since *Adapis parisiensis* agrees in several important features with recent, and most of all with the Malagasy, Lemurs, it may be fairly taken to be in their ancestral line." In 1912 Dr. H. G. Stehlin added to his series of monographs on the mammals of the Swiss Eocene the section on *Adapis*, in which the morphology of the skull and dentition, and the systematic status of the subgenera, species and varieties of the genus, were treated in the most thorough and comprehensive manner, and the relations of the Adapidæ to other groups of primates, including the Notharctidæ, were fully discussed.

In America, the first discovered fossil primate, from the Eocene formation near Fort Bridger, Wyoming, was described by Leidy in 1869 under the name *Omomys carteri*. Leidy gave an excellent description of the lower teeth, but did not recognize the real affinities of the animal, stating that the specimen indicated an insectivorous mammal, probably belonging to the family of the hedgehogs (Leidy, 1869, p. 65).

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[1] The references cited are listed in the bibliography, pages 242, 243, below.

The next year, 1870, Leidy described another fragmentary fossil from the Bridger formation, consisting of the right ramus of a lower jaw, which he named *Notharctus tenebrosus*, the name indicating that the describer recognized that the animal was not a carnivore, in spite of its subcarnivorous appearance. He regarded it as a small extinct "pachyderm." It was the first to be discovered of the subfamily which is the subject of the present work.

The year following, 1871, Professor Marsh described another jaw fragment from the same formation, under the name *Limnotherium tyrannus*. He at first thought it was a small "pachyderm" distantly allied to a certain problematical fossil, the *Hyopsodus paulus* of Leidy, which Leidy had supposed to be related to the suilline family.

In 1872 Marsh described some other fragmentary remains, consisting of lower jaws and upper and lower teeth, basing upon them the genus and species *Thinolestes anceps*. Of this material he speaks as follows:

> The collections made by the Yale party include the remains of a number of small carnivorous mammals, which are apparently very unlike any hitherto known. In dentition, they somewhat resemble several extinct species, supposed to be of suilline affinities, but their carnivorous characters appear unmistakable. All apparently had the angle of the lower jaws inflected, and present other marsupial characters, although in general structure they are very different from any known form of that group. The teeth in the present genus are similar to those of *Limnotherium*, and the two genera are evidently nearly related... (p. 205).

Although he did not understand the relationships of these forms, he saw that they probably represented a distinct family and he accordingly proposed for their reception the family "Limnotheridæ," without formal definition.

In a brief paper dated August 7th, 1872, Professor Cope described a more complete lower jaw, likewise from the Bridger formation, containing most of the teeth of an animal which he named *Tomitherium rostratum*, but which was later referred to *Notharctus*. This jaw was associated with a humerus, a femur, the upper part of the forearm and other fragments. In this first description of *Tomitherium* Cope did not discuss its affinities.

In October, 1872, additional material, including portions of the limb bones, enabled Marsh to place correctly in the order Quadrumana (Primates) the puzzling animals for which he had erected the genera *Limnotherium* and *Thinolestes*. "Although these remains differ widely from all known forms of that group, their more important characters show that they should be placed with them. The genera *Limnotherium*, *Thinolestes*, and *Telmatolestes*, especially, have the principal parts of the skeleton much as in some of the *Lemurs*, the correspondence in many of the larger bones being very close. The anterior part of the lower jaw is similar to that of the Marmosets, but the angle is more produced downward, and much inflected. The teeth are more numerous than in any known Quadrumana. Some of the species have apparently forty teeth, arranged as follows: Incisors $\frac{2}{2}$, canines $\frac{1}{1}$, premolars and molars $\frac{7}{7}$...." (p. 406).

In the same month, October 1872, Cope described a minute jaw from the Bridger Eocene under the name *Anaptomorphus æmulus;* he compared its dental and other characters with those of *Simia* and *Homo*.

In 1873 (pp. 86–90) Leidy published a very full and accurate description of his type lower jaw of *Notharctus tenebrosus*. He speaks of it as a "small extinct pachyderm" and then says: "I at first viewed it as pertaining to a carnivorous animal, and thus referred it, but the anatomical relations of the specimen with those of remains of other animals which have been found in association with it have led me to view the jaw as having belonged to a pachyderm."

At the end of his description of the specimen we find this very noteworthy passage:

> In many respects the lower jaw of Notharctus resembles that of some of the existing American monkeys quite as much as it does that of any of the living pachyderms. Notharctus agrees with most of the American monkeys in the union of the rami of the jaw at the symphysis, in the small size of the condyle, in the crowded condition of the teeth, and in the number of incisors, canines and true molars, which are also nearly alike in constitution. Notharctus possesses one more premolar and the others have a pair of fangs. The resemblance is so close that but little change would be necessary to evolve from the jaw and teeth of Notharctus that of a modern monkey. The same condition which would lead to the suppression of a first premolar, in continuance would reduce the fangs of the other premolars to a single one. This change, with a concomitant shortening and increase of depth of the jaw, would give the characters of the living Cebus. A further reduction of a single premolar would give rise to the condition of the jaw in the Old World apes and man.

In 1873 (pp. 547–548) Cope gave the following interesting discussion of the relationship of his *Tomitherium rostratum,* in which he clearly recognized its primate affinities:

> The first impression derived from the appearance of the lower jaw and dentition, and from the humerus, is that of an ally of the coati, *Nasua.* The humerus, indeed, is almost a fac-simile of that of *Nasua,* the only difference being a slight outward direction of the axis of the head. The same bone resembles also that of many marsupials, but the flat ilium, elevated position of dental foramen, and absence of much inflection of the angle of the lower jaw, etc., render affinity with that group highly improbable. The length of the femur indicates that the knee was entirely free from the body, as in the *Quadrumana,* constituting a marked distinction from anything known in the *Carnivora,* including *Nasua.* The round head of the radius indicates a complete power of supination of the fore foot, and is different in form from that of *Carnivora,* including *Nasua;* and, finally, the distal end of the radius is still more different from that of *Nasua,* and resembles closely that of *Semnopithecus.*
>
> We have, then, an animal with a long thigh free from the body, a forefoot capable of complete pronation and supination, and a form of lower jaw and teeth quite similar to that of the lower monkeys. The form of the humerus and its relative length to the femur, are quite as in some of the lemurs. The most marked difference is seen in the increased number of teeth; but in this point it relates itself to the other *Quadrumana,* as the most ancient types of Carnivora and Ungulates do to the more modern: *e. g., Hyænodon* to the former, and *Palæosyops* to the latter. In its special dental characters it shows a close resemblance to small types of the Eocene, which have been regarded as low Perissodactyles, as *Hyopsodus,* &c.

By this time the affinities of *Notharctus* and its allies with the Quadrumana had been recognized but the misleading suggestion of remote relationship with the "pachyderms" still persisted. In 1876 Cope introduced another very confusing idea which was destined to becloud the real affinities of this group for a long time. Because of an erroneous and accidental association of certain creodont foot bones with the limb bones of *Pelycodus,* Cope inferred that these animals were related to the creodonts:

> It is apparent that the supposed lemurine *Mammalia* of the type of *Tomitherium,* which have the formula of the molar teeth 4–3, cannot be separated by ordinal distinction from the *Creodonta.* They differ from them, it is true, in their wholly tubercular molar teeth, but relate to them in this as the bears and *Procyonidæ* do to other *Carnivora.* I propose therefore to constitute these a distinct group or suborder, intermediate in position between the *Creodonta* and the *Prosimiæ,* under the name of the *Mesodonta.*
>
> I cannot find characters by which to distinguish this division from the Insectivora as an order (*op. cit.,* p. 88).

In the ensuing years, from 1872–1885 inclusive, Cope and Marsh described many other nominal species of Eocene primates, but little was done toward clearing up their precise relationships with modern forms, except that Cope recognized that his genus *Anaptomorphus* was a true lemuroid, referring it to the suborder Prosimiæ.

In 1884 Cope again stated his reasons for erecting the suborder Mesodonta, which he treated as a division of the order Insectivora. "The fragments of the skeletons of two species of. . . . *Pelycodus,* were found, which include numerous bones of the tarsus, and these are identical with corresponding parts in the *Creodonta* and different from those of the Lemuridæ" (p. 214). He then describes the astragalus, portions of the femur and of the humerus, as being closely similar to those of the Creodonta.

In 1885 (pp. 458–461) Cope gave a general review entitled "The Lemuroidea and Insectivora of the Eocene Period of North America," in which he summarized his ideas regarding the relationships of *Notharc-*

tus and the allied *Tomitherium.* At this time he still harbored the idea that the Lemuroidea, the Insectivora, and the Condylarthra were closely related, but he does not mention the group Mesodonta as such; he merely says "In the following pages I will not attempt to distinguish which of the genera are lemuroid and which are insectivorous, since the ungual phalanges are yet unknown. An exception must be made in the case of the genus *Pelycodus*, where a single compressed acute claw is known. This alone does not decide the question, since such a claw exists on the second toe of many Lemuroidea" (pp. 458–459). He referred *Notharctus, Tomitherium,* the European *Adapis,* and four other genera to the Adapidæ, and he speaks of the latter family as "the most primitive type, and the one most nearly allied to the Condylarthra, from which they were probably derived" (p. 459). He left *Pelycodus* "of uncertain reference to this family and order" (p. 460), on account of the supposed creodont character of the feet.

While the number of described species and genera of Eocene primates increased apace, so that by 1902 there were fifty-nine nominal species, very little more had been done in the way of clearing up the precise relationships of these early forms, owing to lack of well-preserved skulls and limbs.

In 1887, however, Dr. Schlosser, in his monographic review of the Apes, Lemurs, Bats, Insectivores, Marsupials, Creodonts and Carnivores of the European Tertiary, expressed a doubt as to the association of the above-mentioned foot material with *Pelycodus.* "The bones are almost too large for *Pelycodus,*" he says, "and I am almost persuaded to refer them to a Creodont" (p. 22, footnote 1). Accordingly, he placed *Pelycodus* along with *Hyopsodus* and *Microchœrus* in the Hyopsodidæ, while *Notharctus* with *Tomitherium* were referred to the Adapidæ, his conclusions being based very largely on the characters of the teeth. He also pointed out the resemblance of Leidy's *Omomys* to the European genus *Necrolemur,* which had been described by Filhol in 1873.

In 1892 Zittel referred all the above mentioned genera to a family "Pachylemuridæ" Filhol, of the suborder Prosimiæ (Lemuroidea), but the error in regard to the creodont characters of the feet of *Pelycodus* was still followed and *Pelycodus* was place next to *Hyopsodus* and *Microsyops.*

In 1899 Dr. W. D. Matthew in his "Provisional Classification of the Fresh Water Tertiary of the West" traced the geological succession of the American Eocene primates and reduced *Limnotherium* and *Tomitherium* to the rank of synonyms of *Notharctus.*

In 1902 Professor Osborn, whose "Revision of the American Eocene Primates" is the basis for all subsequent systematic work on this group, placed *Pelycodus* with *Notharctus* in the family Notharctidæ. This was partly a result of Dr. Matthew's observation, made independently from that of Schlosser, that the feet referred by Cope to *Pelycodus* probably belonged to a creodont. It was also due to the close similarity in dental structure between *Pelycodus* and *Notharctus,* which was revealed by Osborn's and Matthew's comparisons of the successive species of *Pelycodus* in the Lower Eocene and of *Notharctus* in the Middle Eocene. This was an important step toward clearing up the further relationships of these forms. While recognizing the close relationships of *Pelycodus* and *Notharctus,* Osborn defined *Pelycodus* as an earlier and more primitive stage with the upper molars more or less tritubercular and lacking the mesostyle. He regarded the Notharctidæ as a distinct family from the European Adapidæ, distinguished by characters of the dentition. He referred to the genus *Notharctus* Leidy the various species comprising the genera *Limnotherium* and *Thinolestes* Marsh, *Hipposyus* Leidy, and *Tomitherium* Cope, and traced the evolution of the dentition from *Pelycodus frugivorus* of the Lower Eocene to *Telmatolestes crassus* of the Upper Bridger.

Regarding the relationships of the Eocene Primates Professor Osborn said:

> It may be possible with the material now in hand to positively determine the relationships of some of these forms to the existing Anthropoidea or Lemuroidea; but it will require detailed investigation, which I am not able to undertake

> at present. [Footnote]: Dr. J. L. Wortman is now taking up these problems with the rich materials afforded by the Yale Museum Collections. I therefore omit phylogenetic questions here.
>
> Three suppositions are possible: First, that these Primates represent an ancient and generalized group (Mesodonta, Cope) ancestral to both Lemuroidea and Anthropoidea; second, that they include representatives of both Lemuroidea and Anthropoidea, contemporaneous and intermingled; third, that they belong exclusively to one or the other order. There are certain advantages in the revival of the term Mesodonta Cope, a suborder (anticipating the terms Pseudolemuroidea and Tarsii) which would bear somewhat the same relationship to the modern specialized Monkeys and Lemurs that the Condylarthra bear to the Ungulata and the Creodonta to the Carnivora. The serious difficulty with this view is the very considerable separation of these families (*op. cit.*, pp. 176–178).

Accordingly Osborn retained Cope's suborder Mesodonta, including the three families Hyopsodontidæ Schlosser, Notharctidæ Osborn, and Anaptomorphidæ Cope. The Hyopsodontidæ have since been removed by Wortman and by Matthew from the primates, and were referred at first to the Insectivora and finally to the Condylarthra (Matthew, 1914); the Anaptomorphidæ have since been shown to be allied to the existing *Tarsius*.

In the family Notharctidæ Osborn traced the changes in the dentition, beginning with *Pelycodus frugivorus* of the Lower Eocene and culminating in *Telmatolestes crassus* of the Upper Bridger.

In 1904 Dr. Wortman, who had studied the Marsh collection at Yale University, denied the validity of the order Mesodonta:

> As regards the validity of the group Mesodonta of Cope and its suggested revival by Osborn, very little need be said. From the most abundant skeletal materials of both *Adapis* and *Notharctus* we now know that the hallux was almost if not quite as opposable as in any living Primate. Cope's statement, therefore, of its lack of opposability in *Pelycodus*, a genus scarcely distinct from *Notharctus*, must with almost absolute certainty be erroneous. His technical definition of the group, moreover, as well as its dissociation from the Primates, I regard as utterly unsound, illogical, and in no wise warranted by the facts. I do not believe that any such natural group exists, and a revival of the name Mesodonta can result only in confusion. As we have already seen, there are types of very different affinities among these ancient Primates, and this fact in my judgment effectually precludes the possibility of their association into a single group (pp. 409–410).

With reference to the relationship of *Notharctus* and *Adapis* to modern types, Wortman argued as follows:

> What position, then, do *Adapis* and *Notharctus* occupy with reference to these natural groups already outlined? That they can not be consistently placed in the Lemuroidea is evident for the following reasons: The incisors do not exhibit any traces of lemurine modification, but, on the contrary, are like those in typical monkeys; the main entocarotid canal traverses the petro-tympanic chamber as in *Tarsius;* the lachrymal and malar do not unite on the anterior rim of the orbit; the digital lengths of the manus are not known with certainty; but in *Notharctus* the evidence is reasonably conclusive that the fourth was not longer than the third.
>
> On the other hand, their resemblance to the Paleopithecini [*Tarsius*, *Anaptomorphus* and their allies] is more marked. This is seen in the greatly inflated condition of the tympanic bullæ as well as in the outward and backward extension of the external alæ of the pterygoids. These forms differ from the Paleopithecini, however, in having a more reduced lachrymal, in the position of the external opening of the lachrymal canal on or near the rim of the orbit, in having a greater number of premolars, and in general in being larger and of more robust proportions. Thus, it will be seen that they occupy a position intermediate in many respects between the remaining Anthropoidea and the Paleopithecini. In the latter, there seems to have been a marked tendency toward precocious specialization in both tooth reduction and brain enlargement, which are curiously associated with retention of the primitive condition of the lachrymal. *Adapis* and *Notharctus*, on the other hand, exhibit advance in the reduction of the lachrymals, but retain the more generalized features of the dentition and brain enlargement. These are the essential differences between the two lines and mark out very distinctly the trend as well as the possibilities of their future development. It is in just such a group as that which includes *Adapis*, *Notharctus* and *Limnotherium*, that we must seek for the beginnings of the higher monkeys and apes which follow; and while these species, at present the only well-known types of the series, may not have been in the direct line of descent, they can not at the same time have been far removed from it (p. 410).

Here, then, was an important conclusion as to the relationships of *Notharctus* and its allies, namely, that they could not be referred to the Lemuroidea and that they belonged to a group in which we must seek the beginnings of the higher monkeys and apes. As already noted, Leidy in 1873 had observed the significant resemblances in the lower jaw and teeth between *Notharctus* and the higher primates; but Wortman independently arrived at similar conclusions.

In the same paper, Wortman adduced strong evidence for removing *Hyopsodus* from the primates to the Insectivora, and in so doing he freed the remaining primates from this confusing alliance.

In 1903 and 1904 expeditions from The American Museum of Natural History to the Bridger Basin, under the leadership of Mr. Walter Granger, discovered a well-preserved skull, several fragmentary skulls, and partial skeletons representing three or more species of *Notharctus*, which are described below.

In 1911 Schlosser, in Zittel's Grundzüge der Paläontologie, II Abt. (pp. 545–547), placed *Notharctus* and *Pelycodus* with the Adapidæ, and expressed the hypothesis that *Adapis* might be derived from *Pelycodus*.

In 1912 Stehlin (pp. 1287–1290), in the monograph referred to above, showed that the skull structure of *Adapis* was fundamentally the same as in lemurs. In discussing the affinities of *Adapis* he showed that the Notharctidæ and the Adapidæ were sharply distinguished by certain divergent trends in the evolution of the dentition. His conclusions regarding the mutual relationships of these families were expressed as follows (*op. cit.*, p. 1289):

> Ob Adapiden und Notharctiden überhaupt durch ein engeres Band als dasjenige welches alle Primaten verbindet, mit einander verbunden sind, halte ich für fraglich. Jedenfalls lässt sich die Berechtigung einer systematischen Categorie, welche die beiden Gruppen zusammenfasst, auf Grund unserer heutigen Kenntnisse nicht erweisen. Es erscheint vielmehr vorderhand ebensowohl möglich, dass dieselben schliesslich ihren Platz an ziemlich weit von einander entfernten Stellen des Primatensystems finden werden.

In 1913 (pp. 250–251) and again in 1915 (pp. 421–425) the present writer stated that, as regards the majority of its skeletal characters, *Notharctus* is closely allied to the lemurs, differing from modern lemurs in the retention of a smaller brain-case and in the avoidance of the peculiar lemurine specialization of the incisors and canines, but none the less a lemur in the chief structural features of the skull, of the vertebræ, and of the limbs.

In the paper of 1915, above cited, the family Notharctidæ was reduced to the rank of a subfamily of the Adapidæ, the resemblances in the skull and in the skeleton between *Notharctus* and *Adapis* being regarded as an indication of descent from common ancestral stock, which had subsequently split into two distinct subfamilies characterized by divergent tendencies in the evolution of the dentition. It was also suggested that these divergences in the dentition were correlated with differences in the excursion of the mandible in mastication, that of the Notharctinæ being more transverse, that of the Adapinæ more vertical.

In the same paper a new classification of the Lemuroidea was proposed in which the recent and extinct families were grouped under three series: Lemuriformes, Lorisiformes, Tarsiiformes. The Adapidæ (including the Adapinæ and the Notharctinæ) were placed under the Lemuriformes, along with the Lemuridæ, Indrisidæ, and Chiromyidæ. The classification was followed by an abstract of the chief provisional phylogenetic conclusions which had been reached up to that time by the writer in the course of the present studies.

In 1915 Dr. Matthew revised the Lower Eocene species of *Pelycodus* and *Notharctus*, described the new and very primitive species *Pelycodus ralstoni* and *Pelycodus trigonodus*, and gave accurate figures of the dentition of all the species of *Pelycodus* and of the Wind River species of *Notharctus*. After noting Dr. Stehlin's observations on the important distinctions in the character and evolutionary trend of the two groups (Adapidæ and Notharctidæ) he states (p. 434): "Dr. Gregory's morphologic studies of the skulls and skeletons of *Notharctus* and its relatives indicate, however, a somewhat nearer affinity to *Adapis*, so that the two may be considered as divergent phyla of a single family." He accordingly refers the American series to the family Adapidæ.

In 1916 Dr. Stehlin described additional species of *Adapis*, including the primitive *Adapis priscus*, and in discussing the relationship of the Adapidæ and the Notharctidæ emphasized the fact that even the oldest known species of *Pelycodus* had already entered the line of specialization leading to the later members of the Notharctidæ and therefore can not be considered as ancestral to the Adapidæ. The present writer's suggestion that the differences in the molars in the Adapidæ and Notharctidæ were probably correlated with differences in the excursion of the mandible was severely criticized.

In his discussion of the morphological and phylogenetic significance of the tympanic annulus and of the course of the internal carotid artery, which have been used by several authors as a basis for classification, Dr. Stehlin arrived at many other important conclusions which will be considered in the present studies; and the same is true of his discussion of the various parts of the dentition and of his final conclusions on the classification of the primates. The memoir closed with a comparison of the successive primate faunas of the Eocene of Europe and America and with a discussion of the evidence bearing on the possible centers of origin of the Eocene primates of Europe and of the Old World and New World groups.

In 1917 Granger and Gregory revised the numerous Bridger species of *Notharctus*, describing and figuring the types in the Peabody, American, and National Museums, as well as the types of the hitherto undescribed stages *Notharctus matthewi*, *N. osborni*, and *N. pugnax*. Marsh's *Telmalestes* was regarded as falling within the genus *Notharctus*. The sequence and diagnostic measurements of m_1–m_3 of all the species of *Pelycodus* and *Notharctus* were summarized in a table. A new genus, *Aphanolemur*, possibly a member of the Notharctinæ, was established.

To recapitulate, the principal steps in the progress of our knowledge of the Eocene Notharctidæ and their allies, up to the time of the publication of the present work, have been as follows:

1. The early descriptions of fragmentary specimens of jaws and teeth by Leidy, Marsh, and Cope.
2. The observation by Leidy that it would require only minor structural modifications to convert the jaw and teeth of *Notharctus* into those of a South American monkey.
3. The recognition of the primate affinities of "*Limnotherium*" and "*Tomitherium*" by Marsh and Cope, followed by Cope's unfortunate error in regard to the creodont-like structure of the feet of *Pelycodus*.
4. The detection and correction of this error by Schlosser, Matthew, and Osborn.
5. The reduction of *Limnotherium*, *Thinolestes*, *Hipposyus*, and *Tomitherium* to the rank of synonyms of *Notharctus* by Osborn and Matthew.
6. The tracing out of the stratigraphic succession and relationships of the species, ranging from the minute *Pelycodus ralstoni* of the Lower Eocene to the large *Telmatolestes crassus* of the upper Middle Eocene, by Osborn, Matthew, and later by Granger and Gregory.
7. The recognition of the non-primate affinities of *Hyopsodus* and the removal of *Hyopsodus* to the neighborhood of the Insectivora (Wortman), and finally to the Condylarthra (Matthew). This disentanglement clears the way for the recognition of the true affinities of the Notharctidæ.
8. The fluctuation in opinion as to the union or separateness of the Notharctidæ and the Adapidæ, culminating in Stehlin's demonstration that the two families followed different lines of dental evolution and in the writer's conclusion that they may nevertheless be regarded as divergent subfamilies of a single family.

9. Wortman's suggestion that the Adapidæ, including *Notharctus*, stand near to the beginnings of the monkeys and apes, especially the New World monkeys.

10. The discovery of a well-preserved skull and of partial skeletons of *Notharctus*, which, as shown in the present work, exhibit very fully the primitive lemuroid structure of the skull and skeleton.

11. The demonstration by Stehlin of the great variety and wide differentiation of the primates of the European Eocene; his exposition of the complexity and difficult nature of the problem of the relationship of the Eocene families with each other; his conclusions that none of the Eocene families can be positively connected with modern families and that the final consideration of the problem of the place of origin of the order had better be deferred until the fossil records of the Eocene of Asia become available.

THE LIMBS OF *NOTHARCTUS*; A COMPARATIVE STUDY

The general conclusions from the following study of the backbone and limbs of *Notharctus* are stated below (p. 221), but it may also be noted here that this type of skeleton has been preserved with comparatively minor changes in some of the modern lemurs, especially *Lemur*, *Lepilemur*, and *Propithecus*, the chief difference being that these animals have longer hands and feet and longer limb bones. The foot and limb bones of *Adapis*, so far as known, conform to the same general lemuriform type and in many respects are even closer to those of existing lemurs.

In the following description the limbs and vertebræ of *Notharctus* are compared, for the sake of brevity, chiefly with those of *Lemur varius*, *Lemur mongoz*, *Propithecus*, *Cebus*, and *Cercopithecus*, but with frequent reference to other forms. These comparisons, although usually brief, establish the fact that on the whole, in the characters of the vertebræ, pectoral and pelvic arches, and limbs, *Notharctus* stands much closer to the above named lemurs than to the representatives of any other group of primates; also that the South American primates are structurally nearer to *Notharctus* than are the Old World primates.

Every limb bone of *Notharctus* is fundamentally similar in all its parts and processes to the corresponding elements in modern lemurs, the differences being solely in the degree of development of homologous parts. Consequently much definite knowledge of the musculature and limb movements of one of the most primitive known primates can be gained by comparison with modern lemurs, the only necessary assumption being that in rather closely related animals homologous processes and crests are usually connected with homologous muscles. With this purpose in view the limb muscles of a recent *Lemur mongoz* have been carefully dissected and constant use has been made of the beautiful illustrations of the musculature of the indrisine lemurs in Milne Edwards' memoir on the lemurs of Madagascar. (Grandidier and Edwards, 1875).

The skeleton material of *Notharctus* described below comes chiefly from the Lower Bridger formation (Horizon B) of Wyoming. In the principal specimen (Amer. Mus. No. 11474), the paratype of *Notharctus osborni*, all those parts of the backbone, girdles, and limbs are preserved which appear in darker color in Plate XXIII. The remaining parts, shown in light gray color, were restored by Mr. Albert Thomson chiefly from modern lemurs.

A second specimen, Amer. Mus. No. 11478 (Plate XXIV), although very imperfect, supplied some important details which were missing in the first. It was associated with parts of the dentition which were determined as *N. tyrannus* (Marsh). It is somewhat larger than the first skeleton, as shown below, but otherwise the differences between them are trivial.

Parts of skeletons of other members of the subfamily suffice to show that, as in the dentition, there was a gradual increase in size as we pass from the older species of *Pelycodus* near the base of the Lower Eocene to the large *Notharctus crassus* at the summit of the Middle Eocene.

Pectoral Limb

Scapula

Text Fig. 1

This element is represented by the lower part of the blade, the glenoid fossa, and the proximal part of the coracoid process (Fig. 1) of *Notharctus osborni*. By far the nearest resemblances of the part preserved are with the lemurs of Madagascar.

The glenoid fossa, as seen from below, is like a slender pear, only moderately wide at the base. A very similar form of glenoid is seen in a certain specimen of *Lemur mongoz*. In *Cebus*, *Alouatta*, and *Hapale* the glenoid is relatively wider and flatter on the posterior border. The long diameter of the glenoid fossa is 11.3 mm. as compared with 11.5 in a *Lemur mongoz*.

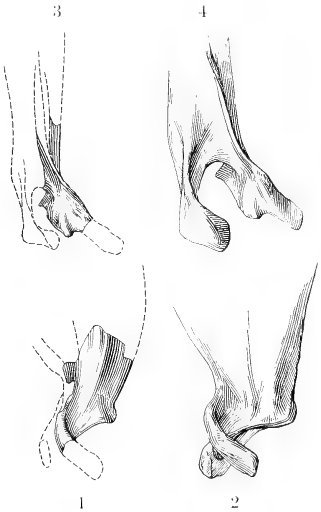

Fig. 1. Comparative figures: lower part of right scapula of *Notharctus* and *Lemur*. Natural size.

1. *Notharctus osborni*. Amer. Mus. No. 11474. Inner side.
2. *Lemur varius*. Amer. Mus. No. 18040. Inner side.
3, 4. Same specimens, front view.

The coracoid process, so far as preserved, closely resembles that of *Lepilemur*. As in that form there was only a slight tuberosity on the front upper border of the coracoid for the coraco-clavicular ligament, whereas in *Cebus*, *Alouatta*, and *Hapale* this tuberosity is very large and prominent.

Immediately above the axillary border of the glenoid is a slight triangular roughening for the tendon of the scapular head of the triceps. This roughening is similar in form to that in a certain specimen of *Lemur varius* (Amer. Mus. No. 18040).

The axillary border, so far as preserved, was not sharply inflected so as to form two sharp ridges with a flat intervening fossa for the tendon of the teres minor, as is the case in *Cebus*, *Alouatta*, and *Hapale*. In *Notharctus*, on the other hand, the merest beginning of this inflection may be indicated in the form of a low swelling on the subscapular surface; there is also a slight swelling of the outer surface of the border, indicating the lower end of the strip for the teres minor. Quite similar details were observed in *Propithecus coquerelli*. Accordingly it can be stated that, at least at the lower end, there was no sharp medially directed ridge on the subscapular surface of the scapula, as there is in *Cebus*, *Alouatta*, and *Hapale;* and that here again the nearest observed resemblances are found in a specimen of *Lemur varius* and in *Propithecus*.

The subscapular surface, so far as preserved, is perhaps nearest to that of *Propithecus*. That part of the surface which was immediately beneath the lower end of the spine is indicated by a gentle concavity flanked posteriorly by a low round eminence, much as in *Lemur*, *Lepilemur*, and *Propithecus*. In *Cebus*, *Alouatta*, and *Hapale*, on the other hand, the subscapular surface presents a widely different appearance due partly to the presence of the sharp medial crest on the axillary border already noted.

So far as indicated by the specimen, the lower end of the pre- and postspinous fossæ were also lemuriform in type.

Clavicle

Plate XXIII

The medial half of the left clavicle is preserved in the type of *N. osborni* (Amer. Mus. No. 11474). It is very similar to that of *Lemur mongoz* but has a stouter, less compressed shaft and a less expanded facet for the sternum. In the Lemuridæ and Indrisidæ the clavicle is but gently curved; in all the Platyrrhini and Catarrhini examined it is more or less S-shaped and is capable of more varied movements, as in brachiation.

Humerus

Plates XXVII, XXVIII; Text Figs. 6, 7, 8

This element is represented by both humeri of *N. osborni*, No. 11474, and by several other humeri belonging to allied species. An extended comparison of the humerus of *Notharctus* shows that it has the following primitive mammalian characters in contrast with the specialized primate characters of anthropoid apes and man:

	Notharctus	*Anthropoid Apes and Man*
1. Shaft, Relative Length	Short	Very long
2. Delto-pectoral Crest	Prominent	Reduced
3. Head	Of moderate size	Large and spherical
4. Inclination and Direction of Head	Chiefly toward the back of the shaft	Largely toward the inner side of the shaft
5. Contour of Bone in Side View	Gently S-shaped	Straight
6. Supinator Crest	Very prominent, extending well up the shaft to a point opposite the lower end of the delto-pectoral ridge	Reduced, ending below middle of shaft
7. Entepicondylar Foramen	Present, very large	Absent
8. Capitellum	Ball-like in center, produced externally toward very inconspicuous external epicondyle	Truncate externally, sharply differentiated from prominent external epicondyle

		Notharctus	*Anthropoid Apes and Man*
9.	Trochlea	Not grooved	More or less deeply grooved with prominent external and internal lips
10.	Olecranal Fossa	Very shallow	Very deep
11.	Spirally Warped Surface on Shaft, for attachment of brachialis anticus muscle	Conspicuous	Inconspicuous
12	Vertically Extended Eminence, for the attachment of the tendon of the teres major on the inner side of the shaft opposite the delto-pectoral crest	Conspicuous	Inconspicuous
13.	Lesser Tuberosity as seen from above	Directed inward and backward	Turned sharply forward
14.	Bicipital Groove	Shallow, wide	Narrow, deep

Fig. 2. *Lemur* sp. Muscles of the chest and throat. After Cuvier and Laurillard.

4 platysma myoides
x sternohyoid
b sterno-cleido-mastoid
a trapezius
6 scalenus anticus

h subclavius
k deltoid
j pectoralis major
j^1, j^2 pectoralis minor

Fig. 3. *Lemur* sp. Superficial muscles of the neck, back and arm. After Cuvier and Laurillard.

$a + a^1$, a^2	trapezius	r, r^1	biceps
d	omotrachelian	v	supinator longus (brachio-radialis)
k, k^1	deltoid	δ	extensor carpi radialis longior
m	infraspinatus	δ^1	extensor carpi radialis brevior
o	teres major	ι	extensor ossis metacarpi pollicis
i	latissimus dorsi	ϵ	extensor communis
t, t^1, t^3	triceps	ρ	adductor pollicis

These contrasts, almost without exception, are correlated with the wide differences in the pose, habitual movements, and musculature of the fore limb, between *Notharctus*, which was a bent-limbed, arboreal quadruped, leaping about on top of the branches, and the Old World primates and man, which are primarily a long-armed, brachiating stock, swinging the arms freely in all directions.

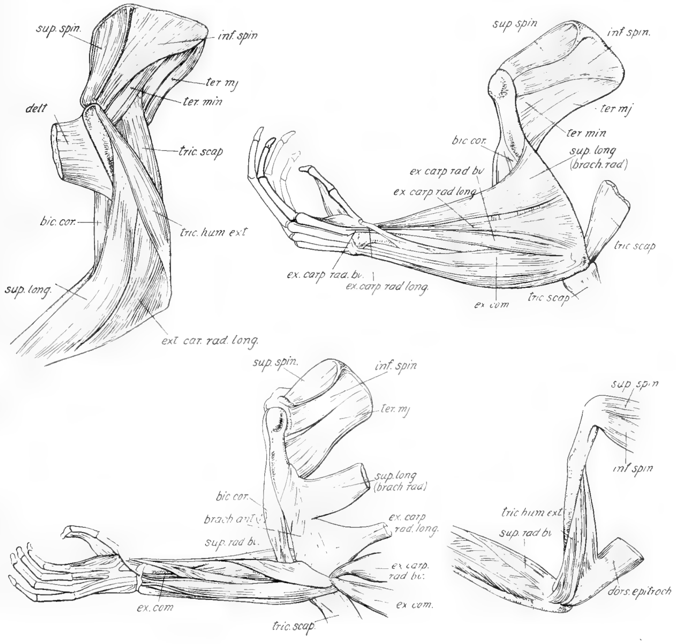

Fig. 4. Arm muscles of *Propithecus diadema*. After Milne Edwards.

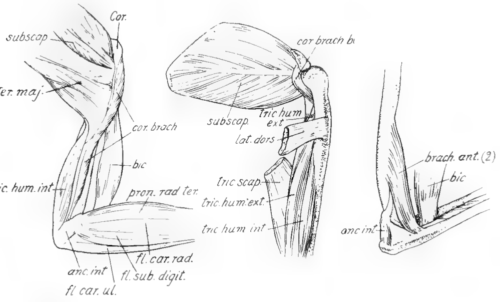

Fig. 5. Arm muscles of *Propithecus diadema* (Continued). After Milne Edwards.

The prominence and extension of the supinator crest of *Notharctus*, for instance, shows that the supinator longus muscle was extended well up the arm, as it is generally in primitive mammals. (See Cuvier and Laurillard's dissections of marsupials, rodents, carnivores, etc.) Milne Edwards (*op. cit.*,

p. 15) has recorded this condition in the indrisine lemurs and has noted that, although it adds greatly to the power to flex the forearm, it makes it impossible to extend the lower arm fully. In the monkeys, on the other hand, says Milne Edwards, the supinator longus much resembles that of man; it is inserted only on the lower part of the humerus, is much more delicate than that of the Indrisinæ, and does not hinder the full extension of the forearm.

That the forearms of *Notharctus* were incapable of extreme extension is also in agreement with the fact that the olecranal fossa is very shallow while in the higher primates, which fully extend the forearm and thus force the coranoid process of the ulna into the back of the upper arm, the olecranal fossa is much deeper.

In correlation with the bent posture of the arms is the fact that the delto-pectoral crest is much more prominent than it is in the higher primates. The "Planches de Myologie" of Cuvier and Laurillard show that in many of the lower mammals the deltoid extends further down the arm than in the higher primates.

A very significant primitive character of the humerus of *Notharctus* is the fact that the moderate-sized head is inclined chiefly toward the back of the shaft, as it is in many primitive mammals with bent limbs, while in the anthropoid apes and man the head has become greatly enlarged on the inner side and inclined toward the inner side of the shaft, because the habits of sitting upright and of walking either upright or in a stooping position causes the elbows to be turned outward and the humerus to be rotated inward so that when the arms are swinging freely the scapula articulates largely with the internal part of the head of the humerus, the rest being covered by the capsule.

The same primitive quadrupedal position of the humerus in *Notharctus* permits the lesser tuberosity to be directed chiefly backward and upward, while in man and anthropoids the frequent outward turning of the elbows and inward rotation of the head of the humerus has pushed the lesser tuberosity around on to the front face of the humerus so that it is finally only separated from the greater tuberosity by a narrow bicipital groove.

In spite of all these primitive mammalian characters the humerus of *Notharctus* still exhibits a number of DIAGNOSTIC PRIMATE CHARACTERS. These may be conveniently exhibited by successive comparisons of the humerus of *Notharctus* with those of various Paleocene, Eocene, and other primitive mammals.

MARSUPIALS. The humerus of *Didelphis* may be taken as the primary type for the Polyprotodontia, that of *Phalangista* as the primary type for the Diprotodontia. Both resemble that of *Notharctus* in possessing a number of primitive characters, such as an entepicondylar foramen, well-developed supinator crest, etc., but both differ from it in several points, especially the following (Plate XXVII):

(1) The supinator crest is more or less angulate at the upper end.

(2) The delto-pectoral crest is more elevated at the lower end and is continued further down the shaft.

(3) The humerus as a whole is shorter and wider with larger proximal end.

Very probably these are PRIMITIVE MARSUPIAL CHARACTERS of the humerus and they may represent a very ancient and primitive arboreal stage following the therapsid stage of mammalian ascent.

CREODONTS. Many creodont humeri have been compared with that of *Notharctus*. They possess all the primitive mammalian characters enumerated above but they differ from *Notharctus* in the following:

(1) The massive flattened deltoid crest terminates below in a prominent deltoid eminence which is wanting in *Notharctus*.

(2) The posteroexternal limit of the deltoid plane is a prominent ridge, while in *Notharctus* no such ridge is present.

(3) The capitellum is large and truncate externally and usually there is not even the beginning of an external lip on the trochlea.

(4) The shaft of the humerus below the deltoid eminence is sharply triangular while in *Notharctus* it is rounder in front.

(5) The entocondylar process is much larger, this indicating great strength and size of the pronator and flexor muscles, as is usually the case in mammals with stout claws.

In all these characters in which *Notharctus* differs from creodonts it agrees with existing lemurs. These characters are all connected with advanced arboreal habits in contrast with the terrestrial habits and unguiculate structure of the most primitive creodonts.

Among recent carnivores, the arboreal Procyonidæ show the nearest approach to *Notharctus* in the general form of the humerus. They differ, however, in many details, especially:

(1) The deltoid crest is much larger and has a spirally warped outer plane, recalling that of other carnivores.

(2) The entocondyle is much larger, this probably implying stouter flexor and pronator muscles as in animals with stout claws.

(3) The capitellum is less ball-like, this implying less developed power of supinating the radius.

In brief, the Procyonidæ may very well be secondarily arboreal derivatives of a *Cynodictis*-like type, while *Notharctus* shows a deeper and more long continued impress of arboreal habits.

TALIGRADA. The humeri of the Paleocene Taligrada *Ectoconus* and *Pantolambda* have all the primitive characters listed above in common with the humerus of *Notharctus*. All their crests and processes, however, are wider and more robust. Their triceps, brachialis anticus, supinator longus, and other arm muscles were of great width and strength. The great size and robustness of the entocondylar process is only exceeded by *Orycteropus* and *Taxidea*, which have very powerful pronator and flexor muscles in connection with earth-scratching habits. The forearm was normally bent approximately at a right angle to the humerus and the degree of maximum extension of the forearm was very limited. The forearm could not be completely supinated. They must have pushed their way through a very resistant medium of some sort, possibly the matted undergrowth of forests (Herbert Lang). Their humerus resembles that of the ground-living *Solenodon* rather than that of the fully arboreal *Notharctus*. (Plate XXVII.)

EDENTATA. Probably the most primitive known edentate is *Palæanodon ignavus* Matthew (1918) from the Lower Eocene. The short, wide humerus of this animal, while sharing many primitive characters, contrasts widely with that of *Notharctus* in its advanced fossorial adaptations. The head of the humerus is an elongate oval, directed backward and permitting free anteroposterior movements. The delto-pectoral crest is much enlarged, flattened and somewhat V-shaped below. The entocondylar process is larger. This is fairly close to the modern armadillo type. At the other extreme of the edentates, the sloths exhibit a somewhat primate-like humerus with an extremely long shaft and degenerate crests and processes but with some curiously reversed characters, associated with the peculiar mode of progression.

RODENTIA. The humerus of the very primitive Eocene rodent *Paramys* is much nearer to that of *Notharctus* than any of those described above and the muscle insertions must have been very similar (Plate XXVII). The chief differences are as follows:

(1) In *Paramys* the delto-pectoral crest is much higher, ending below in a prominent eminence.

(2) The shaft as a whole is straighter, less S-shaped.

(3) The capitellum is less ball-like and is entirely confluent internally with the trochlea.

(4) The entocondylar process is considerably stouter, this implying powerful pronators and flexors.

This indicates that *Paramys* was less completely arboreal in its adaptations than was *Notharctus*. *Paramys* was provided with stout claws, operated by the powerful flexor muscles, which it used in climbing. The humeri of later simplicidentate rodents diverge into easily recognizable arboreal, fossorial-natatorial, fossorial, cursorial, and other types. But no rodent humerus could be mistaken for that of any primate, if closely examined.

INSECTIVORA (LIPOTYPHLA). Among existing Insectivora, *Solenodon* has perhaps the most primitive type of humerus. It is indeed of extremely primitive semifossorial, semiambulatory type, similar to that of the most ancient Carnivora. The head is elongate anteroposteriorly and there is a prominent warped deltoid plane, ending below in a prominent V-shaped eminence. The bicipital groove looks inward rather than forward. The entocondylar process is large; the supinator crest, while well developed, does not flare out at the upper end. From this primitive type the humeri of other Liptotyphla may readily be derived, chiefly by reduction of the crests, but in some phyla by new specializations, as in the Talpidæ.

MENOTYPHLA. I refer to this group the family Plesiadapidæ, on the basis of skeletal material of *Nothodectes gidleyi* Matthew (1917) which the describer has generously placed in my hands for examination.

The humerus (Plate XXVII), while more like that of *Notharctus* than any of those described above, has the following special characters:

(1) The delto-pectoral crest is very thin and acutely V-shaped, as seen from the outer side, ending below in a prominent pointed tip.

(2) The supinator crest is not so large as it is in *Notharctus* and does not extend up to the level of the deltoid tip.

(3) The trochlea is relatively larger and more extended vertically.

(4) The tuberosity for the teres major, on the inner side of the shaft, is much larger and more sharply defined.

The humerus of the existing *Ptilocercus* might readily be derived from the *Nothodectes* type by the lengthening of the shaft and slight reduction of the supinator crest. The *Ptilocercus* humerus still retains much that is reminiscent of a *Nothodectes*-like type, but in *Tupaia* the crests are further reduced; in *Rhynchocyon* a cursorial type of humerus, with a prominent greater tuberosity and hinge-like distal joint, is finally evolved.

The humerus of *Nothodectes* thus gives evidence, which is strengthened by that from many other parts of the skeleton, for the following conclusions:

(1) The Plesiadapidæ are Menotyphla, not Lemuroidea.

(2) The Menotyphla are the nearest known relatives of the primates.

(3) They represent the specialized descendants of a Cretaceous pre-primate, unguiculate stock, less perfectly adapted for perching on the branches than were the Eocene Lemuroidea.

PRIMATES. The foregoing comparison of the types of humeri in various primitive mammals also adds some evidence for the following conclusions, which were long since arrived at from other evidence.

(1) The Mesozoic placental forerunners of the Creodonta, Taligrada, Insectivora, etc., were ungui-

culate, pentadactyl mammals with short hands and feet. They had powerful pronators, flexors, supinators, extensors, brachialis anticus, pectoralis, deltoid, and scapular muscles.

(2) They could probably climb, dig, run, and swim, but not in the specialized ways of their remote descendants.

(3) Those which were ancestral to the creodonts and certain other Paleocene orders were probably small animals, perhaps not as large as a common opossum.

(4) The Mesozoic ancestors of the primates were among the very small arboreal forms and were of insectivorous-frugivorous habits. Even as late as the Lower Eocene, after the primitive primates had become differentiated into several families, they were still of very small size; but in one phylum, the Notharctinæ, they increased rapidly in size in ascending levels, finally becoming about as large as an *Indris*.

(5) The ancestral stock, represented to some extent by the Menotyphla, remained small and indifferently adapted to arboreal life.

(6) The progressive lemuroid stock acquired primitive primate characters, which all relate, in the locomotor apparatus, to adaptations for perching and leaping among the branches.

The humerus of *Notharctus* differs from those of all other primitive mammals and resembles those of the Eocene Adapinæ and some modern lemurs in the following characters (Plate XXVII; Figs. 6, 7):

(1) The delto-pectoral crest is not V-shaped and does not end below in a raised pointed tip. It is, on the contrary, a low delicate crest with a thin edge, which runs down gently into the more or less flattened cylindrical shaft.

(2) On the inner side of the delto-pectoral crest opposite the tuberosity for the teres major is a more or less vertically extended, shallow, oval fossa for the tendon of the latissimus dorsi muscle. (Plate XXVIII.)

(3) The supinator crest extends much further up the shaft than do those of the Menotyphla and Eocene Rodentia and it is relatively wider transversely than those of the Creodonta. It is not curved so sharply backward as are those of the primitive Taligrada, Edentata, Rodentia, Insectivora. (Plate XXVII.)

(4) The great tuberosity is relatively smaller than it is in primitive creodonts, taligrades, edentates, rodents, insectivores, and Menotyphla. (Plate XXVII.)

(5) The entocondylar process is relatively smaller than that of other Paleocene and Eocene mammals, this implying that the pronator radii teres, and flexor muscles were less robust than in primitive unguiculates. This is doubtless correlated with the presence of nails rather than claws. (Plate XXVII; Fig. 5.)

(6) The trochlea humeri is provided with a low external lip which tends to separate it from the capitellum, whereas in other Eocene mammals, except the Menotyphla, capitellum and trochlea are entirely confluent. This difference is correlated with differences in the normal pose of the radius and ulna. In the other Eocene mammals the forearm is habitually pronated so that the low coronoid process of the ulna articulates with the inner lip of the trochlea. In such forms the head of the radius is extended transversely, the capitellum is less ball-like, and there is no outer lip on the trochlea. In the primates, on the other hand, in consequence of their perching and climbing habits, the arm is more often partly supinated. This rotates the shaft of the ulna, so that the large coronoid process now presses against the outer part of the trochlea; hence, an outer lip is developed on the trochlea while the inner lip is much lower than in animals with

Fig. 6

Fig. 7

> strongly pronated forearms. So too, the head of the radius in primates becomes circular, so that it can the more easily rotate within the orbicular ligament, and it is the head of the radius which articulates with the groove that now separates the outer lip of the trochlea from the ball-like capitellum.[1] (Plate XXVII.)

All these considerations are in harmony with other evidence to the effect that in *Notharctus* the forearm was habitually partly supinated, as a part of the limb-grasping series of adaptations.

Special resemblances between the humeri of *Notharctus* and a certain humerus referred to *Adapis magnus* by Filhol are as follows (Figs. 6, 7):

(1) In both types the supinator crest extends much further up the shaft than it does in modern lemurs.
(2) The middle part of the shaft is less elongate than in most lemurs.
(3) The entocondylar process extends further inward than in modern lemurs.
(4) The capitellum is more ball-like and the outer lip of the trochlea less defined.
(5) The tuberosity for the teres major is more conspicuous.

But a certain humerus catalogued as "*Adapis parisiensis*" (Amer. Mus. No. 10018) has a straighter, less flaring supinator crest, more like that of *Propithecus;* and in the specimen of *Adapis magnus* (?) figured by Filhol the middle of the shaft is approaching the cylindrical lemuriform type. Thus these humeri referred to *Adapis* are a stage nearer to the lemuriform type than are those of *Notharctus.*

Among recent Lemuridæ, *Lepilemur* has a humerus (Fig. 8) which is very like that of *Notharctus* in many respects, but differs in the following:

(1) The shaft as a whole is straighter.
(2) The edge of the pectoral crest is curled over and the crest projects more prominently at the lower end.
(3) The head is an elongate oval.
(4) The tuberosity for the teres major is further up the shaft, nearer the prominent lesser tuberosity.
(5) The mid-shaft is longer and rounder in section.
(6) The supinator crest flares less, is straighter, and does not extend so far up the shaft.
(7) The trochlea is smaller, has a smaller inner lip and a larger outer lip, this implying a greater degree of supination.
(8) The entocondyle is directed slightly upward instead of straight inward.

Characters (1), (2), (4), (5) and (6) also hold good in *Lemur varius* and *L. mongoz.* In these, however, the head is larger, the trochlea has two nearly parallel lips and extends further around on the back of the shaft, the olecranal fossa being deep; this implies free supination and extension. The entocondyle is shorter and thicker (Figs. 6, 7).

Fig. 6. Comparative series: humeri of *Notharctus*, *Adapis*, *Lemur.* Back view. Natural size.

1. *Notharctus osborni.* Amer. Mus. No. 11474.
2. "*Adapis parisiensis.*" After Filhol.
3. *Lemur mongoz.* Amer. Mus. No. 22886.

Fig. 7. Comparative series: humeri of *Notharctus* (1), *Adapis* (2, 3), *Lemur* (4), *Cebus* (5), *Hapale* (6), *Macacus* (7). Front view. Natural size, except Nos. 6, 7.

1. *Notharctus osborni.* Amer. Mus. No. 11474. × $\frac{1}{1}$.
2. "*Adapis parisiensis.*" After Filhol. × 1.
3. "*Adapis parisiensis.*" Amer. Mus. No. 10018. × $\frac{1}{1}$.
4. *Lemur mongoz.* Amer. Mus. No. 22886. × ^{1}.
5. *Cebus hypoleucus.* Amer. Mus. No. 14016. × $\frac{1}{1}$.
6. *Hapale* sp. Amer. Mus. No. 17574. × $\frac{3}{2}$.
7. *Macacus nemestrinus.* Amer. Mus. No. 14012. × $\frac{2}{3}$.

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[1] These opposite lines of specialization are well shown by comparing the distal end of the humerus of a sloth with that of a dog. The former indicates extreme supination, the latter extreme pronation.

In *Microcebus*, of the same family, which has very delicate limbs, the supinator crest flares backward somewhat as in *Tarsius*, but otherwise the humerus is like that of other lemurs.

The humerus of *Propithecus* is more specialized than that of *Notharctus* in the following characters:

(1) The shaft is elongate.

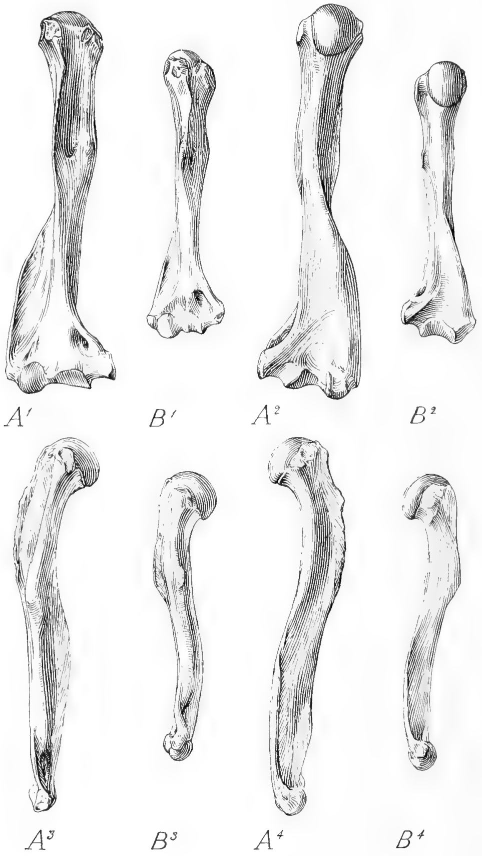

Fig. 8. Comparative series: right humeri of *Notharctus* and *Lepilemur*. Natural size.

A^1. *Notharctus osborni*. Amer. Mus. No. 11474. Front view.
B^1. *Lepilemur mustelinus*. Amer. Mus. No. 31251. Front view.
A^2, B^2. Back view of same specimens.
A^3, B^3. Inner side view.
A^4, B^4. Outer side view.

(2) The deltoid crest is small and limited to the upper third of the shaft; it has a curled-over pectoral edge, protruding along the middle portion of the crest, above the fossa for the tendon of the latissimus.

(3) The shaft is flattened in its mid-section.

(4) The supinator crest is less flaring and narrower transversely.

(5) The inner lip of the trochlea is abortive, as the forearm is habitually supinated.

But these specializations cannot conceal the very evident relationship of structural ancestor and descendant.

The humerus of *Chiromys* emphasizes certain features already foreshadowed in *Notharctus* and is also allied to the *Propithecus* type, but more primitive. The supinator crest ends above in an angulate corner. The outer lip of the trochlea is well developed but not the inner lip, this indicating that the forearm could be supinated further than it could be in *Notharctus*.[1]

In *Galago crassicaudata* the humerus is obviously derived from a more primitive *Notharctus*-like type by slight changes in proportions. The head is large, the delto-pectoral crest has a fairly prominent eminence, the small entocondyle is directed partly backward. In the delicate *Galago alleni* the humerus is elongate, with narrow upper end but sharply marked low crests. In the potto (*Perodicticus potto*) the great tuberosity is low and the deltoid plane much flattened. In *Loris* the humerus is long with abortive crest. It will be recalled that all the members of this family are good climbers but that the galagos are exceedingly active while the lorises are sluggish, clinging tightly to the branches.

In *Tarsius* the humerus is rather different from any of those hitherto noted. The supinator crest flares backward, abolishing the depression which in *Notharctus* lies between the edge of the supinator crest and the shaft. The bridge over the entepicondylar foramen is nearly vertical (i. e., more nearly parallel to the shaft than is the case in *Notharctus*). The entocondyle is delicate and slightly curved downward; the tuberosity for the teres major is near the upper end of the shaft. There is no distinct round pit for the tendon of the teres minor; the deltoid plane is fairly well indicated. Comparison of the humerus of *Tarsius* with those of *Nothodectes* and *Notharctus* shows that in the upper end of the humerus *Tarsius* is more like *Notharctus* while the flaring supinator crest on the lower half is a point of resemblance with *Nothodectes*.

Comparison of the humerus of *Notharctus* with those of *Hapale* (Fig. 7.6), *Callithrix*, *Lagothrix*, *Alouatta*, *Chrysothrix*, and *Cebus* (Fig. 7.5) shows that in these platyrrhine genera the humerus has progressed away beyond the primitive *Notharctus*-like stage, in the direction of the higher primates. *Cebus*, *Chrysothrix*, *Callithrix* retain the entepicondylar foramen; while in the Hapalidæ it is variable and in *Alouatta* and *Lagothrix* it is absent, at least in the few specimens at hand. The humerus of *Alouatta*, a typical platyrrhine, differs from that of *Notharctus* as follows:

(1) The shaft is long and straight.
(2) There is a long, very flat deltoid plane, lateral to the very low and barely distinct delto-pectoral ridge.
(3) The bicipital groove is but faintly indicated.
(4) The tuberosity for the teres major is not defined.
(5) The supinator crest is barely indicated and is long and straight.
(6) The shaft below the delto-pectoral ridge becomes flattened.
(7) The entocondyle is massive and is directed partly downward.
(8) The entepicondylar foramen is entirely absent.
(9) The inner lip of the trochlea is sharply pronounced and there is no outer lip.
(10) The capitellum is larger.
(11) The trochlea extends further around on to the dorso-posterior side and the olecranal fossa is deeper.

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[1] The humerus lends no support to Dr. Wortman's view (1903, p. 411) that *Chiromys* represents a separate grand division of the Primates coördinate with the Lemuroidea and the Anthropoidea.

(12) The head is larger and somewhat more spherical.

(13) The greater and lesser tuberosities are nearer together and the bicipital groove is narrower at top.

Thus the humerus of *Alouatta* may be regarded as in many respects a degenerate and de-differentiated derivative of that of *Notharctus*. These characters in general indicate more ape-like ways of using the arms, fuller extension, freer movements at the shoulder, stronger and more frequent pronation of the forearm, greater strength in flexing the carpus.

In *Cebus* and *Chrysothrix* the humerus is less highly specialized, since a well-developed entepicondylar foramen, an outer lip of the trochlea, and a better developed supinator crest are retained; but here a characteristic ape-like specialization is the gentle bending of the upper part of the shaft toward the inner border of the humerus. In the Hapalidæ the deltoid plane is flattened and more or less V-shaped and the humerus as a whole could easily be derived from the *Notharctus* type, but close affinity with the *Cebus* type is evident.

Hence it is quite obvious that with regard to the form of the humerus the Platyrrhini are not as near to *Notharctus* as are the lemuriform genera, especially *Adapis*, *Lepilemur*, *Lemur*, *Chiromys*, and *Propithecus*.

The catarrhine types of humerus (including those of Old World monkeys, apes, and man) have already been compared with the *Notharctus* type (p. 64 above). They show rather close resemblances to the platyrrhine types, but usually have a better developed trochlea with prominent inner and outer lips. There is no trace of the entepicondylar foramen and the supinator crest is inconspicuous. The deltoid plane is accented and so is the bicipital groove. The head is more or less spherical. Brachiating[1] and the habit of sitting upright, culminating in the anthropoids, are chiefly responsible for these differences. (Plate XXVII; Fig. 7.7, *Cebus*, *Pan*.)

This series of comparisons makes clear the morphological importance of the very primitive primate humerus of *Notharctus*, which, while retaining many primitive mammalian characters, is well differentiated from the humeral types of marsupials, creodonts, carnivores, taligrades, edentates, rodents, insectivores and others. Its nearest structural ally outside of the primates is *Nothodectes*, which is now referred to the Menotyphla. Within the order Primates the humerus of *Notharctus* again is extremely primitive, and fitted to give rise in turn to the humeral types of the Lemuriformes, Lorisiformes, Tarsiiformes, Platyrrhini and Catarrhini as understood by the writer. But the nearest structural resemblances are to be found among the Lemuriformes, especially among the Adapidæ and Lemuridæ. Hence the humerus of *Notharctus*, as well as the great majority of all other elements of the skeleton, is plainly in a lemuriform, or better, in a pre-lemuriform stage of evolution.

The humeral type of the Adapinæ is very close indeed to that of *Notharctus*.

The humeral types of the Cebidæ have departed more widely from the primitive *Notharctus* type: in the greater elongation and cylindrical form of the bone, in the marked reduction of the external epicondylar ridge, delto-pectoral crest, and entocondyle; the entepicondylar foramen is often absent; the trochlea and capitellum now form one widely extended, almost cylindrical joint. These details of the humerus of the Cebidæ, taken in connection with the characters of the manus, indicate that in general these animals do not have so tight a grip upon the branches but that this inferiority is more than compensated by a superior quickness and agility. Here, as in many other lines of primates, the progressive advance in brain capacity has been associated with progressive adaptations for versatility and agility at the expense of robustness and passive clinging power.

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[1] Progressing by swinging from branch to branch with the forearms. (Compare Keith, 1899, Proc. Zool. Soc., Mar. 7, p. 305.)

Relation of the Humeral Index to Habits

	BREADTH	LENGTH	INDEX
Semifossorial Types			
Dasypus	26	60	23
Orycteropus	67	155	23
Taxidea	34	90	26
Solenodon	19	45	24
Ambulatory to Cursorial Types			
Clænodon	44	143	32
Dissacus	63	187	30
Felis	20	88	44
Urocyon	22	109	50
Cynælurus	34.5	178	51
Primitive Arboreal Types			
Didelphis	21	66	31
Phalangista	21	71	34
Nothodectes	11	37.5	34
More Specialized Arboreal Type			
Tupaia	5.5	29.5	51
Secondarily Arboreal (climbing by use of claws)			
Paramys	25	80	32
Nasua	24	80	33
Cercoleptes (= *Potos*)	24	73	30
Cholœpus	31	163	52
Primitive Primate Types			
Notharctus osborni, No. 11470	20	71	35
" *tenebrosus*	24	77	32
Adapis (?) *magnus*	19	74	38
Lepilemur	15	52	34
Lemur mongoz	20	86	43
" *varius*	26	108	41
Propithecus coquerelli	23	94	40
Brachiating Types			
Hapale	10	46	46
Cebus	22	108	49
Alouatta	30	162	54
Macacus	25	146	58
Cercocebus	22	122	55
Anthropopithecus	65	324	50
Hylobates	27	226	84
Homo	54	326	60

These figures demonstrate the following facts:

(1) Semifossorial humeri are very short and broad.

(2) A primitive ambulatory type has about the same index (32) as the most primitive arboreal type (31), but progressive, cursorial, unguiculate types exhibit a marked elongation of the humerus, the index rising to 51 in *Cynælurus*.

(3) The really primitive arboreal types have the humerus of moderate width (index 31–34), but in advanced arboreal types the humerus invariably lengthens to a greater or less degree.

(4) In those secondarily arboreal forms which use the large compressed claws in clinging the humerus is moderately wide.

(5) Among the Lemuriformes there is a steady rise in the humeral index, as we pass from the more primitive forms with wider humeri to the specialized lemurs with long humeri.

(6) In the brachiating series the index rises rapidly from 49 in the Cebidæ to 84 in *Hylobates*, which has the longest humerus of the series. In *Hapale* the humerus is perhaps secondarily widened through the use of the claws in climbing.

Radius

Text Fig. 10

This element is represented by the right radius and the distal end of the left radius of *N. osborni*, Amer. Mus. No. 11474, by the right radius and portion of the left radius of *N. tyrannus*, Amer. Mus. No. 11478, as well as by other specimens. Resemblance to the radius of *Lepilemur* is extremely close and detailed. The principal difference is that the shaft is wider, especially at the lower end. and there is no groove for the tendon of the extensor ossis metacarpi pollicis, such as is present in *Lepilemur* and *Lemur*. About the middle of the shaft on the anterior border there is a gentle eminence to which the tendon of the pronator radii teres [1] was very probably attached; this eminence is better developed than in recent

Fig. 9. Arm muscles of *Lemur* sp. After Cuvier and Laurillard.

n	subscapularis	*q*	coracobrachialis	δ	extensor carpi radialis longior	α	palmaris
o	teres major	*t*, *t*², *t*³	triceps			β	flexor carpi unlaris
i	latissimus dorsi	*u*¹	anconeus internus	μ	flexor profundus digitorum	ξ	abductor pollicis brevis
*r*¹, *r*	biceps	*v*	supinator longus	γ	flexor carpi radialis	ρ	adductor pollicis
s	brachialis anticus	*x*	pronator radii teres	κ	flexor sublimis digitorum	*R*	annular ligament

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[1] Dr. Wood Jones (1916, p. 38) notes that the pronator radii teres has but a single head (arising from the upper surface of the internal epicondyle of the humerus) in lemurs, in monkeys, and in most placental orders. On the other hand, a second head is present (arising from the coronoid process of the ulna) in primitive amphibians and reptiles, in *Tupaia* and *Crocidura*, in most chimpanzees, in many gorillas, in the orang, and usually in man. He therefore regards the bicipital condition of the pronator radii teres as primitive.

While it may possibly be true that man and the anthropoids retain a primitive muscle slip which has been lost in the lemurs, it is practically certain that, with regard to the form of the humerus, of the radius, and of the ulna, the lemurs as a whole are much more primitive than the anthropoid-man group. Dr. Wood Jones (p. 44) speaks of "the primitive type of every bone and joint of the human fore-limb." In view of the fact that Eocene and even modern lemurs retain very many characters in humerus, radius, and ulna, which are found in other quadrupedal Eocene mammals, but are absent in the semierect to erect man-anthropoid group, the phrase noted above appears to be most misleading. (Cf. Plate XXVII.)

lemurs. The interosseous ridge, from which was stretched the interosseous membrane running to the ulna, is well marked but not so sharp as it is in *Lemur*. The anterior border of the shaft is not nearly so thick as it is in *Lemur* and *Lepilemur;* the styloid process was less produced downward and there was no distinct groove for the tendon of the extensor ossis metacarpi pollicis. The process for the attachment of the supinator longus was more prominent. The marked bowing of the radius and ulna in opposite directions afforded space for robust extensor and flexor muscles of the carpus and pollex.

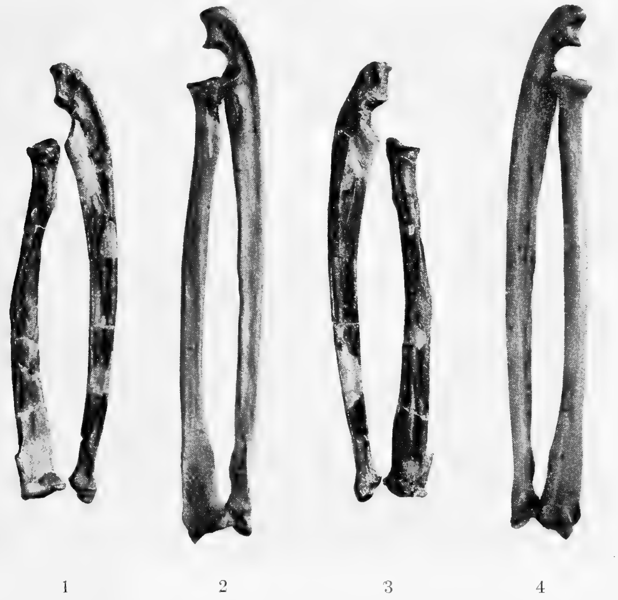

Fig. 10. Comparative series: right radius and right ulna of *Notharctus* and *Lemur*. Natural size.

1. *Notharctus osborni*. Amer. Mus. No. 11474. Inner, or flexor, side of forearm bones.
2. *Lemur mongoz*. Amer. Mus. No. 22886. Inner, or flexor, side.
3, 4. Outer, or extensor, side of same specimens.

The radius of *Propithecus*, except for its greater length, in all views is strikingly similar to that of *Notharctus;* it is also curved anteroposteriorly as in *Notharctus* and is but little modified by the further flattening of the distal end and the rounding of the shaft. As in *Notharctus*, there is a distinct process on the anterior border near the lower end, for the tendon of the supinator longus, and both genera lack the deep groove for the extensor ossis metacarpi pollicis which is seen in *Lepilemur* and *Lemur*. In *Propithecus* the groove for the extensor communis digitorum is converted into a tunnel beneath the dorsal ligament.

The radius of *Cebus* and *Alouatta* as compared with that of *Notharctus* is much longer and has a cylindrical shaft; distally it is much thicker in section; the region of the styloid process is more produced downward and inward. But only a small change, i. e., the conversion of a flattened shaft into a cylindrical one, would be required to transform a *Notharctus*-like radius into the cebid type.

The marmosets vary considerably in the length of the radius. The longer straighter radii distinctly suggest the *Callithrix-Cebus* type; the shorter radii have the shaft curved about as much as it is in *Notharctus*, but they have the styloid process shaped more as it is in *Cebus*. The head of the radius is circular rather than oval and its outer rim does not protrude so much as it does in *Notharctus*.

Comparative Measurements

	N. osborni No. 11474	*N. tyrannus* No. 11478	*L. mongoz* No. 22886	*L. mongoz* No. 31254	*L. varius* No. 18040
Total Length of Radius from distal to proixmal articular facets	67.	67 (est.)	87.	85.	98.
Greatest Transverse Diameter of Head of Radius	7.5	7.3	7.5	6.8	10.
Greatest Width of Distal End of Radius across articular facets	9.5	9.7	8.	7.9	11.

Ulna

Text Fig. 10

The ulna is represented by the right and a portion of the left in *N. osborni*, Amer. Mus. No. 11474, and by the right in *N. tyrannus* (No. 11478). The chief difference from *Lemur* and *Lepilemur* is the shortness and marked curvature of the shaft; they also have the posterior border wider and flatter. The great sigmoid notch is similar to that of *Lemur mongoz*, but somewhat less expanded transversely, in correlation with the relative narrowness of the humeral trochlea; it is confluent with the small sigmoid cavity for the reception of the head of the radius, whereas in *Lemur* these two are divided by a sharp ridge. In *Lepilemur*, however, this ridge is less pronounced. The olecranon closely resembles that of *Lemur varius* but its medial apex is more produced inward; as seen from the proximal end the olecranon is less rounded than it is in *Lemur*. The styloid process and the rest of the distal end recall this region in *Lepilemur*.

The ulna of *Propithecus* is especially close in all parts to that of *Notharctus*, the principal difference being the flattening of the flexor border in *Propithecus*, which contrasts with the sharp edge in *Notharctus*. The olecranon of *Propithecus* is also rounder and more truncate and the sigmoid notch is wider.

The ulna of *Cebus* is elongate and straighter, its olecranon massive and truncate, the coronoid process higher, and the back of the shaft behind the sigmoid notch wide, with sharply projecting edges. The interosseous border is not so sharp; there is no sharply rimmed fossa for the pronator quadratus. The styloid process is larger and more ball-like.

In *Alouatta* the ulna is remarkable both for length and stoutness; the shaft is roundly oval in section, the olecranon wide and truncate, the styloid process very ball-like.

The ulna of the marmosets is allied to the cebid type and has an expanded truncate olecranon.

Manus

Plate XXIX; Text Figs. 11, 83

The description of the manus of *Notharctus* may be preceded with advantage by a description of the manus of *Lemur* and of *Cebus*.

The manus of *Lemur* is strongly prehensile, especially in the following characters: in the dried skeleton the stout pollex (I) diverges widely from the elongate digits III and IV; the slender digit II is often placed midway between I and III; III and IV are close together, IV being the longest and heaviest and V shorter than III. The carpus is narrow proximally and wide distally; the scaphoid is wide, the lunar very narrow and small, the trapezium large, the magnum narrow and extended vertically; the unciform is large and even more extended vertically. The wide shallow centrale lies between the unciform, magnum and trapezoid below and the lunar and scaphoid above; it has contact with the unciform, a specialization which may be correlated with the extreme divergence of the pollex and the crowding of the carpal elements toward the ulnar side. The metacarpal of digit I is stout and short; metacarpals II–V are slender, II being considerably shorter than III, which is a little longer than IV. The proximal phalanges are stout and long, the middle row in digits II–V stout; the distal row are very short and bear flattened, crescentic expansions for the flat nails and for the expanded finger tips below.

In many of these characters *Lemur* parallels the opossums: e. g., in the fan-like arrangement of the digits, in the divergent pollex, in the small size of the lunar, in the widening of the distal row of the carpals, in the vertical extension of the magnum and of the unciform, in the elongation of the fourth digit and in its association with the third, etc.

Huxley, Dollo, Anthony and others have shown how such features in the opossum render the manus of that animal especially effective in firmly grasping the branches of trees. The primitive primates exhibit similar characters and also have the advantage of expanded finger tips and greatly expanded pads on the palm of the hand.

In *Cebus* these presumably primary adaptations, or palæotelic characters, have been partly obscured by several adaptations and functions which are probably cænotelic. First, *pari passu* with the increasing versatility which is expressed in the larger brain and in the form of the humerus, the manus has perhaps become better adapted for running lightly along the surface of the branches, as shown in the more symmetrical development of the digits on either side of digit III and possibly in the shortening of the digits. Secondly, the mode of progression which has been designated as "brachiation," and which consists in swinging the body from branch to branch partly by means of the forearms, the hands being held above the head, the palms facing each other and the digits well flexed, has been adopted in moderate degree by *Cebus*, and is perhaps indicated by the widening of the carpus, by the more symmetrical arrangement of the digits on either side of digit III, by the less divergence and greater mobility of the pollex, by the globular expansion of the distal ends of the metacarpals, and by the narrowing of the distal phalanges, the claws being bent up almost into nails. In correlation with the lessened divergence of the pollex there has been a readjustment of the carpals so that the lunar is widened and the magnum separates the centrale from contact with the unciform.

All these readjustments result in the transformation of the manus from a mere grasping organ, used chiefly for clinging to the branches, into a true hand, provided with a more or less opposable thumb and capable of delicately coördinated motions. The dexterity of a cebid monkey in the use of its hands is well illustrated in the following incident related by Thomas Belt in his "Naturalist in Nicaragua."

> 'Mickey's' actions were very human-like. When anyone came near to fondle him, he never neglected the opportunity of pocket-picking. He would pull out letters, and quickly take them from their envelopes. Once he abstracted a small bottle of turpentine from the pocket of our medical officer. He drew the cork, held it first to one nostril then to the other, made a wry face, recorked it, and returned it to the doctor.

The exercise of this function is especially facilitated by the globular form of the heads, or distal facets, of the metacarpals and by the drawing in of the pollex toward the remaining digits.

The manus of *Notharctus*, (Figs. 11, 83) so far as indicated by the fragmentary remains, appears to be somewhat more primitive than that of any modern lemurs: (1) the unciform is not so deep vertically, (2) the magnum is relatively deeper, (3) the facet for the lunar on the radius is thicker anteroposteriorly. Hence, by inspection of the surrounding elements, it is probable that (4) the lunar was not so much reduced as it is in lemurs, (5) the centrale probably had little if any contact with the unciform, and possibly (6) the pollex was somewhat less divergent. These presumably primitive characters are retained in the modern platyrrhine monkeys which, however, have also specialized in the opposite direction by the further enlargement of the lunar and by the widening of the upper end of the magnum.

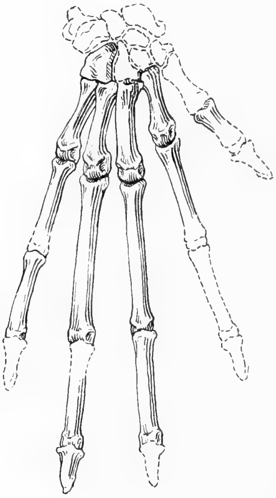

Fig. 11. Dorsum of right manus of *Notharctus tyrannus*. Amer. Mus. No. 11478. Natural size. For manus of *N. osborni* see Fig. 83.

The metacarpals of *Notharctus* are very short and most like those of the modern *Perodicticus*, but much shorter. The long slender phalanges almost suggest those of *Indris* or of *Chiromys* rather than the flattened phalanges of either the typical platyrrhine monkeys or the modern Lemuridæ.

The single known ungual phalanx, which is provisionally mounted on digit IV, is strangely asymmetrical. Its exact counterpart was not found in any of the primates compared with it. The nail was evidently longer and narrower than those of Lemuridæ, Indrisidæ, Lorisidæ, but not so narrow as those of *Chiromys*. It was, however, essentially lemuroid in shape, and the ungual phalanx itself differs from those of the Cebidæ, which have very feeble shafts and very small round tips.

The following additional details concerning the structure of the manus of *Notharctus* seem worthy of record. In *Notharctus osborni* the manus is represented only by some of the carpals and scattered elements of the digits. In *Notharctus tyrannus* the left hand is represented by carpals 2–5, proximal phalanges 2–5, and the unciform and other fragments. The right hand is represented by the fifth metacarpal, the fourth proximal phalanx of the fourth digit, the middle phalanges apparently of the third and fourth, and a single distal phalanx which may belong with the fourth. What is apparently the first metacarpal is preserved in *Notharctus osborni;* it is similar to that of *Lemur*, and on the inner side of the distal end shows a small facet which may have lodged the sesamoid to which is attached the tendon of the adductor pollicis muscle, which is very strong in lemurs. The metacarpals are shorter and stouter than those of either *Lemur* or *Cebus*, this betokening powerful muscles of the palm. The metacarpal which is identified as number II is a third shorter than metacarpal III, whereas in *Lemur*, metacarpal II is only a little shorter than metacarpal III, and in *Cebus* it is nearly equal to it. This disparity in length between II and III is further emphasized in the modern *Chiromys* and is very probably a primitive character. The short metacarpals are retained in *Lepilemur*, although here they are thinner than those of *Notharctus*.

In conclusion, it seems hardly necessary to give a fuller and more detailed description of each individual known element of the manus of *Notharctus*. It may suffice to state that the writer has made careful comparisons of every such element with the homologous elements of representative Lemuridæ and Cebidæ; and that with regard to the detailed conformation of each element, *Notharctus*, with few exceptions, is nearer to *Lemur* than to *Cebus*.

Comparative Measurements

	N. tyrannus No. 11478	*Lepilemur mustelinus* No. 31251	*Lemur mongoz* No. 31254	*Lemur varius*
Metacarpal I, Length	—	8.5	11.	16.4
" I, Breadth of Distal End	—	3.3	4.3	5.7
" II, Length	13.5	10.	18.6	26.4
" II, Breadth of Distal End	4.6	3.2	3.6	5.7
" III, Length	20.5	11.	19.6	27.
" III, Breadth of Distal End	5.5	3.4	4.	5.3
" IV, Length	18.	14.3	19.6	27.3
" IV Breadth of Distal End	5.7	3.4	4.5	5.5
" V, Length	14.3	12.	17.3	23.5
" V, Breadth of Distal End	4.5	3.	4.5	5.
Proximal Phalanx of Digit I	—	7.	11.	16.5
" " " " II	—	10.	14.3	24.3
" " " " III	25.5 est.	12.5	17.3	27.5
" " " " IV	27.3	15.5	18.5	28.
" " " " V	—	12.5	15.	24.

PELVIC LIMB

Pelvis

Plates XXXII, XXXIII; Text Figs. 12, 13, 14

The pelvis of *Notharctus* is preserved in Nos. 11474, 11478 and 11479. It is essentially of lemurine type, differing chiefly in the shorter, wider ilia, and relatively longer ischia. It differs in many particulars from the pelvis of New World monkeys, Old World monkeys, apes, and man; it is in each case more primitive — that is, very close to the tupaioid or Menotyphla type.

1. As viewed from below, the opposite halves of the pelvis of *Notharctus* form a sort of lyre, the blades of the ilia diverging anteroexternally beyond the first sacral vertebra. In all lemurs this feature is still more pronounced. In the New World monkeys, on the other hand, in the ventral view the opposite ilia are more parallel to each other and do not diverge anteriorly, but their ventral surfaces are spread

out behind the sacrum. The ilia of the Old World monkeys diverge slightly in front, but are wider on the ventral surface. In the top view, likewise, the ilia of *Notharctus* diverge anteriorly, while those of the Cebidæ and Hapalidæ are more parallel to the backbone. (Plate XXXII.)

2. The ventral border of the ilium in the lemurs, in side view, is deeply concave, while in Cebidæ, Hapalidæ and Old World monkeys it is nearly straight. (Plate XXXIII; Fig. 13.)

Fig. 12. Comparative figures of the pelvis of *Notharctus* and *Lemur*. Natural size.

1. *Notharctus osborni*. Amer. Mus. No. 11474. Ventral aspect.
2. *Lemur mongoz*. Amer. Mus. No. 22886. Ventral aspect.
3. *Notharctus osborni*. Amer. Mus. No. 11474. Left side, with sacrum.
4. *Lemur mongoz*. Amer. Mus. No. 22886. Left side.
5. *Notharctus osborni*. Amer. Mus. No. 11474. Right ilium and ischium, medial aspect, showing articular surface of the sacrum.

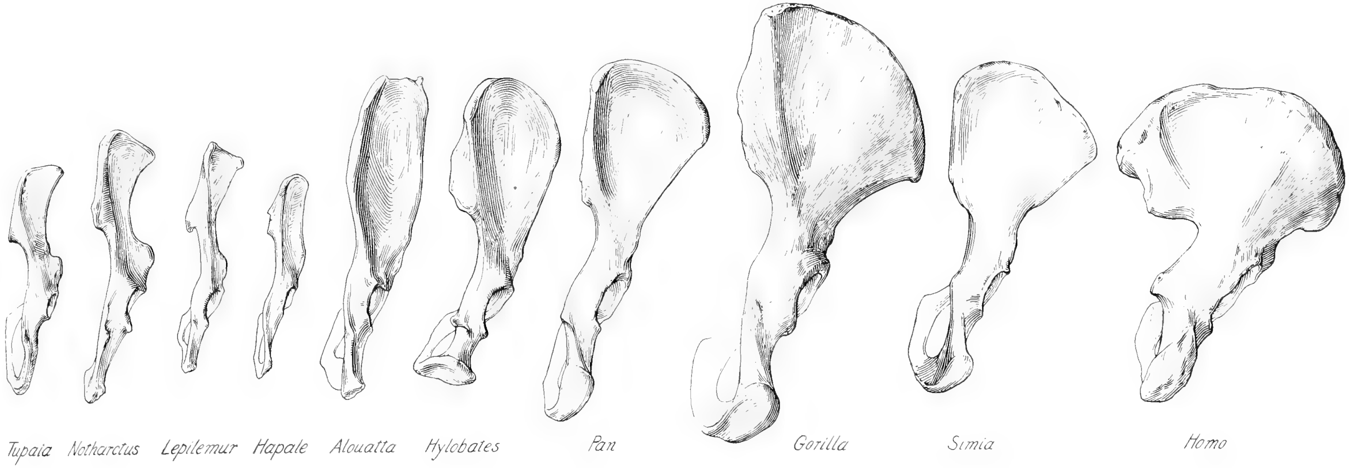

Fig. 13. Comparative series: right os innominatum of *Tupaia, Notharctus, Lepilemur* and higher primates. Dorsolateral aspect. Scales various.

3. The blade of the ilium of lemurs, in side view, is narrow, and the gluteal fossa is deeply excavated, while in the Cebidæ it is flatter and considerably more expanded, the gluteal fossa being shallow.

4. Immediately in front of the acetabulum in *Notharctus* and in the lemurs there is a very prominent process, homologous with the anterior inferior spine of the ilium of man; it is elongated anteroposteriorly, compressed laterally and roughened along its summit; in recent lemurs this process serves for the attachment of a strong ligament that runs forward and is attached to the anteroinferior process of the iliac crest; this ligament extends the area of origin of the gluteal and of the iliacus muscles, and also gives the partial attachment to the sartorius muscle. The process itself also gives attachment in part to the sartorius muscle, and immediately behind this to the powerful rectus femoris muscle. The anterior border of the process runs forward into the sharp concavity of the lower border of the ilium. In the Hapalidæ this anterior inferior process is still present, although less defined than in *Notharctus*. In the Cebidæ it is confluent with the anterior border of the ilium; in the Cercopithecidæ it is barely or not at all visible. Vestiges of it may be seen in the gibbons and in some old gorillas and chimpanzees; it is practically absent in a young gorilla; it is a little better developed in the orang. The enlargement of the process in man is no more to be regarded as a primitive character than is the wide expansion of the ilium. (Fig. 13.)

5. The articular surface for the sacrum, on the inner side of the ilium, which is best shown in No. 11479, is almost identical in form with that of the *Lemur*, and is much shorter than that of the Cebidæ, since it articulates only with a single vertebra. (Fig. 12.)

6. The pubis of *Notharctus* is not preserved, but from the close similarity of both the ilium and the ischium to those of lemurs, it is quite likely that the pubis was less extended anteroposteriorly than it is in *Cebus*, and that the anterior pelvic opening, or pelvic inlet, was more restricted dorsoventrally. The anterior opening or inlet of the pelvis in *Notharctus* and in the lemurs is also bounded by a sharp rim on the ilium, which is reduced in South American monkeys. (Fig. 12.)

7. The ischium resembles those of lemurs, especially *Lepilemur*, except that it is larger; it differs markedly from the ischium of the New World monkeys in not having the ischial tuberosity widely averted, because the lemurs do not sit upright. A small ischial spine is present, similar to that of *Lepilemur*. It probably gave attachment on the inner side to the ischio-coccygeus and on the outer side to the gemmelli (cf. the dissection of *Propithecus*, Milne Edwards, Pl. 68, fig. 3) as it does also in other primates, including man. (Figs. 13, 14.)

8. The acetabulum with regard to both form and position closely resembles that of *Lemur*, and differs from those of the Cebidæ in that the anterior and posterior lips of the acetabulum are elevated, and the contour as a whole is less circular. (Fig. 12.)

The whole configuration of the pelvis of *Notharctus* indicates that the animal was an arboreal quadruped which did not sit fully upright but leaped about on all fours among the branches.

With regard to the musculature of the pelvis, the form of the ilium shows that the gluteal series and the iliacus, in form and proportion, were like those of modern lemurs. The narrow lower face of the blade of the ilium indicates corrresponding proportions for the iliacus and psoas muscles, the areas for which are much wider in monkeys. The widely everted anterior blade of the ilium, which leaves a wide space between the blade and the lumbar centra, gives space for the widely extended transverse processes of the lumbars and for bulky quadratus lumborum, psoas, erector spinæ, superior and inferior sacro-coccygeal muscles. In *Cebus* the blade is not everted and the transverse processes of the lumbars are less extended transversely. The marked prominence of the anteroinferior process of the ilium is a primitive lemuroid character present also in the Menotyphla; it implies the presence of a strong ligament between this process and the tip of the ilium, and, together with the ligament, it gives a firm support for the ilio-psoas, sartorius, deep gluteal and rectus femoris muscles, which are all used in leaping. (Figs. 12, 14, 24.)

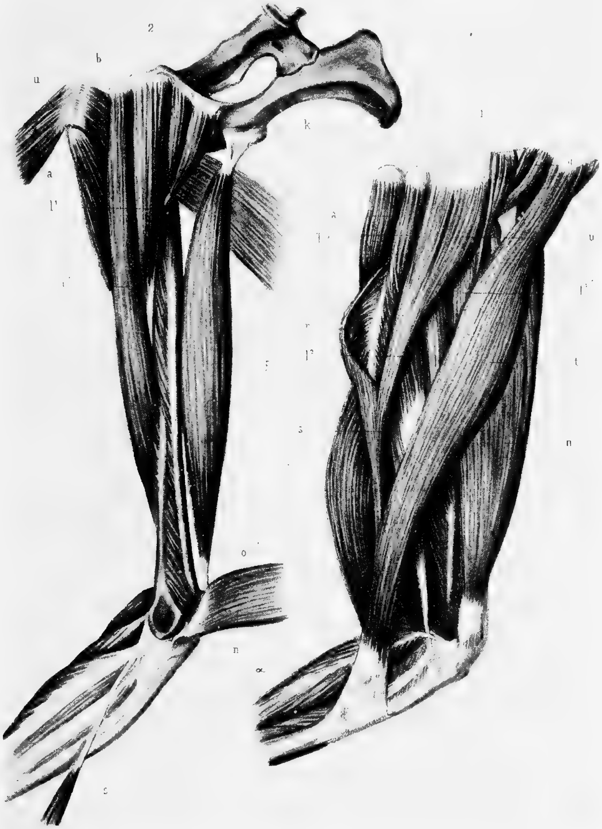

Fig. 14. Muscles of the inner side of the thigh of *Propithecus diadema*. After Milne Edwards. Compare Fig. 24.

1. Superficial muscles

n	vastus internus	*u*	gracilis
t	sartorius	*q*, *s*	common fascia of origin of biceps and semitendinosus
g	psoas magnus	*r*	semitendinosus
l^1,l^2	adductors	*s*	semimembranosus

2. Deep muscles after the removal of biceps, semitendinosus and semimembranosus, gracilis, etc.

p rectus femoris (its tendon arising from the anterior inferior spine of the ilium).

o	crureus	l^1, l^2	adductors
k	pectineus	*a*	gluteus maximus

The non-expansion of the ischial tuberosities indicates that the *Notharctus* pelvis is less adapted for sitting upright than is that of the South American monkeys, while the shortness of the ischium in lemurs and *Notharctus*, and the restriction of the pelvic inlet, indicates that the true pelvis is relatively small and that possibly the newborn young may have had the brain-case less expanded than that of higher primates.

The pelvis of *Propithecus* is slightly modified from the *Notharctus* type in the wider divergence of the ilium, in the prolongation of the anterior inferior process of the ilium, and in the relative shortening of the ischia. Thus *Propithecus* is a little more specialized for leaping. In all palæotelic features of the pelvis the agreement is remarkably close. (Plate XXVI.)

The pelvis of *Chiromys* is also slightly specialized away from the *Notharctus* type through the narrowing and elongation of the ilium, but is fundamentally similar to it, and contrasts widely with the pelvic types of the New World and Old World monkeys.

The pelvis of the Old World monkeys is much nearer to the New World type than to that of lemurs. The iliac blade is progressively widened and everted, finally attaining a very wide expansion in man; this is no doubt correlated with the habit of sitting upright, with the relatively heavy abdomen and with the widening of the gluteus medius and minimus. The anterior inferior spine of the ilium is confluent with the anterior expanded border; in correlation with the sitting habit the ischial tuberosities are widely expanded and everted.

In man the very widely expanded and everted blade of the ilium is associated with the fully erect posture both in sitting and walking; the capacious false pelvis affords support to the voluminous abdominal viscera, the areas for the gluteus medius, gluteus minimus and iliacus are much increased, the lines of insertion of the external transverse and oblique abdominal muscles on the crest of the ilium are greatly widened; the eversion of the anterosuperior spine of the ilium is associated with a more vertical pull of the tensor vaginæ femoris, of the sartorius, and of the ilio-femoral ligament, in standing and progressing.

Comparative Measurements of the Pelvis

	Notharctus osborni No. 11466	*Notharctus osborni* No. 11479	*Lemur mongoz* No. 31254	*Cebus hypoleucus* No. 14017
Total Length from anterior tip of ilium to ischial tuberosity		73.	81.5	83.
Length of Ilium from middle acetabulum to anterior dorsal tip		48.5	56.	57.
Length of Ischium from middle acetabulum to ischial tuberosity		25.5	24.5	26.5
Width of Ilium, anterior end		19.	18.5	19.
Iliac Index (width/ length)		.39	.30	.30
Anteroposterior Diameter of Acetabulum	14.5	——	11.	12.
Anteroposterior Diameter of Thyroid Foramen		13.	16.5	17.
Ilio-ischial Ratio		1.90	2.28	2.15

These measurements emphasize the relative shortness in *Notharctus* of the ilium as compared with the ischium, the large size of the acetabulum and the small size of the thyroid foramen or fenestra.

Femur

Text Figs. 15, 16

The right femur is preserved in *Notharctus osborni,* No. 11474, and less completely in other specimens of *N. tyrannus* and *N. tenebrosus.* They are, on the whole, close to those of *Lemur mongoz,* which are only a little longer. It is surprising that while the humerus of the modern *Lemur mongoz* has become considerably elongate, the femur is only a little longer than that of *Notharctus*. The humero-femoral ratio of *Notharctus osborni* is .60, as compared with .65 in *Lemur varius*, .75 in *Cebus capucinus*, and 1.05 in *Brachyteles arachnoides*. The progressive elongation of the humerus in this series is in harmony with the crouching position normally assumed by *Notharctus* as inferred from other evidence, in contrast with the upward slope of the backbone in the normal pose of *Brachyteles*.

The head of the femur is smaller and much less ball-like than that of *Lemur;* it is located somewhat more in line with the long axis of the shaft, whereas in *Lemur* it is more sharply set off from and inclined to the axis of the shaft. The head is thus somewhat more sessile and the neck less constricted. When the pelvis and the femur are placed in their normal articular relations it is seen that, in the resting pose, the femur of *Notharctus* was held out from the body at only a gentle angle, whereas in *Lemur* the femur is more abducted. Here, therefore, as in so many other characteristics, *Notharctus* represents a less advanced stage of arboreal adaptation. In *Lepilemur* the head of the femur is extended further inward toward the digital fossa on the posterior side of the femur than is the case in *Notharctus*. In *Lepilemur*

Fig. 15. Comparative series: right femora of *Notharctus*, *Adapis*, *Lemur*, *Cebus*, *Hapale*, *Macacus*. Front view.

1. *Notharctus osborni*. Amer. Mus. No. 11474. × $\frac{1}{1}$.
2. "*Adapis parisiensis*." After Filhol. × $\frac{1}{1}$.
3. *Lemur mongoz*. Amer. Mus. No. 22886. × $\frac{1}{1}$.
4. *Cebus hypoleucus*. Amer. Mus. No. 14016. × $\frac{1}{1}$.
5. *Hapale* sp. Amer. Mus. No. 17574. × $\frac{3}{2}$.
6. *Macacus nemestrinus*. Amer. Mus. No. 14012. × $\frac{2}{3}$.

this condition is connected with the fact that the animal can reach further forward and upward with the hind limb than was the case in *Notharctus*, which is again more primitive than the modern type.

The great trochanter is much less expanded than that of *Lemur* and lies below the level of the head, whereas in *Lemur* it projects widely above it. When the femur is articulated with the pelvis and compared with those of *Lemur* it is seen that in *Notharctus* the space for the deep gluteal muscles was more restricted and that these muscles were shorter, while their locus of insertion, the great trochanter, was smaller. Hence, in all probability, *Notharctus* could not leap so far in proportion to its body weight as the modern *Lemur varius* can.

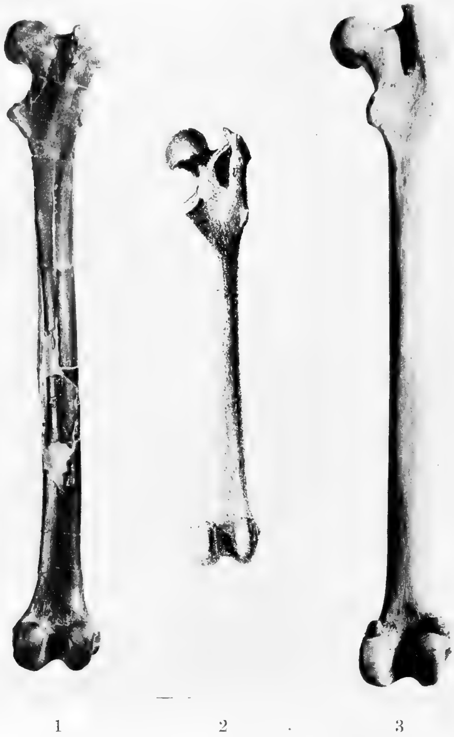

Fig. 16. Comparative series: right femora of *Notharctus, Adapis, Lemur*. Back view. Natural size.

1. *Notharctus osborni.* Amer. Mus. No. 11474.
2. "*Adapis parisiensis.*" After Filhol.
3. *Lemur mongoz.* Amer. Mus. No. 22886.

The external tip of the lesser trochanter is more slender and acute than that of *Lemur;* this probably implies that the ilio-psoas muscle was less powerful than it is in *Lemur,* just as the leaping power of *Notharctus* was supposedly somewhat less. The third trochanter is similar to that of *Lemur,* but smaller and less protuberant; hardly different enough, however, to indicate any marked difference in the gluteus maximus and quadratus femoris muscles which were attached to this process on the outer and inner sides respectively. The digital fossa is somewhat less extended vertically than that of *Lemur mongoz,* this perhaps implying that the obturator internus, gemelli, obturator externus and other adductors of the femur were somewhat less robust than those of *Lemur*.

The long shaft of the femur is cylindrical in mid-section and is similar to that of *Lemur varius*. The shaft as a whole has a slightly less straight and more irregular contour than that of *Lemur*. The linea aspera, or adductor ridge, is represented by a long vertical groove running down the posteromedial side of the shaft from below the lesser trochanter to a point about two-thirds the distance down the shaft. About fifteen millimeters below the lesser trochanter the arterial foramen opens in this groove. Traces of such a groove are found in *Lemur mongoz* and *Lemur varius*. The groove and the lips on either side of it in *Lemur* serve for the insertion of the adductor longus muscle. No distinct crest for the insertion of the lower part of the gluteus maximus is present either in *Notharctus* or in *Lemur*, although in the latter this muscle is widely extended from the third trochanter downward to near the lower end of the shaft. The popliteal surface on the back of the shaft above the condyles resembles that of *Lemur*.

The distal end of the femur is relatively smaller than that of *Lemur varius;* the external condylar ridge or keel is a little more protuberant and is slightly less reflected on to the front face of the femur; the patellar facet is narrower; the external tuberosity is a little more prominent, and the whole distal portion of the femur is a little less symmetrical than it is in *Lemur*. The intercondylic notch is narrower; nevertheless a close comparison of the articular relations of the femur, tibia, and patella in *Notharctus* and *Lemur* leads to the conclusion that there was little difference in the range of flexion and extension at the knee, that of *Lemur* being perhaps a little greater.

Thus the general resemblance of the femur of *Notharctus* to that of *Lemur* is so strong that we may be quite sure that the arrangement of the muscles was substantially identical in the two animals, the differences being mostly differences of proportion. With regard to the normal perching pose of the hind limb, *Lemur* may ordinarily abduct the thighs a little more than did *Notharctus*, and in leaping it may have extended the leg a little more, but on the whole the postures and movements of the limb of *Notharctus* were extremely *Lemur*-like.

The femur is also fairly similar to that of *Lepilemur mustilenus*, with which it has frequently been compared during the course of this study; it differs only in the proportions of certain parts which need not be specified.

The femur of *Adapis* is even closer in appearance to that of *Notharctus* than is the femur of *Lemur*, as may be seen in the accompanying figures. The lesser trochanter is even more pointed than that of *Notharctus*, the third trochanter is a little less prominent. (Figs. 15, 16.)

Comparative Measurements of the Femur

	N. osborni No. 11474	*N. tenebrosus* No. 1727	*L. mongoz* No. 31254	*L. mongoz* No. 22886	*L. varius* No. 18940	*Cebus apiculatus* No. 30290
Total Length of Femur	122.	138.	122.	128.	152.	145.
Greatest Diameter of Proximal End, head to greatest trochanter	20.	24.	22.	23.5	29	25.
Greatest Diameter of Distal End	16.5	19.	17.	17.5	22.	21.

The femur of *Propithecus* is fundamentally similar to that of *Notharctus*, but more specialized. The shaft is longer and more circular in section, the second trochanter is more expanded, the head more globular, the neck more constricted, the external condyle or trochlear keel is widely expanded. These characters are probably associated with the freer movement at the acetabulum and superior leaping power of *Propithecus.*

The femur of *Cebus* differs radically from that of *Notharctus* in many characters: the third trochanter is obsolete or entirely absent, the head is spherical, the neck sharply constricted, the great trochanter is more in line with the shaft and the width of the whole proximal part of the bone is relatively less; the second trochanter has a much thicker tip, the digital fossa is much deeper, the adductor groove on the back of the femur is barely indicated, the whole distal end is widely expanded, the patella face is wider and the trochlear keels lower. These characters are accentuated in *Alouatta,* which has also a widened shaft.

These differences in the femora of *Notharctus* and of *Cebus* are doubtless correlated with differences in the musculature and in the action of the limbs. In *Notharctus* the stout gluteus maximus was doubtless attached as it is in lemurs, not only to the third trochanter, but also all down the shaft below the third trochanter; and the quadratus femoris, which is inserted on the back of this process is a stout muscle. In *Cebus* the gluteus maximus muscle is less developed, especially the lower part, and the quadratus femoris is weaker. In *Lemur* and *Notharctus* the narrow patellar facet and high trochlear keels tend to limit the motion of the leg at the knee to an anteroposterior plane. In *Cebus,* on the contrary, the wide patellar facet and low trochlear keels permit a greater twisting of the leg upon the femur. All this is correlated with the fact that *Lemur* and *Notharctus* were specialized for leaping, while *Cebus* has become somewhat de-differentiated and has more mobile limbs. These differences are still more accentuated in *Alouatta,* which has the great trochanter small, the third trochanter absent, the distal end very wide and permitting wide twisting at the knees. In the marmosets the femur is essentially of cebid type (Fig. 15.5).

Patella

Text Fig. 17

The patella is represented in *N. osborni* (No. 11474) and in *N. tyrannus* (No. 11478). It is a small nodule of bone narrower than the patella of *Lemur* and still narrower than those of *Cebus* and *Alouatta,* in conformity with the narrowness of the patellar facet in the femur. It is much less produced below than that of *Lemur.* Its lower end is asymmetrical while that of *Cebus* is more symmetrical and rounded, in accordance with the greater freedom of the knee-joint.

In *Propithecus* the patella is essentially similar to that of *Lemur.*

Tibia

Text Fig. 17

Both tibiæ are well preserved in *N. osborni,* No. 11474; the right tibia is nearly complete in *N. tenebrosus* (A. M. 1727); several other less complete tibiæ are known. As compared with those of *Lemur mongoz,* they are much shorter, more robust, and more curved, especially in the anteroposterior plane. There is a prominent eminence, or tuberosity, on the front face of the tibia, about one-third of the way down the shaft, which may be designated as the "lower anterior tuberosity" of the tibia (the cnemial tuberosity being the "anterior tuberosity" of human anatomy): the lower anterior tuberosity is much better developed in *Notharctus* than it is in *Lemur.* In *Lemur* this tuberosity is farther dorsad; it lies beneath the upper part of the strong fascia which covers the tibialis anticus muscle, and is especially associated with the band-like tendon of the conjoined sartorius and gracilis muscle, which passes over its anterior surface and is inserted on its outer margin. The front of the shaft of the tibia is flatter in *Notharctus*. The distal end of the tibia is narrower than that in *Lemur varius*, but not much different from that of *Lemur mongoz*. As in other primates the internal malleolus ends below in a prominent hook. The cnemial or anterior tuberosity is much higher and narrower and terminates above in a sharp spine. This condition is correlated with the narrower intercondylic notch and narrower distal end of the femur.

Fig. 17. Comparative figures: right tibia, fibula, and patella of *Notharctus* and *Lemur*. Natural size.

1. *Notharctus osborni*. Amer. Mus. No. 11474. Front view.
2. *Lemur mongoz*. Amer. Mus. No. 22886. Front view.
3, 4. The same specimens, back view.

The tibia of *Notharctus tenebrosus*, No. 1727, is much longer than that of *N. osborni*, and is as long as that of *Lemur mongoz*, but much stouter. The stoutness of the tibia and bowing apart of the tibia and fibula imply a corresponding development of the muscles of the leg and foot and, in fact, the feet are relatively large.

In general, the tibia of *Notharctus* is essentially lemurine, differing chiefly in its more robust character.

Comparative Measurements of the Tibia

	N. osborni No. 11474	*N. tenebrosus* No. 1727	*L. mongoz* No. 31254	*L. mongoz* No. 22886	*L. varius* No. 18040	*Cebus apiculatus* No. 30200
Length of Tibia, distal to proximal facets	101.	112.	110.	115.	134.6	131.
Tibio-femoral Ratio	.82	.81	.82	.89	.88	.90

The tibia of *Propithecus* is more elongate and slender than that of *Notharctus*, but is otherwise similar. The lower anterior tuberosity is less pronounced and is much nearer the upper end of the shaft. (Plate XXVI.)

The tibia of *Cebus* is longer and straighter than that of *Notharctus*, the proximal end is flatter with a lower spine, the lower anterior tuberosity is much less prominent, the distal articular facet has deeper concavities for the trochlea of the astragalus, the internal malleolus is more produced downward, the distal end as seen from the rear is wider and flatter at the lower edge.

Fibula

Text Fig. 17

The fibula of *Notharctus* is essentially similar to that of *Lemur;* as in recent lemurs and indrisines the external malleolus is produced outward more than downward, and the facet for the astragalus is gently inclined to the vertical plane in correlation with the gentle inclination of the external facet of the astragalus. The fibula differs from that of *Lemur mongoz* in its sharply curved shaft and relatively more robust and distal ends.

In *Propithecus* the fibula is essentially the same as that of *Notharctus*, but more elongate and somewhat less curved. (Plate XXVI.)

Cebus and its allies have the fibula much more elongate and slender, with almost straight shaft. The external malleolus is produced downward rather than outward, and extends down nearly to the level of the internal malleolus. The facet for the astragalus is nearly vertical in correlation with the subvertical plane of the external facet of the astragalus.

The fibula of the marmosets is essentially the same as that of *Cebus;* the distal end of the fibula is closely appressed to and bound by the interosseous membrane to the tibia; occasionally the junction with the tibia a centimeter up the shaft. The external malleolus is nearly level with the internal malleolus, and the facet for the astragalus is vertical.

Pes

Plates XXX, XXXI; Text Fig. 84

The pes of *Notharctus* is represented by a number of specimens, pertaining chiefly to *N. osborni*, *N. tyrannus* and *N. tenebrosus*, which afford knowledge of every element of the foot except certain of the phalanges. The principal specimens are as follows: No. 11474 (part of the paratype skeleton of *N. osborni*) the greater portion of the right pes and portions of the left; No. 11466 (associated with type skull of *N. osborni*), left calcaneum, right entocuneiform; No. 11478 (part of skeleton referred to *N. tyrannus*), right pes lacking phalanges, except on hallux, left astragalus, calcaneum, meso- and ectocuneiform, and parts of metatarsals I and III; No. 13024 (associated with lower jaw and limb bones, referred to *N. tenebrosus*), right tarsus with parts of metatarsals and phalanges, left calcaneum, astragalus and fragments of phalanges; field number 420 (from near Millersville, Lower Bridger, referred to *N. pugnax*), left astragalus, calcaneum, cuboid ento- and ectocuneiform, proximal end of metatarsal I. The different species of *Notharctus* differ in the pes only in size and in minor characters.

From the pes of the much older and more primitive *Pelycodus frugivorus* of the Wasatch, that of *Notharctus* is distinguished by the lengthening of the lower half of the calcaneum and by the antero-posterior widening of the entocuneiform. From the pes of "*Adapis parisiensis*," that of *Notharctus* is distinguished by the much greater length of the lower half of the calcaneum and by the narrowness of the astragalus. (Fig. 21.)

The pes of *Notharctus* offers important evidence in favor of the view that this animal should be classified under the suborder Lemuroidea rather than under the Anthropoidea as by Wortman (1904, pp. 172–174), since the pes is incontestably lemuroid rather than anthropoid in type. Here, as in other parts of this work, the writer is not opposing the view that *Notharctus* is structurally ancestral to the South American monkeys, in the pes as well as in all other parts of the skeleton. Such a derivation of the South American monkeys as suggested by both Leidy and Wortman, seems indeed to be very probable. But this does not alter the fact that *Notharctus* is in a lemuroid stage of evolution in the great majority of its known characters.

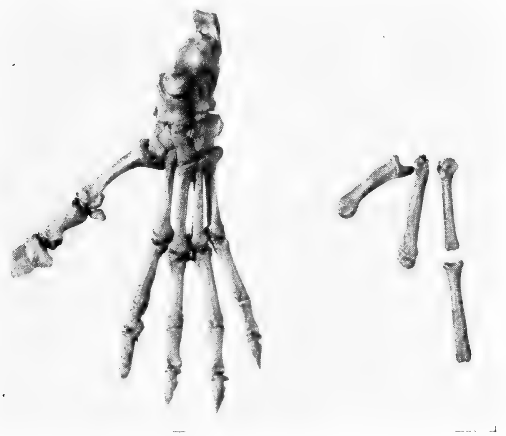

Fig. 18. Left pes of *Lepilemur mustelinus*, Amer. Mus. No. 31251. Fragments of left pes of "*Adapis parisiensis*," Amer. Mus. No. 10016. Natural size.

Broadly speaking, the pes of *Notharctus* differs from that of the modern *Lepilemur* chiefly in the much greater length and narrowness of the phalanges, in the stoutness of the metatarsals, and in the more vertical position of the meso- and ectocuneiform.

In the description of the several elements of the pes which immediately follows, comparisons are made only with *Lemur* or allied forms. The comparisons with *Cebus* and other primates are given afterward (pp. 106, 107).

Astragalus

Plate XXX; Text Fig. 19

The astragalus also is essentially similar to that of *Lemur* in all views. In both genera the trochlea is rather narrow and extends far backward, ending above or posteriorly, in a groove for the flexor longus hallucis muscle flanked by an internal and an external tubercle. The concavity of the trochlea is slight and the internal lip or rim is well defined but not as large as the external rim. The facet for the fibula is oblique, not vertical, in correlation with the oblique position of the corresponding facet on the fibula.

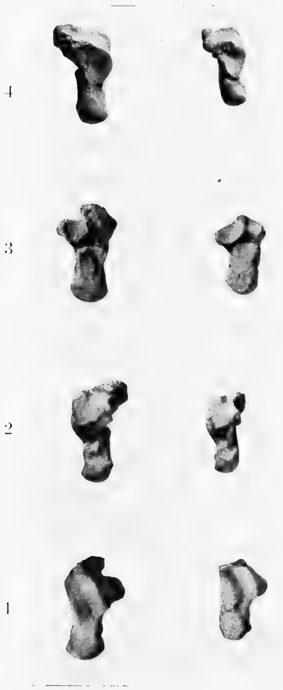

Fig. 19. Comparative figures: right astragalus of *Notharctus tenebrosus* (Amer. Mus. No. 13024) and *Lemur mongoz* (Amer. Mus. 3769). Natural size.

1. Dorsal or front view.
2. Fibular or outer side view.
3. Plantar or back view.
4. Tibial or inner side view.

The movement of the astragalus on the tibia and fibula is hinge-like and limited to an anteroposterior plane. In *Lemur* the posterior astragalo-fibular ligament runs transversely from the inner side of the lower tip of the fibula to a pit on the outer side of the astragalus just behind the facet for the fibula. This ligament forms the outer part of a transverse axle upon which the astragalus turns in its hinge-like movement upon the tibia and fibula. The inner part of the axle is formed by the strong, posterior astragalo-tibial ligament, which runs from a rough surface on the inner surface of the astragalus behind the facet for the tibia to the back part of the internal malleolus.

The above-mentioned pit for the posterior astragalo-fibular ligament, on the outer side of the astragalus, and the rough surface for the posterior astragalo-tibial ligament, on the inner side of the astragalus near the proximal end, are both well defined in *Notharctus*.

The neck of the astragalus in both *Lemur* and *Notharctus* is elongate and slants obliquely downward and inward in the direction of the hallux, so that it crosses the straight shaft of the calcaneum. When the foot is fully extended upon the tibia the neck of the astragalus is more nearly in line with the tibia, but as the foot is flexed the neck assumes a more and more oblique position. It is forced to do so by the pressure of the fibula upon the oblique astragalo-fibular facet, and by the pressure of the navicular upon the head of the astragalus. The same movement of the fibula causes the astragalus to rock upon the calcaneum as a base, the concave, oblique, ectal, or posterior calcaneal, facet of the astragalus sliding over the sharply convex, ectal facet of the calcaneum; while the flattened oval sustentacular, or middle calcaneal, facet of the astragalus slides over the corresponding facet of the calcaneum. In *Lemur* the astragalus is tied to the calcaneum during these movements by the interosseous calcaneo-astragaloid ligament. This short ligament arises from the "interosseous groove" (sulcus calcanei) on the front or upper surface of the calcaneum between the ectal and the sustentacular facets of the calcaneum, and is inserted on the back or lower face of the astragalus, between the ectal and sustentacular facets of the astragalus. Both these pits or grooves are well marked in *Notharctus*.

The head of the astragalus is spheroid to ovate in shape, more or less flattened on the inner side.

This conformation of the head permits of a certain amount of twisting of the navicular upon the astragalus. The articular surface of the head is somewhat produced upward on to the front face, but this part rubs on the under side of a ligament running from a certain tubercle on the front of the neck of the astragalus to the dorsal surface of the ectocuneiform. This ligament is homologous with the dorsal astragalo-scaphoid and scapho-cuneiform ligaments of man. The tubercle in question is present in both *Lemur* and *Nŏtharctus*. The posteroinferior part of the head, above the navicular facet and below the sustentacular facet, articulates with, and rests upon, the broad tibio-navicular ligament.

Fig. 20. Right astragalus of "*Adapis magnus*." After Filhol. Natural size.

The astragalus of *Notharctus* differs from that of *Lemur* in the following details: the neck is relatively longer, the trochlea narrower, the facet for the fibula is more concave, the concavity of the ectal facet is more pronounced, the pit for the posterior astragalo-fibular ligament is deeper. But these are all minor differences of no importance in comparison with the fundamental agreements observable in every part of the bone.

To sum up with regard to the function of the astragalus in *Notharctus* and in later primates, this bone transmits the weight of the body from the tibia and fibula above to the calcaneum and navicular below. In leaping, on the contrary, the astragalus transmits the thrusts from these elements upward. The joint at the trochlea is hinge-like and permits motion chiefly in the plane of the tibia. The crossing of the astragalus and calcaneum, so that the neck of the astragalus is sharply inclined from without inward and downward, seems to be connected chiefly with the inverted position of the pes, the sole of the foot being appressed to the outer side of the supporting trunk or branch and the hallux, on the inner side, raised on a higher level; as a result of this the navicular through the pressure of the entocuneiform stands on higher level than the cuboid, so that it carries with it the head of the astragalus, the neck of the astragalus consequently assuming an oblique position. In specialized cursorial animals, on the other hand, the crossing of the astragalus upon the calcaneum is less pronounced, and the neck of the astragalus tends to get in line with the tibia.

For similar reasons the head of the astragalus is twisted around toward the inner side, that is because the whole inner side of the tarsus is twisted toward the inner side along with the hallux. The rocking of the astragalus upon the calcaneum, and the cog-tooth relation of the ectal astragalo-calcaneal facets have been mentioned above, as well as the axle-like function of the posterior astragalo-fibular and the posterior astragalo-tibial ligaments. The ball-like head of the astragalus permits a wide degree of flexion of the foot and considerable twisting of the navicular upon the astragalus.

Such were the chief morphological and functional characteristics of the astragalus of these relatively primitive Eocene primates. Together with other evidence, they indicate a long course of arboreal adaptation preceding the lemuroid stage.

Calcaneum

Plate XXXI; Text Fig. 21

While the joint between the tibia and fibula and the astragalus serves as a hinge, the calcaneum serves as a lever to throw the body forward in leaping. We may, therefore, consider the tibio-astragaloid joint as the fulcrum of a lever of the first class, the pull of the muscles of the calf as the power, and the reaction of the supporting medium against the thrust of the foot as the resistance. In order to gain great speed the fulcrum would be placed near the power and so we find that the power-arm of the lever, represented by the length of the tuber calcis, is short, while the resistance arm, which is the distance from the astragalo-tibial joint to the ground, is long. This relation, already established in *Notharctus*, is emphasized in many modern lemurs and carried to an extreme in *Tarsius* and the Galagos.

The calcaneum of *Notharctus* is fully as lemur-like as is the astragalus. The back of the tuber calcis is ovoid, with a pointed upper end, and a dorsoventrally convex surface for the tendo Achillis. The inner side of the tuber is concave where it curves around the tendon of the flexor longus hallucis. The ectal and sustentacular facets are substantially similar, and so is the interosseous groove between them. The wide lower or anterior part of the upper surface is roughened for the external calcaneo-astragaloid ligament and for the short extensors of the digits. The lower or distal end has a concave facet for the cuboid and in some specimens there is a pit for the calcaneo-cuboid ligament. The outer side of the

Fig. 21. Comparative series: left astragalus of *Notharctus pugnax*, "*Adapis parisiensis*," and *Pelycodus frugivorus*. × $\frac{3}{2}$.

1. *Notharctus pugnax*, Amer. Mus. No. 11721. Outer side.
2. "*Adapis parisiensis*." Amer. Mus. No. 10016. Outer side.
3. *Pelycodus frugivorus*. Amer. Mus. No. 16852. Outer side.

4, 5, 6. The same specimens, front, or dorsal view.

shaft is flattened, sometimes bearing a roughened peroneal spine below the ectal facet. Between this spine and the sustentaculum is a prominent groove for the flexor longus hallucis. The posterior surface near the lower end bears a tuberosity for the attachment of the short plantar ligament.

Thus the calcaneum of *Notharctus* is only a little less specialized for arboreal leaping than is that of *Lemur,* the chief difference being that the sustentaculum tali is nearer the lower end than it is in the modern genus.

Cuboid

Plates XXX, XXXI

The cuboid of *Notharctus* is equally lemuroid in type. It is flattened dorsoventrally, is subrectangular, with the long axis continuous with that of the calcaneum. The cuboid affords a firm base for the calcaneum and receives the lateral thrusts of the navicular and ectocuneiform. It rests in turn upon digits IV and V. There is but little motion between the cuboid and the elements around it. It can twist upon the lower end of the calcaneum by means of a subconical elevation which is received into a corresponding depression of the lower end of the calcaneum. It abuts laterally against the navicular and ectocuneiform by means of flattened or slightly convex articular surfaces. Externally it bears a prominent projecting tubercle which is deeply grooved by the tendon of the long peroneal muscle; this tendon prevents lateral displacement of the cuboid. On its lower or posterior face the cuboid is tied to the calcaneum by the calcaneo-cuboid ligament. The groove for the peroneus longus passes obliquely downward and inward across the posterior face of the cuboid, and is covered by the cubo-metatarsal ligament. The concave distal end receives the convex facets of metatarsals IV and V.

The principal difference from the cuboid of *Lemur* is that in *Notharctus* this element is narrow transversely in proportion to its height.

Navicular

Plate XXX; Text Fig. 22

This bone forms a base for a system of converging elements, which comprises the three cuneiforms and their attached digits. Thus it receives the thrusts from these elements below and from the calcaneum above. The bone slants sharply inward, backward and downward in such a way that its under surface flanks medially the deep gutter for the flexor tendons on the under side of the tarsus. But the slanting position of the navicular is especially connected with the turned-in position and the thumb-like character of the hallux. On the under side, the navicular is held in place especially by the strong wide tibio-navicular ligament, which runs from the proximal, internal tip of the navicular beneath the head of the astragalus to the sustentaculum tali and to the lower end of the internal malleolus. The navicular abuts against the cuboid laterally by a flat facet on its outer side at the lower end. On its front surface, immediately above the ectocuneiform, it bears a low rounded eminence to which is attached the scapho-cuneiform ligament. This eminence is more pronounced in *Notharctus* than it is in *Lemur.* Just above the facet for the entocuneiform on the posteroinferior corner of the bone, there is a smooth articular surface for the tendon of the tibialis posticus muscle which is inserted on the under side of the navicular and on the dorsointernal rim of the entocuneiform.

The surfaces and facets of the navicular of *Notharctus* are all peculiarly lemurine in type. It has a deeply concave facet above for the head of the astragalus and this concave border runs dorsointernally into a process for the attachment of the tibio-navicular ligament. The bone bears below a triad of facets, of which the inner two, for the ento- and mesocuneiform respectively, are convex, the outer concave. The middle one, however, is more convex than the homologous facet in *Lemur* and is not displaced posteriorly but is in line with the other two, these differences being correlated with certain differences in the mesocuneiform to be noted below.

Ectocuneiform

Plate XXX

The ectocuneiform forms the keystone of the transverse arch of the instep. It is compressed laterally between the mesocuneiform internally and the cuboid externally, and it is extended vertically (or anteroposteriorly when the foot is flat on the ground). It receives the oblique transverse thrusts from the hallux, which are transmitted through the mesocuneiform and through the upper end of metatarsal II, and in turn it distributes these thrusts to the navicular, cuboid and digits III and IV. It also transmits proximodistal thrusts from the navicular to digits III and IV and vice versa.

On the dorsum of the foot the ectocuneiform is decidedly narrower at the upper or proximal end than it is at the lower or distal end. The narrow upper end bears a slightly concave facet for the anterior pedicle, or dorsolateral facet, of the navicular. The wide lower end bears a concave triangular facet for metatarsal IV. The inner or flat side bears near the upper end a proximodistally extended, slightly concave, narrow facet for the mesocuneiform, and near the lower end a flat facet for metatarsal II. The outer or lateral side, as seen on the dorsum of the foot, is concave near the upper end and bears a flat upper facet for the cuboid. The sinus, or concavity, on this outer side is partly filled by the cubo-ectocuneiform ligament; below, or distally, the lateral side bears a concave lower facet for the cuboid.

The plantar aspect of the bone on the under side of the tarsus is very narrow, while the sides of the bone beneath the dorsum and facing the mesocuneiform and the cuboid respectively are, as it were, pressed in towards each other.

The deep portion of the upper or proximal end, deep to the convex facet for the navicular already mentioned, ends proximally in a narrow keel bearing on its outer or lateral side a facet for the deep surface of the cuboid, and on its inner side a flat facet for the deep portion of the mesocuneiform. Thus the deep portions of the cuboid and of the mesocuneiform arch over the deep upper end of the ectocuneiform and are in contact above it. This is a result of the lateral folding of the foot so that the plantar surface of the hallux inclines toward those of the other digits. To the prominent tubercle, which is immediately below or distal to the above described keel, and which is compressed laterally and extended proximodistally, may have been attached a transverse ligament, running from the entocuneiform to the meso- and ectocuneiforms, and a proximodistal ligament running down to the back of metatarsal III.

The foregoing description of the ectocuneiform of *Notharctus* also applies word for word to that of *Lemur*. Nevertheless, there are a few quite minor differences that distinguish the ectocuneiforms of these two genera. In *Lemur* the dorsal aspect of the bone is more rectangular and the sinus that separates it from the cuboid is less conspicuous. The proximal facet for the navicular is wider and the tubercle on the plantar surface is much less prominent. The facet for metatarsal II on the inner side of the bone does not extend nearly so far up toward the proximal end of the bone, as metatarsal III is not thrust upward so far between the ento- and the ectocuneiform.

Mesocuneiform

Plate XXX; Text Fig. 22

This bone being wedged in between the ento- and ectocuneiform forms part of the transverse arch of the instep, consisting of the cuboid and the three cuneiforms. In the front view the mesocuneiform of *Notharctus* is rectangular, the long axis being nearly vertical, while in modern lemurs the bone is of varying shape but always more oblique in position, so that it widely overlaps the entocuneiform on account of the wider divergence of the hallux in the modern genera. But, in some respects, there are greater differences in the position and form of the mesocuneiform within the genus *Lemur* than there are between a certain specimen of *Lemur varius* and the specimens of *Notharctus*.

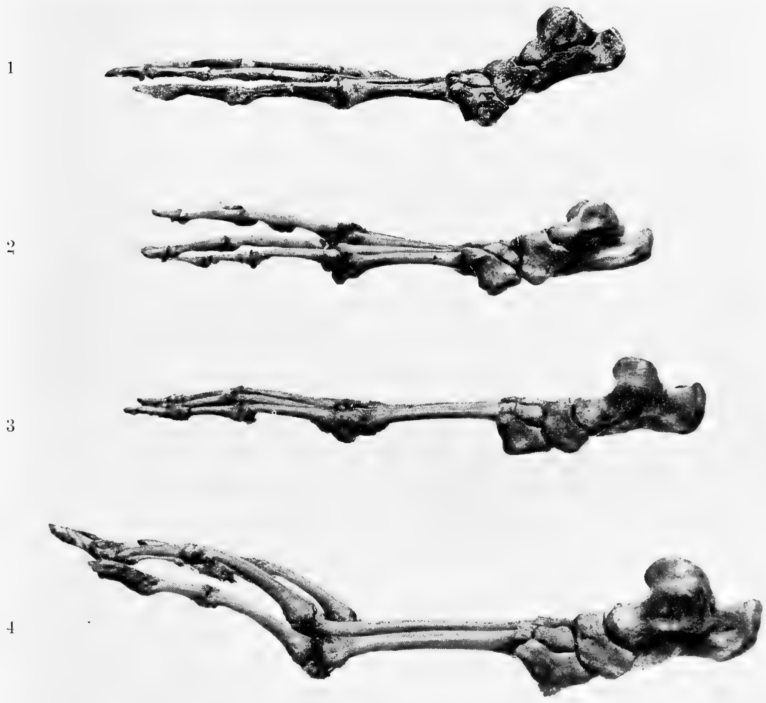

Fig. 22. Comparative series: right pes, inner side, of *Notharctus, Lemur, Cebus, Macacus,* after the removal of the hallux. Natural size.

1. *Notharctus osborni.* Amer. Mus. No. 11474.
2. *Lemur mongoz.* Amer. Mus. No. 22886.
3. *Cebus hypoleucus.* Amer. Mus. No 14016.
4. *Macacus nemestrinus.* Amer. Mus. No. 14012.

The general form of the mesocuneiform of *Notharctus* is irregularly wedge-like, the narrow edge being on the plantar aspect of the tarsus. The bone is fastened in place on the dorsal aspect by transverse ligaments and on the plantar aspect by the deep plantar ligaments, attached to the tubercle at the upper end. The bone is less warped and twisted than that of *Lemur*, a condition which is again correlated with the sharper divergence of the hallux in that genus.

Entocuneiform

Plates XXX, XXXI; Text Fig. 22

The internal cuneiform affords a wide base for the very large hallux. It is typically lemuroid in form, differing chiefly in the more bulging contour of its posterior surface. Its most conspicuous feature is the wide concavoconvex facet for the hallux. On its front face it bears a round conspicuous tubercle for the attachment of a stout ligament connecting it with the upper end of the hallux (homologous with the lateral tarso-metatarsal ligaments of man), and on its rear margin it bears a prominent compressed eminence with an articular surface for the tendon of the flexor longus hallucis and for the fascia of the flexor brevis hallucis. The (external) side of this tuber near the base gives insertion to ligaments running transversely to the ectocuneiform, while in front of this was a ligament that was attached to the mesocuneiform.

The facet for the navicular, which occupies the whole upper surface of the bone, is concave. The posterosuperior rim of the bone gives insertion to the tendon of the tibialis posticus muscle.

The entocuneiform takes part with the cuboid and with the other cuneiform bones in the formation of a deep gutter for the flexor tendons of the foot. It abuts laterally against the upper end of the second metatarsal and against the mesocuneiform.

Hallux

Plates XXX, XXXI; Text Figs. 22, 23

As already stated, *Notharctus* progressed chiefly by leaping from branch to branch, grasping the branches at the end of each leap with the hands and feet, but especially with the latter, as do modern lemurs.

The hallux of *Notharctus* is a highly specialized organ of locomotion which in functional importance was equivalent to all the remaining digits together, since it constituted one half, and that the more active one, of a pair of pincers, the remaining digits collectively forming the opposing and more passive half. By means of the powerful flexors and of the massive adductors of the hallux the great skin pads on its plantar surface were pressed against the supporting branch, while the corresponding pads on the sole of the foot were pressed against the branch in an opposing direction.

The first metatarsal ends proximally in a very large and transversely extended concavoconvex articular surface for the entocuneiform. This articular surface is guarded in front by a raised rim, culminating dorsally in an obtuse process, the rim and process together giving attachment to the ligaments that fasten the hallux to the entocuneiform and to the navicular respectively. The same articular surface is continued dorsoposteriorly on to the anterior face of the great process for the tendon of the peroneus longus muscle. This process is markedly asymmetrical, curving upward posteromedially. Its upper end, which gives insertion to the peroneus tendon, projects into the lower end of the deep gutter on the plantar surface of the foot described above. The anterolateral portion of this peroneal process bears an articular surface, marking the area of contact with the plantar surface of the second metatarsal. The presence of the metatarsal element at this point and its consequent contact with the peroneal process limits the adduction of the hallux, which thus could not be drawn in parallel to the other digits but always diverged markedly from them.

The shaft of the first metatarsal below the proximal expansion narrows rapidly, the anterolateral border being nearly straight, the posteromedial deeply incurved. The shaft is moderately short. Toward the distal end it again becomes very asymmetrical. The anterolateral border of this swelling is roughened for the internal lateral ligament, which connects the first metatarsal with the proximal phalanx. The posteromedial border of the lower part of metatarsal I bears a rounded pit probably for the external lateral ligament, which also passed to the proximal phalanx.

Fig. 23. Comparative series: right hallux of *Notharctus, Lemur, Cebus, Macacus.* Natural size.

1. *Notharctus osborni.* Amer. Mus. No.11474.
2. *Lemur mongoz.* Amer. Mus. No. 22886.
3. *Cebus hypoleucus.* Amer. Mus. No. 14016.
4. *Macacus nemestrinus.* Amer. Mus. No. 14012.

5, 6, 7, 8. Same series, top view.

The extreme distal end of metatarsal I bears a convex facet for the first phalanx; this facet is slightly extended on to the dorsal surface to permit extension of the hallux.

The plantar aspect of the distal end of metatarsal I bears two concave facets, or grooves, separated by a compressed ridge. Both the inner and the outer facets respectively articulated with the great sesamoids which were imbedded in the fibrous plate, on the plantar side of the capsule enclosing the metatarso-phalangeal joint. These sesamoids also gave insertion to the inner and outer tendons of the powerful flexor brevis hallucis muscle. (Fig. 25.) The articular surface of the median ridge between the sesamoids was worn smooth by the movement of the fibrous plate itself.

3 2 1

Fig. 24. Muscles of the hind limb of *Lemur*. After Cuvier and Laurillard.

1. Outer side, superficial muscles.
2. Outer side, after the removal of vastus externus and biceps.
3. Inner side of thigh and leg.

Abbreviations

a	gluteus maximus + agitator caudæ	α	gastrocnemius
a^1	gluteus medius	β	soleus
i	iliacus	δ	tibialis anticus
k, k^1	pectineus	δ^1	tibialis posticus
l, l^1, l^2	adductors	ε	peroneus longus
m	vastus externus	ϵ^1	peroneus brevis
o	crureus	ϵ^2	extensor quinti digiti brevis
p	rectus femoris	ζ	extensor digitorum longus
q	biceps	η	abductor hallucis
r	semitendinosus	κ	flexor brevis digitorum
s	semimembranosus	ν	adductor obliquus hallucis
t	sartorius	ν^1	adductor transversus hallucis
u	gracilis	π	lumbricales

The proximal end of the first phalanx is also asymmetrical, being produced into a shorter process on the anterolateral and a longer process on the posteromedial side. To the plantar surface of these processes were attached by ligament the lower end of the joint capsule, containing the sesamoids above mentioned and the two tendons of the flexor brevis hallucis. To the smaller anterolateral process was also attached the tendon of the adductor obliquus hallucis and to the larger posteromedial process the tendon of the abductor hallucis.

Fig. 25. Deep muscles of the plantar surface of the foot of *Propithecus diadema*. After Milne Edwards.

ι	flexor longus digitorum	μ	abductor brevis hallucis
ι^1	flexor longus hallucis	ν	adductor obliquus hallucis
λ^1	flexor brevis hallucis	ν^1	adductor transversus hallucis
λ^2–λ^5	flexor brevis digitorum	π	lumbricales

The shaft of the first phalanx is nearly as wide as that of metatarsal I; it is convex above and flat below. Distally it bears a spreading asymmetrical expansion which is produced posteromedially into a prominent process.

The plantar surface of this distal end bears a facet for the distal phalanx and for the large sesamoid of the joint capsule. This facet is convex distally, for the distal phalanx, and concavoconvex on the plantar aspect, for the sesamoid. The sesamoid was developed in the tendon of the powerful adductor transversus muscle.

The asymmetrical distal phalanx spreads widely at the proximal end, its anterolateral process being much the larger of the two. Onto its flattened plantar surface was inserted the tendon of the flexor longus hallucis. The distal end was spade-shaped and bore a large flat nail.

The foregoing description of the hallux of *Notharctus* would apply literally to that of *Lemur*, the chief difference being that in the modern genus the distal phalanx is more expanded. *Lepilemur* has the distal phalanx and nail still more expanded. The *Propithecus* hallux is very similar to that of *Notharctus*, but there are minor differences in proportion, the metatarsal in *Propithecus* being long.

The remaining digits of the pes of *Notharctus*, so far as known, require only brief notice, the chief differences from *Lemur* being the shortness of the metatarsals, the length and slenderness of the phalanges and the narrowness of the distal phalanges; the second metatarsal is not thrust up into the tarsus as far as it is in *Lemur*. The respective lengths of the digits are not positively known, but digit IV was probably the longest as in lemurs.

From the foregoing description and accompanying illustrations it is evident that the astragalus, the calcaneum, the navicular and the entocuneiform of *Notharctus* differ only in minor details and proportions from those of *Lemur;* the mesocuneiform is broader and more vertical in position and the ectocuneiform is narrower at its upper end. The cuboid is closely similar to that of *Lemur*, and likewise exhibits on its outer side a groove for the tendon of the peroneus longus. The hallux is not quite so divergent as that of *Lemur*, the metatarsals are shorter and much stouter; all the phalanges of digits II–V are more slender and narrow.

The pes of *Notharctus* is somewhat less specialized than that of any modern lemur. It is obviously also much more primitive than that of *Propithecus*, the chief specializations of which are the massive character of the tarsals and the great elongation of the metatarsals. The hallux of this genus is essentially similar to that of *Notharctus*. Evidently in *Propithecus* as well as in *Notharctus* the adductor hallucis, adductor obliquus hallucis and adductor transversus hallucis were very powerful, as indicated by the large size of the phalanges of the hallux. The internal process on the proximal end of metatarsal I is even heavier in *Propithecus* than it is in *Notharctus;* this process abuts against the mesocuneiform and metatarsal II when the digit is adducted; it interlocks with the surface of the cuneiform and metatarsal II, and offers a firm attachment for the tendon of the peroneus longus. This muscle was doubtless very effective in pressing the hallux and its pads against the side of the branches.

The pes of *Notharctus* differs in many important details from that of *Cebus*, the latter being less pincer-like and with a more mobile hallux, less widely divergent. The hallux of *Cebus* is held more parallel to the other digits than that of *Notharctus;* in correlation with this, the distal facet of the entocuneiform is less saddle-shaped and more convex and faces distally rather than medially. The entocuneiform of *Cebus* lacks the prominent posterior process seen in *Notharctus*. The metatarsal of the hallux in *Cebus* has the peroneal process much reduced; while the ectocuneiform is much shorter vertically. The cuboid is more rectangular; the groove on the back of the cuboid for the tendon of the long peroneal muscle is much broader and deeper. The astragalus has a more delicate neck and a wider trochlea. The calcaneum is widened and flattened on the plantar surface below and has an expanded tuber. Metatarsals II–V are all elongate and of subequal length. The distal phalanx of the hallux is narrow instead of broadly spatulate; the distal phalanges of digits II–V are very slender and slightly extended distally; they evidently carried very narrow nails which in *Cebus* are often almost claw-like.

Hapale differs from *Notharctus* in the markedly less divergent hallux, which is held nearly parallel to the other digits; in correlation with this the peroneal process of the end of metatarsal I is much reduced and all the digits end in claw-like nails, the first showing some traces of the flattening. For reasons given elsewhere it seems probable that these "claws" of *Hapale* are secondarily compressed nails and that *Hapale* is merely a specialized cebid with squirrel-like habits.

The pes of the Old World monkey *Macacus* differs from that of *Notharctus* as follows: the trochlea of the astragalus is widened, with a sharp internal rim; the neck diverges less from the trochlea and the head is more expanded; the calcaneum is shorter and wider; the navicular is much wider and has nearly parallel upper and lower facets; the distal facet of the entocuneiform is broadly convex rather than concave or saddle-shaped; the peroneal process of digit I is wide but less elongate; the cuboid is shorter and broader and so also are the meso- and ectocuneiform. The proximal phalanges are more sharply curved and flattened beneath; the distal phalanges are pointed, but show no superior dorsal groove. All these characters of *Macacus* are probably correlated with its more or less terrestrial and subcursorial habits.

Comparative Measurements of Pes

	Notharctus osborni No. 11474	*Notharctus tyrannus* No. 11478	*Lemur mongoz* No. 12822	*Lemur mongoz* No. 31254	*Lemur varius* No. 18040
Metatarsal I, Length	22.	25.	25.	—	38.
" I, Width of Distal End	6.4	7.	7.	—	6.4
" II, Length	23.	22.	27.	25.	36.
" II, Width of Distal End	4.	7.	4.3	4.3	5.3
" III, Length	23.5	21.	26.5	24.3	35.
" III, Width of Distal End	4.3	5.	4.	3.7	5.4
" IV, Length	—	21.	26.5	24.	33.
" IV, Width of Distal End	—	4.6	4.	4.7	5.3
" V, Length	20.	19.5	25.	23.	32.
" V, Width of Distal End	4.3	3.8	3.9	3.7	5.
Hallux, Length	44.	47.5	48.5	—	51.
Astragalus, Length, trochlea to head	14.5	14.5	16.	—	18.5
Calcaneum, Length	22.	—	23.	23.	29.
Navicular, Mid-length	6.5	—	7.	7.	8.
" Breadth	9.2	—	9.6	9.5	12.
Cuboid, Length	8.4	—	9.	9.	12.
" Breadth	7.5	8.	7.3	7.3	11.

THE VERTEBRAL COLUMN OF *NOTHARCTUS*

The principal specimens in which the backbone is represented are Amer. Mus. No. 11474, the type of *Notharctus osborni;* No. 11478, referred to *Notharctus tyrannus;* and No. 11473, referred to *N. osborni.* A few vertebræ are associated with other specimens of *Notharctus.* In no individual is the column completely preserved, but by a careful comparison of these specimens with each other and with those of existing lemurs and other primates the chief features of the backbone are revealed.

The vertebræ were worked out and restored by Mr. Albert Thomson, who used the vertebral column of *Lemur mongoz* as a model in restoring the missing parts. While further study has revealed many minor characters in which the vertebræ of *Notharctus* differ from those of *Lemur*, yet, in the main, that is the nearest available pattern.

The parts represented either by fragments or by more or less complete vertebræ are indicated in the following table.

Vertebræ Represented

	N. osborni No. 11474	*N. osborni* No. 11473	*N. tyrannus* No. 11478
C 1	+	0	+
C 2	0	0	+
C 3	+	0	
C 4	+	0	
C 5	+	0	
C 6	0	0	0
C 7	0	0	0
D 1	+	0	0
D 2	+	0	0
D 3	+	0	
D 4	+	0	
D 5	+	0	
D 6	+	0	
D 7	+	0	(?)+
D 8	+	0	(?)+
D 9		+	
D 10		+	
D 11	0	0	
?D 12	0	+	
L 1	0	+	0
L 2	+	0	+
L 3	+	0	+
L 4	+	0	+
L 5	+	0	+
L 6	+	0	+
L 7	+	0	+
L 8	0	0	0
S 1	+	0	+
S 2	0	0	+
S 3	+	0	+
Cd 1	(?)+	0	+
Cd 2	(?)+	0	0
Cd 3	(?)+	0	(?)+
Cd 4	(?)+	0	0
Cd 5	0	0	(?)+
Cd 6	0	0	0
Cd 7	+	0	0
Cd 8	0	0	0
Cd 9	0	0	(?)+
Cd 10	(?)+	0	(?)+
Cd 11	0	0	(?)+
Cd 12	(?)+	0	(?)+
Cd 13	(?)+	0	(?)+
Cd 14	(?)+	0	(?)+
Cd 15	(?)+	0	(?)+
Cd 16	(?)+	0	(?)+
Cd 17	(?)+	0	(?)+
Cd 18	0	0	(?)+
Cd 19–28 (?)	0	0	0

It is probable that the vertebral formula of *Notharctus* was very nearly, or actually, the same as that of *Lemur*, and that it may be written as follows:

C 7, D 12, L 8, S 3, and Cd ?

In *Lemur mongoz* it is:

C 7, D 12, L 6–8, S 3, Cd. 28.

In *Lemur varius* it is:

C 7, D 13, L 6, S 2–3, and Cd 27–29.

Thus, in the genus *Lemur* generally the lumbar vertebræ are 6 or 7, rarely 8, and the sacrals are usually 3, rarely 2.

The vertebral column in general approaches that of *Lemur mongoz* in the proportions of the cervicals, dorsals and lumbars; but the coccygeal vertebræ are considerably lighter and the tail much more slender.

The column is distinguished from that of the Cebidæ, as typified by *Cebus*, in having the dorsal centra narrower and shallower, the zygapophysial processes less extended transversely; the lumbars are more elongate, with wider parapophyses; the tail is very much lighter, more slender and is not prehensile; the sacral vertebræ are smaller and less expanded laterally. In the marmosets (Hapalidæ) the lumbar centra are relatively narrower than those of *Notharctus*, but both the sacrals and the caudals are in some respects intermediate in form between those of *Notharctus* and of *Cebus*. In the Old World monkeys, represented by the macaques, the dorsal and lumbar centra are much wider transversely, as well as the zygapophysial processes.

ATLAS.— The atlas of *Notharctus* is represented by two incomplete specimens associated respectively with *N. osborni*, Amer. Mus. No. 11474, and *N. tyrannus*, No. 11478. This atlas, so far as preserved, is clearly of the primate type, and differs from that of creodonts in having the transverse process much smaller and narrower, the neural arch narrower anteroposteriorly, and the posterior facets for the axis smaller; these characters being associated with the less powerful neck muscles of the primates. The atlas agrees closely with that of *Lemur mongoz*, No. 31254, except in the following points. (1) The smaller

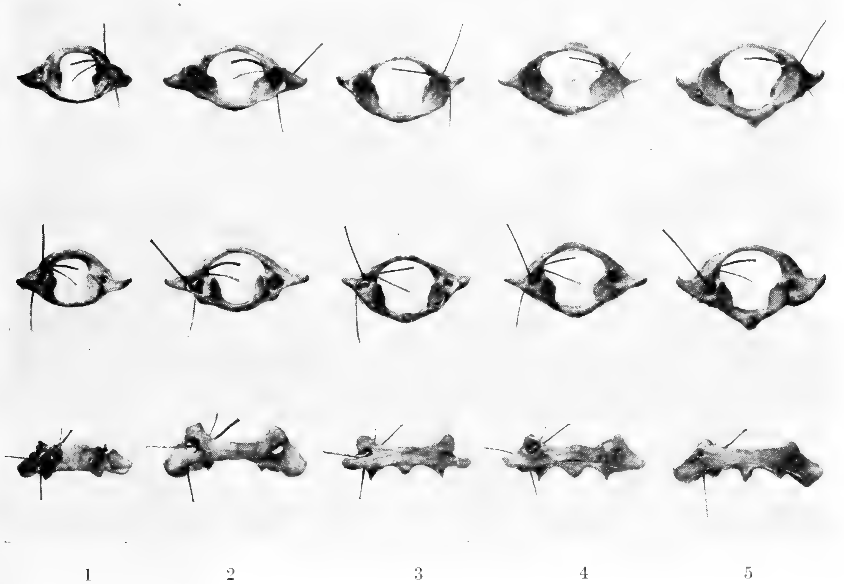

Fig. 26. Comparative series: atlas of *Notharctus* (1), *Lemur* (2), *Cebus* (3, 4), *Macacus* (5). Natural size.

Top row: anterior or cephalic view.
Middle row: posterior or caudal view.
Bottom row: dorsal view.

1. *Notharctus osborni*. Amer. Mus. No. 11474.
2. *Lemur mongoz*. Amer. Mus. No. 22886.
3. *Cebus apiculatus*. Amer. Mus. No. 30200.
4. *Cebus hypoleucus*. Amer. Mus. No. 14016.
5. *Macacus nemestrinus*. Amer. Mus. No. 14012.

The general course of the vertebrarterial artery and of the suboccipital nerve in relation to the foramina of the atlas are indicated by black and white threads respectively.

size of the cotylus for the occipital condyle, its flatness and more anteroposterior direction. (2) The stoutness and greater expansion anteroposteriorly of the transverse process. (3) The foramina and canals for the vertebral artery and for the suboccipital nerve are smaller. (4) The transverse process does not bridge over anteriorly the common canal for the vertebral artery and the suboccipital nerve, whereas in *Lemur* it does bridge over this canal and is thus joined to the anterior rim of the atlas. Another specimen of *L. mongoz*, No. 22886 (Fig. 26.2), is far more slender and the openings for the vertebral artery and suboccipital nerves are much expanded, while the neural arch is very narrow. Thus the difference between these two atlases of *Lemur mongoz* is greater than the difference between one of them and that of *Notharctus*.

The atlas of *Notharctus* in general is not dissimilar to that of *Propithecus*, except for the wide openings in the latter for the nerves and arteries.

As compared with the atlas of *Cebus*, that of *Notharctus* is stouter in all its parts; the facet for the occipital condyle is smaller and the openings for the nerve and artery are far more restricted; also the canal for the spinal cord was probably much smaller. As compared with the atlas of the macaque, similar differences obtain; the latter is of more slender structure and the openings for the spinal cord and for the vertebral artery and suboccipital nerve are much more expanded; the transverse process is also more delicate and pointed and the hypapophysis is extended ventrally, this implying a stout longus colli muscle.

Figures 26.1–5 show the course of the vertebral artery in these primates. As in other mammals it pierces the transverse process posteriorly, then turns sharply inward and joins the canal for the suboccipital nerve, again turning sharply forward and running into the brain-case through the foramen magnum. In *Notharctus* the smaller size of the openings for the spinal cord, for the suboccipital nerve, and for the vertebral artery is in harmony with its smaller brain and probably smaller blood-vessels; the existing forms, *Lemur*, *Cebus*, *Macacus* and the higher primates, showing a progressive enlargement of these elements.

Axis (Pl. XXXII).—The base of the axis is preserved in No. 11473, referred to *Notharctus osborni*. It agrees so closely with that of *Lemur mongoz* that in all probability the neural arch and neural spine displayed an equal resemblance. The lemur type of axis contrasts sharply with that of the creodont or of the modern carnivore in being much shorter anteroposteriorly, with smaller odontoid and with the neural arch and spine shorter and less expanded; the transverse process also is less expanded. These characters are correlated with the more slender occipital and cervical muscles of the lemurs, in contrast with the powerful neck of the carnivores.

The axis of *Notharctus* differs from that of *Lemur mongoz* in the more delicate odontoid process, in the less pronounced median hypapophysial ridge, and in the lack of a median posterior process. *Lemur varius* has all these characters more pronounced and progressive. The transverse processes in *Lemur* point backward more sharply than do those of *Notharctus*.

Cebus has the base of the axis widely produced posteriorly in the median line, in correlation with the more sharply curved neck, and the transverse processes are much larger and more divergent; the neural arch is more slender and the odontoid heavier, all these characters being associated with the expanded occiput and with the more upright pose of the animal. (Plate XXXII.)

Macacus (Pl. XXXII) has the odontoid larger and more protuberant; the transverse processes, as seen from below, form a pair of large sharply pointed wings, and the median ventral portion is widely produced posteriorly in correlation with the marked curve of the neck and upright pose of the head; the neural arch is very high and the neural opening very large; the posterior zygapophysial facets are more vertical and elongate and the opening for the vertebral artery is large. Thus, the axis of the Old World monkey is widely different from those of *Notharctus* and of *Lemur*, but is not so dissimilar to that of *Cebus*, except in minor characters. It differs widely from that of *Mycetes* (*Alouatta*), which is very massive, with a wide neural spine and heavier transverse processes, in correlation with the more powerful neck muscles.

CERVICALS 3 to 7.— The *Notharctus* and lemurine neck vertebræ differ from those of carnivores in being more depressed and extended anteroposteriorly with more delicate and shorter neural spines. The transverse processes are more elongate anteroposteriorly, less twisted dorsoventrally and more appressed laterally to the centra; the cervical vertebræ as a whole articulate in such a way that the head is held more upward, while in carnivores it is more inclined downward.

The third cervical vertebra is represented by a part of the neural arch and the zygapophysial facets in No. 11478; it resembles that of *Lemur* in the anteroposterior elongation of the neural arches, but the zygapophysial facets are somewhat more inclined dorsoventrally.

As compared with the third cervical of *Cebus*, that of *Notharctus* is stouter and more elongate; the zygapophysial facets are less vertical; it differs from that of *Macacus* in the greater elongation of the neural arch and spine and in the smaller vertical diameter of the neural tunnel.

THE FOURTH CERVICAL is represented by the neural arch in No. 11474 and is, on the whole, closest to that of *Lemur mongoz*. From that of *Macacus* it differs in having the anterior zygapophysial facet much smaller and less extended vertically; the neural arch is also wider anteroposteriorly and the neural tunnel smaller.

THE FIFTH CERVICAL.— The centrum and neural arch are much as in *Lemur mongoz* but the vertebrarterial canal is smaller and the neural arch heavier than those of *Cebus* and *Macacus*.

In the anteroposterior width of the neural arches *Notharctus* is much surpassed by *Alouatta* in which the powerful cervical vertebræ broadly overlap each other and are provided with large neural spines and broad transverse processes. A comparison with *Cebus*, however, suggests that these peculiarities of *Alouatta* are not directly inherited from a lemurine type like *Notharctus*, but are merely a specialization of the cebid type in adaptation to the great muscular development of the skull, neck, throat, and thorax, all these in turn possibly being a result of the enormous development of the vocal organs and lungs. Cervicals 3, 4, and 5 of *Alouatta* differ from those of *Notharctus* in having the zygapophysial facets more horizontal, the transverse processes much larger, and the posteroinferior prolongations of the centra much more pronounced.

Cervicals 6 and 7 are not preserved in *Notharctus*. In *Lemur* the sixth cervical differs from those of *Cebus* and *Macacus* in having the inferior lamella of the transverse process much elongate anteroposteriorly. In the seventh cervical of *Lemur* the diameter across the transverse processes is less than in *Cebus* and much less than in *Macacus*.

While regrettably incomplete, the fragmentary cervical vertebræ of *Notharctus* indicate that the neck differed only in minor details from that of *Lemur*. As compared with those of *Cebus* and *Macacus*, the individual vertebræ were probably narrower across the neural arches and transverse processes and longer anteroposteriorly, and the neural and arterial openings were more restricted.

DORSALS.— The first dorsal is known only from the centrum of No. 11474 which is nearest in form to that of *Lemur mongoz;* however, the anterior facet of the centrum is more nearly at right angles to the long axis of the centrum, whereas in *Lemur mongoz* it is more inclined. The centrum is much less expanded transversely than is the case in *Macacus*, is flatter inferiorly than that of *Cebus*, but is not nearly so flat or wide as that of *Alouatta*. Very probably the transverse processes in *Notharctus* were smaller and less extended laterally than are those of *Cebus* and still less than those of *Macacus*.

Dorsals 2 to 8 are represented by the centra in No. 11474, which agree so closely with those of *Lemur mongoz* that it is highly probable that the transverse processes, neural arches, and other features were equally lemurine. (Plate XXXII; Fig. 27.)

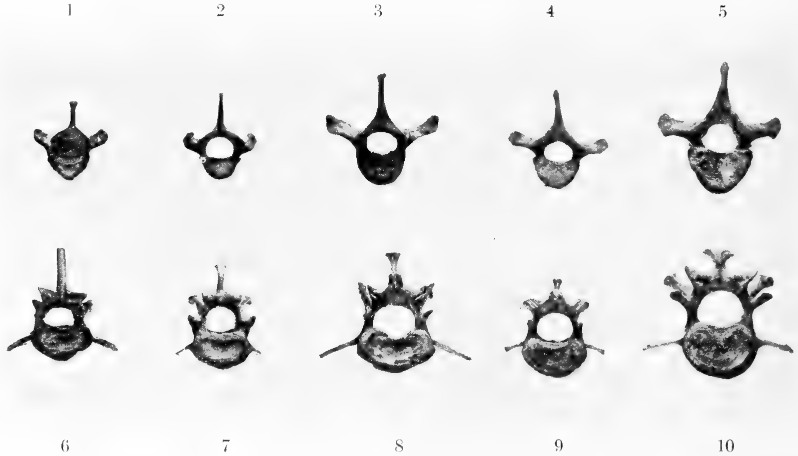

Fig. 27. Comparative series: single dorsal and lumbar vertebræ of *Notharctus* and other Primates. Posterior or caudal view. Natural size.

1. 8th (?) dorsal; 6. 3rd (?) lumbar — *Notharctus osborni*. Amer. Mus. No. 11474.
2. 8th dorsal; 7. 3rd lumbar — *Lemur mongoz*. Amer. Mus. No. 22886.
3. 7th dorsal; 8. 3rd lumbar — *Cebus hypoleucus* Amer. Mus. No. 14016.
4. 7th dorsal; 9. 3rd lumbar — *Cebus apiculatus*. Amer. Mus. No. 30200.
5. 9th dorsal; 10. 3rd lumbar — *Macacus nemestrinus*. Amer. Mus. No. 14012.

These lemurine dorsal vertebræ contrast with those of carnivores in having the centra more constricted or angulate in the median line below and the neural spines very much lower, especially in the anterior dorsals, the neural arches being more elongate, flatter and wider on top; the metapophyses, which lie external to the zygapophyses, in the lemurs, as seen from above, are directed forward rather than outward and are more protuberant and rounded; in the carnivores they are often more elongate anteroposteriorly; in the lemurs the facets for the ribs at the end of the transverse processes are larger and more circular. These and other differences in the neural arches and zygapophyses are associated with the markedly different shape of the thorax, which in lemurs, as in other arboreal animals, is widely bowed outward and shallow vertically, whereas in carnivores the thorax is typically compressed and deep.

The dorsals of *Notharctus* and *Lemur* are relatively smaller than those of *Cebus* and *Macacus*.

The centra are more compressed below and are excavated anteroposteriorly, whereas in *Cebus* they are flatter on the lower surface, and still more so in *Macacus*. The transverse processes are far less extended laterally, also the column narrows very rapidly from the lumbars to the mid-dorsal region, whereas in *Macacus*, and to a less extent in *Cebus*, it narrows very gradually as we pass forward.

Alouatta, in correlation with the great size and muscular development of the thorax, has the dorsal centra and neural spines very heavy, the latter closely imbricating; the facets for the tubercles of the ribs are very wide; the anterior dorsal centra are somewhat compressed below. In all these features *Alouatta* appears to be a specialized cebid rather than a primitive derivative of the lemurs.

In the marmosets the dorsal centra appear to be relatively shorter and wider than those of *Notharctus* and *Lemur*, the regional differentiation of the neural spines is sharper; but everywhere there is a fundamental resemblance with the dorsals of *Notharctus*.

Musculature of the Cervical and Dorsal Regions.— The agreement in form of the cervical, dorsal, lumbar and sacral vertebræ of *Notharctus* with those of lemurs, taken in conjunction with the similar agreement in the limb bones, is so close that we may confidently infer that the modern lemur (Fig. 2) has preserved the musculature of the Eocene lemur with very little change.

The neck of *Lemur* is much longer than that of either the South American monkeys or the catarrhines. In general, the neck muscles are arranged in such a way that the head is held more forward and not so much at right angles to the column as it is in the higher primates, as is indicated also by the fact that in the latter the neck vertebræ are compressed anteroposteriorly and widened transversely.

The thorax is less expanded than that of higher primates, the ribs being shorter and less robust; consequently the dorsal vertebræ are also less robust and have less widely extended transverse processes.

The eighth dorsal is the anticlinal, at which point the dorsal muscles end and the lumbar muscles become predominant.

Lumbars.— In contrast with those of carnivores, the lumbars of *Notharctus* and of *Lemur* differ in the form of the transverse processes; these are short and anteroposteriorly broad, whereas in typical carnivores they are long, narrow and sharply turned forward, a condition which is perhaps correlated with the superior cursorial powers of the hind limbs of carnivores. The centra of the carnivore lumbars are also flatter inferiorly than are those of lemurs.

Of the lumbar vertebræ of *Notharctus* the first and eighth are absent in Nos. 11474 and 11478, but lumbars 2–7 are represented in both specimens by more or less complete vertebræ. The lumbar centra are lemur-like: shallow vertically (Fig. 27), elongate anteroposteriorly (Plate XXXIII), with more or less sharp median inferior keels; whereas in *Macacus* they are deeper vertically and much wider inferiorly, with median keels reduced or absent. *Cebus* is to some extent intermediate, but the centra are deeper vertically and wider transversely than they are in lemurs.

The neural spines of *Notharctus* are stout and forwardly directed as in *Lemur*, although somewhat heavier than in *L. mongoz;* in *Macacus* the neural spines are much lengthened anteroposteriorly with depressed tips. In *Cebus* they are intermediate in form between those of *Notharctus* and of *Macacus*. The bases of the neural spines exhibit no traces of the paired "hyperapophyses" (Mivart) on either side of the mid-line which are characteristic of *Cebus* and *Alouatta*.

As in other primates, the lumbars of *Notharctus* bear posteriorly directed processes (anapophyses) immediately external to and beneath the postzygapophyses. The transverse processes, so far as preserved, are similar to those of *Lemur* but somewhat wider at the base; they spring from the sides of the centrum and are directed outward and downward, whereas in *Macacus* they are smaller, spring from points higher up on the sides of the centra, or even from the bases of the neural arches, and are less inclined downward. In *Cebus* the transverse processes are on the whole more like those of *Macacus* than like those of *Lemur*. In *Alouatta* they spring almost from the base of the neural arches. The lumbars of the marmosets may be regarded as modifications of the primitive lemurine type, but the neural spines and transverse processes are more delicate.

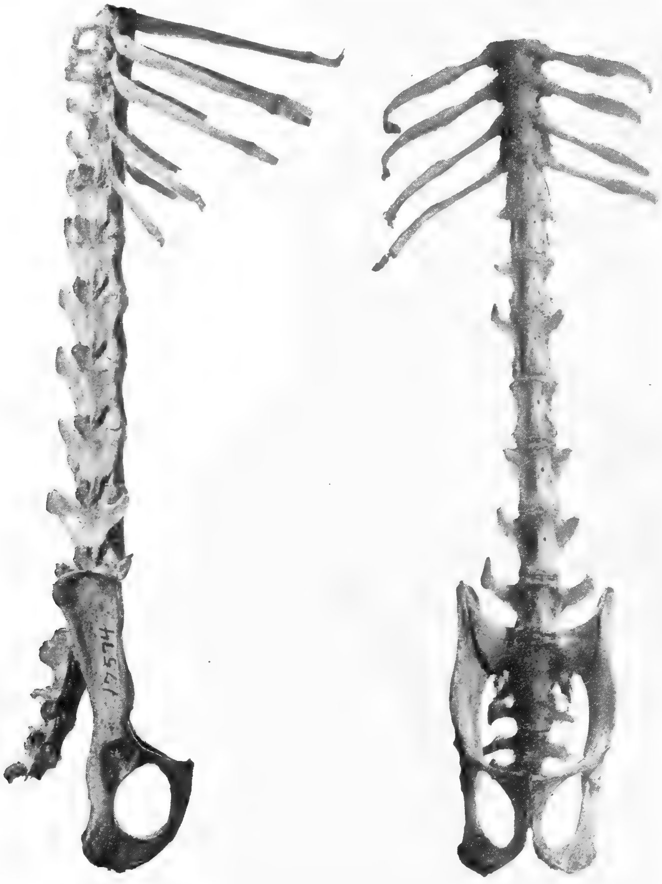

Fig. 28. Pelvis and vertebræ of *Hapale jacchus*. Amer. Mus. No. 17574. Lateral and ventral aspects. $\times \frac{3}{2}$.

MUSCULATURE OF THE LUMBAR REGION.— The form of the lumbar centra of *Notharctus* and *Lemur*, which are elongate, narrow and vertically shallow, are associated with a more horizontal pose of the body in resting; while the short, broad and vertically shallow lumbar centra of *Macacus* are associated with the habit of sitting upright and with the presence of expanded ischial tuberosities. In man these features of the lumbar centra are accentuated. *Cebus*, in the form of its lumbar centra, is perhaps nearer to *Macacus* than to the lemurs. *Hapale*, on the other hand, is somewhat nearer to the lemurs. Likewise the long forwardly directed neural spines of the lumbars in *Notharctus* and *Lemur* are associated with a more horizontal pose, whereas the widened and erect neural spines of the lumbars of *Macacus* are associated with a more upright pose in sitting. This line of specialization of the lumbar spines is carried gradually through the Old World monkeys and great apes and culminates in man, in which the lumbar spines are either vertical or directed backward. From these vertical or backwardly directed lumbar spines in man slips of the erector spinæ muscle pass forward, or upward, toward the dorsal vertebræ, and assist in extending the backbone, i. e., in throwing the lumbar region into a ventrally convex curve; they therefore render important service in the act of sitting upright as well as in bipedal locomotion. In the more quadrupedal lemurs, on the other hand, these muscular slips, passing from the forwardly directed lumbar spines, are especially useful in the act of leaping, by raising the fore part of the body.

The varied form and position of the transverse processes of the lumbar vertebræ in lemurs and higher primates are likewise associated with differences in methods of locomotion and consequently in the form and proportions of certain muscles, especially the quadratus lumborum and psoas. In man the quadratus lumborum arises in part from the crest of the ilium and from the transverse processes of the lumbar vertebræ (except the first and second?) and is inserted into the last rib and the transverse processes of lumbars 1, 2; the transverse processes of the human lumbars are directed dorsally so that the quadratus lumborum assists in extending the column and thus in maintaining the upright pose. In lemurs, on the other hand, the transverse processes of the lumbars are directed downward and forward and the quadratus lumborum doubtless assists in flexing the column, in the act of leaping. The psoas in man arises from the ventroexternal region of the posterior dorsal and lumbar vertebræ, especially from the transverse processes; it passes caudad in front of the pelvis and is inserted on the lesser trochanter, on the inner side of the femur; it coöperates with the iliacus and other muscles in flexing or pulling forward the femur, and in preventing the body from falling over backward. In the quadrupedal primates it is especially powerful in drawing the femur forward, and is attached to the posterior branch of the transverse processes.

In short, the lemurs, including *Notharctus*, in correlation with their superior leaping powers and more horizontal pose in sitting, have the stout lumbar neural spines directed forward, apparently in correlation with the forward pull of the erector spinæ; they have the lumbar transverse processes broad and forwardly directed, this implying powerful quadratus lumborum muscles, used in flexing the lumbar region in leaping; and finally, the transverse processes are provided with posterior branches for the insertion of the powerful psoas muscles, used in drawing the femora forward.

Differences in the form and arrangement of the muscles of the dorsal and lumbar regions no doubt determine in part not only the characteristic differences between dorsal and lumbar vertebræ, but also the more or less transitional character of the posterior "dorsals" and anterior "lumbars"; for in this region the muscles of the ribs and diaphragm, as well as the longissimus dorsi and the spinalis dorsi, give place to the quadratus lumborum, the psoas and the erector spinæ.

SACRUM.— The sacrum is partially preserved in Nos. 11474 and 11478. The closest resemblances are with *Lemur*, but the second and third sacrals are smaller, in correlation with the more slender tail. As in *Lemur*, the articular surface for the ilium is borne almost entirely by the first sacral vertebra (Plate

XXXII), whereas in *Cebus* it is borne by sacrals 1 and 2 and in *Macacus* and *Alouatta* all three sacrals broadly share the articular surface.

As compared with that of carnivores, the sacrum of lemurs differs chiefly in the greater length of the centra and in the more rectangular outline of the sacrum as a whole, which is caused by the flattening and widening of the transverse processes of the second and third sacrals and by the anteroposterior direction of the iliac articulation, which in the carnivores is more obliquely placed.

CAUDAL VERTEBRÆ (Plate XXXIV).— In No. 11474 the coccygeal vertebræ are represented by four centra and by some portions of the neural arch and zygapophyses. In No. 11478 (*N. tyrannus*) part of the zygapophysis of caudal 2 and the centrum and left zygapophysis of caudal 3 are preserved. The coccygeal vertebræ of *Notharctus*, as well as the more posterior caudals, are notably smaller than those of *Lemur*, this indicating a much more slender tail. The centra of the first three coccygeals of *Notharctus* are flattened below, with gently rounded anterior faces and flattened posterior faces. In *Macacus* the first and second coccygeal vertebræ have relatively very short centra, which are deeply excavated, or concave, below, and have the anterior and posterior faces strongly convex; the chevrons are comparatively slender. The third coccygeal vertebra in *Notharctus* and lemurs is flattened below; in *Macacus* it is longer and deeply excavated below, with strongly convex anterior faces.

The transverse processes in the coccygeals of *Lemur* and probably of *Notharctus* were widened anteroposteriorly, but in *Macacus* they are relatively narrow anteroposteriorly.

No chevrons were preserved in *Notharctus* but they were probably shaped much as in *Lemur*.

The fifth coccygeal vertebra of *Notharctus* had the centrum widened and flat below, as in *Lemur*.

In *Cebus* the coccygeal vertebræ are on the whole intermediate between those of *Macacus* and of lemurs. In *Alouatta* they are exceptionally large and massive.

The sixth caudal vertebra, following the last coccygeal, is not preserved, but in all probability it was shaped as in *Lemur*, namely, with a very flat wide centrum and with the lateral processes running the whole length of the centrum, the zygapophyses widely spreading and the neural arch extremely low and reduced. The reason for inferring this similarity between *Notharctus* and *Lemur* in the sixth caudal is that the seventh, which is preserved in *Notharctus osborni*, No. 11474, is essentially of the lemur type, except that it is not so much expanded transversely and is much smaller in all dimensions. This vertebra shows the last vestiges of the extremely reduced neural arch, which in the next vertebra is represented merely by a groove.

The seventh caudal differs from that of *Macacus* in having the centrum flat beneath and the anterior zygapophyses smaller. The ends of this vertebra differ from those of *Macacus* in not having two sharp downwardly projecting median processes. The greatest differences, however, are seen in comparison with *Cebus* and *Alouatta;* in these the seventh caudal is widely expanded at the anterior and posterior ends; the transverse processes and zygapophysial processes are far heavier, and the chevrons are borne on two prominent ventral processes which are lacking in *Cebus*.

The remaining tail vertebræ of *Notharctus* are more cylindrical, less depressed dorsoventrally than those of *Cebus* and have much smaller transverse processes. They differ from those of *Macacus* in minor details.

A detailed comparison of the posterior caudal vertebræ with those of *Lemur* indicates that in No. 11474 the seventh (?) and the twelfth (?) to the seventeenth (?), inclusive, are represented by more or less perfect vertebræ. In No. 11478 the twelfth (?) to the twentieth (?), inclusive, are represented. All these vertebræ are narrower and less depressed than those of *Cebus* and are shorter than those of *Lemur*, the cross section of the vertebræ being less angular; but they are a little more vigorously developed than those of *Propithecus*, which are very slender cylinders almost without transverse processes.

The functional significance of these structural details may be elucidated by a brief comparative survey of the musculature of the tail of various mammals.

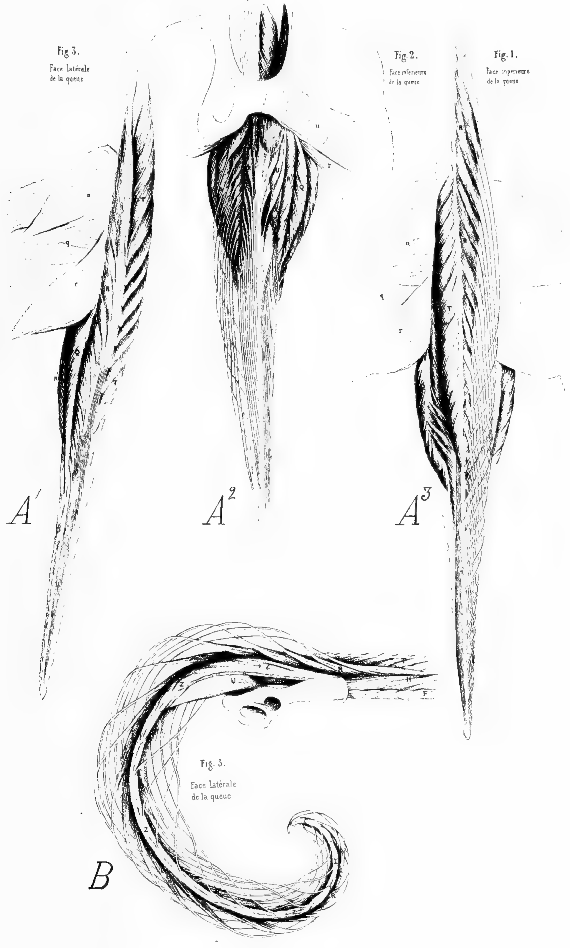

Fig. 29. Tail muscles of mammals. After Cuvier and Laurillard.

A^1 *Castor*, lateral view, left side.
A^2 The same, ventral view.
A^3 The same, dorsal view.
B *Cebus*, lateral view, right side.

Musculature of the Sacral and Caudal Regions.— Cuvier and Laurillard (Recueil de Planches de Myologie) give dissections of the tail of several animals with prehensile tails, such as *Cebus*, *Nasua*, *Tamandua*, and of others, such as the kangaroo, the beaver, and the *Ornithorhynchus*, which have very heavy tails adapted for other purposes. From these plates (Fig. 29) may be derived the following general conception of the musculature and mechanism of the tail in mammals:

1. *Extensor caudæ medialis.*— The deepest layer of muscles, on the dorsal aspect of the tail, consists of the *superior interspinal muscles* (T, " interépineux supérieurs" or "lumbo-sacro-coccygien" = extensor caudæ medialis, Reighard and Jennings) which lie around the dorsal spines and are serially homologous with the spinalis dorsi and multifidus spinæ. They are continued forward over the sacrum, on to the lumbar region, and extend back some distance behind the coccyx, becoming gradually weaker in the posterior tail vertebræ. Each segment of this series rises from the sides of the neural spine and from the metapophysis, or prominence above the prezygapophysis; it runs over the next following vertebra and is inserted around the base of the neural spine of the second vertebra following. This muscle assists in raising the tail.

2. *Extensor caudæ lateralis.* The *superior sacro-coccygeal muscles* (R, "sacro-coccygien supérieurs" or "lumbo-sus-caudien").— This series extends over the lumbar, sacral, and caudal vertebræ, becoming reduced posteriorly. Each segment rises from the area lying between the base of the prezygapophysis and the transverse process; it is thus lateral to and more superficial than the superior interspinal muscles. Each segment of this series ends in a long thin tendon, and these tendons form a large longitudinal bundle running along the upper side of the tail; they are inserted into or near the posterior ends of the transverse processes along with the intertransversal muscles (Z). The superior sacro-coccygeal muscles (R) together with the superior interspinals (T) cooperate in raising the tail, and are hence named by many authors levator caudæ internus and levator caudæ externus, respectively.

3. *Abductor caudæ internus.* The *intertransversals* (Z, "intertransversaires").— These deep-seated muscles form a wedge-shaped series arising from the sides of the posterior sacral, coccygeal and caudal vertebræ, immediately above and below the transverse processes and ventral to the superior sacro-coccygeal muscles. Each one passes backward and is inserted into the posterior swelling of the transverse process of the next following vertebra. They are the chief agents in curving the tail from side to side.

4. *Inferior interspinal series* (V, "sous-caudien, interépineux inférieurs").— These arise from the ventral surfaces of the centra and from the transverse processes of the sacral, coccygeal and caudal vertebræ, and each segment is inserted posteriorly into the chevron of the second following vertebræ. They assist in flexing the tail.

5. *Ischio-coccygeal* (Q, "ischio-coccygien externe" abductor caudæ ventralis).— This ischio-coccygeal muscle arises from the dorsal rim of the ilium above and behind the acetabulum; it passes upward and backward and is inserted into the transverse processes of the coccygeal and first few caudal vertebræ.

6. *Ilio-coccygeal* (U, "iléo-sous-caudien," part of levator ani group).— Arises from the ischial spine above and behind the acetabulum; it passes upward and backward and is inserted into the ventral surface of the upper caudal vertebræ. These muscles (Q, U) are broadest opposite the coccygeal and upper caudal vertebræ, which have the largest chevrons, and diminish rapidly in the posterior caudal vertebræ. They act powerfully to lower the proximal end of the tail; they are immensely developed in the kangaroo and of moderate size in the lemurs.

7. *Inferior sacro-coccygeal series* (R′ "sacro-coccygien inférieur) or "lumbo-sous-caudiens").— This is the chief antagonist of the superior sacro-coccygeal series; it arises from the inferior surfaces of the sacrum and of the transverse processes of the caudal vertebræ. The fleshy belly of each segment is continued posteriorly into a long tendon and these tendons together form a prominent bundle on the

lower lateral surface of the tail. Each segment passes backward and upward and is inserted into the transverse process of the next following vertebra. This series tends to depress the tail and to flex each segment on the one in front of it, and with the superior sacro-coccygeal series is powerfully developed in all animals with prehensile tails.

To sum up the general positions and functions of these muscles, we have (1) around the neural spines and metapophysial processes of the lumbar, sacral, and caudal vertebræ, the superior interspinals (T) (extensor caudæ medialis); (2) lateral to these the superior sacro-coccygeal (R) series (extensor caudæ lateralis), lying between the zygapophyses and the transverse processes and serving to raise the tail; (3) the intertransversal muscles (Z), (abductor caudæ internus), lying above and below the transverse processes and on the sides of the centra, forming a wedge-shaped series which move the tail from side to side; (4) the *inferior interspinal* (V) series on the ventral surface of the centra, attached to the chevrons and serving to lower the tail; (5) the *ischio-caudals* (Q) and the *ilio-coccygeals* (U) rising from the inner surface and dorsal rim of the ischium and ilium respectively, and being inserted into the transverse processes and chevrons, especially of the coccygeal and upper caudal vertebræ, pulling the tail powerfully downward and more or less laterally; (6) the *inferior sacro-coccygeal* series rising from the transverse processes and ridges of the caudals and inserted into the transverse processes of the second following vertebra, along with the intertransversals.

The myological significance of the characters of the tail vertebræ of *Notharctus* is therefore as follows. The slender coccygeal vertebræ, with narrow transverse processes, and the smaller size of the facets for the chevrons, all indicate more slender muscles at the root of the tail (especially the superior sacro-coccygeal, ilio- and ischio-coccygeal and intertransversals). The subcylindrical form of the more posterior caudals, their small transverse processes and small zygapophysial processes, in contrast with the depressed vertebræ and strong lateral and zygapophysial processes of *Cebus*, all indicate a non-prehensile tail with weak intertransversals, superior and inferior sacro-coccygeals; it was probably almost whip-like as in *Propithecus*, less muscular than in *Lemur*, and far less than in *Cebus*.

Measurements of the Vertebræ

	N. osborni No. 11474	*N. osborni* No. 11473	*N. tyrannus* No. 11478	*L. mongoz* No. 22886	*L. mongoz* No. 31254	*L. varius* No. 35396
	mm.	mm.	mm.	mm.	mm.	mm.
Total Length of Lumbar Vertebræ (L2–L7)	92.	—	93. est.-	—	91.5	119. est.
Atlas, anteropost diam., above vertebrarterial foramen	5.5	—	6.5	—	6.5	—
Cervical 3, anterior zygapophysis to posterior zygapophysis	6.	—	—	—	5.5	8.
Cervical 4, prezygapophysis to postzyg. facet, ant. post. diameter	6.	—	—	—	5.5	8.
Dorsal 1, ant. posterior diam. of centrum	7.5	—	—	—	6.	7.5
" 1, transverse " " "	7.4 est.	—	—	—	9.	
" 2, ant. post. " " "	8.	—	—	—	5.9	7.6
" 2, transverse " " "	8.	—	—	—	8.3	10.2
" 3, ant. post. " " "	7.8	—	—	—	6.8	8.7
" 3, extreme trans. " " "	8.5	—	—	—	7.4	10.
" 4, ant. post. " " "	8.3	—	—	—	6.	10. est.
" 4, transverse " " "	7.	—	—	—	8.	—
" 5, ant. post. " " "	7.3	—	—	—	7.	9.5 est.

Measurements of the Vertebræ (*Continued*)

	N. osborni No. 11474	*N. osborni* No. 11473	*N. tyrannus* No. 11478	*L. mongoz* No. 22886	*L. mongoz* No. 31254	*L. varius* No. 35396
Dorsal 5, transverse diam. of centrum	7.5 est.	—	—	—	7.3	10.5
" 6, ant. post. " " "	7.8	—	—	—	7.3	—
" 6, transverse " " "	8.2	—	—	—	7.7	—
" 7, ant. post. " " "	8.5	—	7.3	—	7.3	9.3
" 7, transverse " " "	8.	—	8.	—	6.8	9.
" 8, ant. post. " " "	8.2	—	7.4	—	7.5	9.5
" 8, transverse " " "	8.3	—	8.2	—	7.4	10.
" 9, ant. post. " " "	—	8.5	—	—	8.	9.8
" 9, transverse " " "	—	8.2	—	—	7.9	11.
" 10, ant. post. " " "	—	10.	—	—	8.7	10.7
" 10, transverse " " "	—	8.3	—	—	7.9	10.
" 11, ant. post. " " "	—	—	—	—	10.	—
" 11, transverse " " "	—	—	—	—	9.5	—
" 12? ant. post. " " "	—	12.2	—	—	11.	12.5
" 12? transverse " " "	—	9.2	—	—	9.6	11.4
First Lumbar, ant. post. " " "	—	13.	—	—	12.4	—
First Lumbar, transverse " " "	—	14.	—	—	10.3	—
Second Lumbar, ant. post. " " "	13.3	—	14.	—	13.4	16.3
Second Lumbar, transverse " " "	10.	—	11.	—	10.9	14.
Third Lumbar, ant. post " " "	14.8	—	14.3	—	13.7	16.2
Third Lumbar, transverse " " "	11.5	—	12.	—	11.1	14.3
Fourth Lumbar, ant. post. " " "	15.5	—	15.5	—	14	16.4
Fourth Lumbar, transverse " " "	11.6	—	13.5	—	12.5	14.3
Fifth Lumbar, ant. post. " " "	—	—	16.	—	15.	17.
Fifth Lumbar, transverse " " "	—	—	—	—	12.	15.3
Sixth Lumbar, ant. post. " " "	15.5	—	15.5	—	15.3	16.
Sixth Lumbar, transverse " " "	12.7	—	12.3	—	12.3	15.
Seventh Lumbar, ant. post. " " "	13.5	—	14.7	—	14.3	15.7
Seventh Lumbar, transverse diam. of centrun	12.	—	13.3	—	12.7	15.
Eighth Lumbar, ant. post. " " "	—	—	—	—	11.4	13.5
Eighth Lumbar, transverse " " "	—	—	—	—	12.	13.5
First Sacral, ant. post. " " "	11.4 est.	—	11	11.	10.5	12.5
First Sacral, trans. diam. of centrum, across process	—	—	—	28.5	22.5	29.
Second Sacral, ant. post. diam. of centrum	—	—	10.	10.5	10.	10.5
Second Sacral, trans diam. of centrum, across process	—	—	—	22.	18.2	20
Third Sacral, ant. post. diam. of centrum	9.3	—	10.2	10.	9.5	11.6
Third Sacral, transverse " " "	—	—	—	10.	8.6	11.5
Third Sacral, trans. diam. of centrum, across process	—	—	—	27.	19.	22.
Caudal 1 (coccygeal), ant. post. diam. of centrum	8.4	—	—	8.7	—	—
Caudal 1 (coccygeal), trans. diam. of centrum	7.	—	—	9.	—	—
				24.5 (across process)		
Caudal 2, ant. post. diam. of centrum	8.2	—	—	9.5		
				27. (tr. across process)		
Caudal 3, " " " " "	8.5	—	—	9.		
				24		
Caudal 4, " " " " "	10.4	—	—	10.5		
				21.4 (" " ")		
Caudal 5, " " " " "	—	—	—	11.3		

Measurements of the Vertebræ (*Continued*)

	N. osborni No. 11474	*N. osborni* No. 11473	*N. tyrannus* No. 11478	*L. mongoz* No. 22886	*L. mongoz* No. 31254	*L. varius* No. 35396
Caudal 5, transverse diam. of centrum			8	17.		
“ 6, ant. post. “ “ “				18.5		
“ 6, trans. diam. across process				14.		
“ 7, ant. post. diam. of centrum	17.4			24.		
“ 7, trans. diam. across process				12.5		
“ 8, ant. post. diam. of centrum	—	—		28.		—
“ 8, trans. diam. across process		—		11		
“ 9, ant. post. diam. of centrum		—		28.5		
“ 9, trans. diam. across process				11.4		
“ 10, ant. post. diam. of centrum				29		
“ 10, trans. diam. across process				9.4		
“ 11, ant. post. diam. of centrum				28.5		
“ 11, trans. diam. across process	—			8.5	—	
“ 12, ant. post. diam. of centrum	25.5		25.3	28.	—	
“ 12, trans. diam. across process				8.	—	
“ 13, ant. post. diam. of centrum				28.	—	
“ 13, trans. diam. across process				7.5		
“ 14, ant. post. diam. of centrum	21.6			26.		—
“ 14, trans. diam. across process	—		—	6.8		—
“ 15, ant. post. diam. of centrum	25.5		20.8	26.		—
“ 15, trans. diam. across process				5.5		—
“ 16, ant. post. diam. of centrum				24.4		—
“ 16, trans. diam. across process				5.		—
“ 17, ant. post. diam. of centrum				23.	—	
“ 17, trans. diam. across process				4.8	—	
“ 18, ant. post. diam. of centrum				22.	—	
“ 18, trans. diam. across process		—		4.	—	—
“ 19, ant. post. diam. of centrum			—	19.	—	—
“ 19, trans. diam. across process				3.5	—	

THE DENTITION AND MANDIBLE OF *NOTHARCTUS* AND ITS ALLIES; COMPARISON WITH THE ADAPINÆ

ADULT DENTITION [1]

In order to place on record a detailed description of the dentition of the Notharctinæ and at the same time to interpret the facts from an evolutionary viewpoint, the writer has endeavored to trace the evolution of each tooth, in so far as it is shown in the species of Notharctinæ from successive horizons of the Lower and Middle Eocene. Next, the mechanical relations of each tooth, with the articulating teeth of the opposite jaw are considered. Then, the structure, evolution, and mechanical relations of the corresponding teeth of the Adapinæ are treated in order to exhibit the evidence for the common origin and diverse trends of evolution of the two subfamilies.

Incisors

Text Figs. 30, 31, 32, 35

The *central upper incisor* (i^1) is preserved *in situ* in a specimen of *Notharctus venticolus* (Amer. Mus. No. 14656). It has a compressed oval crown 4.2 mm. in length and 1.9 mm. in breadth, the long axis running obliquely from the lingual to the labial side. The crown is gently convex and smooth on the labial side, which is sharply truncate below by the elongate cutting edge, which runs forward to the bluntly worn anterior tip; the gentle concavity of the lingual surface of the crown is interrupted by a downwardly pointing V-shaped region of low relief. The crown is supported by a long procumbent cylindrical root, which in side view is sharply inclined to the anteroposterior axis of the crown. By comparison with *Adapis, Propithecus* and *Chirogale* it seems improbable that the central upper incisor touched its fellow of the opposite side; in other words, there was very probably a small median diastema. The central incisor is obviously less specialized than that of *Adapis parisiensis*, in which the cutting edge has become much more extended.

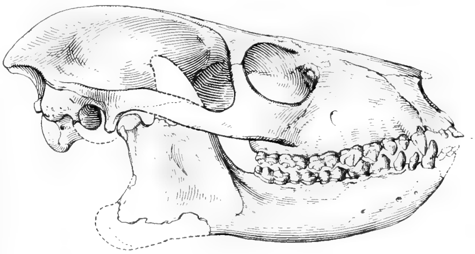

Fig. 30. Skull and lower jaw of *Notharctus osborni*. Amer. Mus. No. 11466. Middle Eocene (Lower Bridger beds) Bridger Basin, Wyoming. Natural size.

Lacrymal region and incisors partly restored from other specimens.

The *lateral upper incisor* (i^2) is preserved in *N. venticolus* (No. 14656) and in the type of *Notharctus, osborni* (No. 11466). Its crown is small, low and asymmetrical, the tip low and obtuse, the labial surface strongly convex, the lingual surface gently concave or flattened, but bearing a slight central ridge

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[1] For a summary of the characters of the dentition see pages 181, 225.

(*N. venticolus*). The long axis of the crown inclines gently toward the mid-line of the skull; it measures 2.2 mm. in this direction and 2 mm. in thickness. Its root is subcylindrical and less procumbent than that of i^1. It is thus less specialized than that of *Adapis*, which has become more like the wide-edged i^1. It was separated by well-marked diastemata from both the central incisor and the canine, whereas in *Adapis* (according to Stehlin's figures) the widened crown of i^2 was nearly or quite in contact both with the central incisor and with the canine. So far as one can judge from imperfect material the opposite incisor series of *Notharctus* were somewhat less inclined toward each other than was the case in *Adapis*, especially *Adapis magnus*.

A second upper incisor of a species of *Pelycodus* (Amer. Mus. No. 15034) from the Wasatch formation is much like that of *Notharctus;* the single-fanged canine also resembles that of the female of *Notharctus osborni*, save that it is less robust. Taken in connection with other evidence this indicates that the general construction of the muzzle and of the dentition even in the most primitive species of *Pelycodus* was not dissimilar to that of *Notharctus*.

The *lower incisors* are all preserved *in situ* in the paratype of *Notharctus pugnax* (Amer. Mus. No. 11480); the lower incisors of one side are preserved in the type of *N. rostratus* (Amer. Mus. No. 5009) and in *N. venticolus* (Amer. Mus. No. 14655); in all these cases they are much more worn than the premolars, this suggesting that they erupted very early, along with the molars, as in *Adapis;* the only little-worn lower incisors known to the writer are in the type jaw of *N.* ("*Thinolestes*") *anceps* Marsh in the Yale Museum. These are gently procumbent with short spatulate crowns. The crown of i_1 is broadly spatulate, truncate at the tip, 2.6 mm. in width; that of i_2 is obliquely spatulate, width 3.2, with a round edge. The lateral tips of the crowns of i_1 and i_2 were in contact. The much worn lower incisors of *N. pugnax*, type, are all separated from each other by diastemata of somewhat less than a millimeter in width, while the diastema between i_2 and the canine is about 2 millimeters. The unworn crowns were moderately expanded transversely and may have been in contact. In *Adapis* all the diastemata are small and the wide flat crowns are nearly or quite in contact. (Cf. Stehlin, 1912, p. 1173, figs.)

The *central lower incisors* (i_1) are moderately procumbent. The half-worn crown bears a transversely extended worn edge, but the unworn crown probably has a bluntly pointed tip. The cutting edge articulated with the chisel-like edge of i^1 and was no doubt more or less rubbed by the under surface of the tongue. In old animals the worn surfaces of the procumbent lower incisors face upward and forward, showing that they were partly overhung by the upper incisors.

The *lateral lower incisors* (i_2) are much larger than i_1; when well worn the crowns are oval antero-posteriorly; when unworn they probably ended above in a rounded truncate tip rather than in a very wide chisel-like edge; they articulated with the lingual surface of i^2. The slender roots of the central pair of incisors extend about one-third the way down the length of the symphysis and are parallel and quite near to it. The much stouter but short roots of the lateral incisors occupy the triangular area between the roots of the canines and those of i_1.

From the construction and articulating relations of the upper and lower incisors and from the relative size and positions of their roots in *Notharctus* I think it may be safely inferred that the third upper and lower incisors of the complete Eutherian formula are the ones which are missing in *Notharctus* and in all other primates. Modern representatives of the eighteenth century "école des faits" may object that until the Paleocene or earlier ancestors of the primates shall be discovered we cannot *know* that the ancestral formula for the incisors was $I\frac{3}{3}$. This matter will be discussed later, but meanwhile it may be noted that the absence of i_3 in the lower jaw is associated with (I do not say conditioned by) the enlargement of the canine, the procumbency of i_1 and the consequent restriction of the space for the roots of i_2,

i_3; in the upper jaw the tip of the enlarged lower canine occupies the space which would be filled by i^3 if present, and this is true even in female skulls with small canines.

Canines

Plate XLII; Text Figs. 30–32, 35

The large *upper canines* in supposed males have a long, nearly straight, pointed crown and a massive root. In a specimen of *N. venticolus* (Amer. Mus. No. 14655) the crown and root together measure 22 mm. in length. In the earlier species of *Pelycodus* the canines of supposed males were less robust in proportion to the size of the jaw; in the latest species of *Notharctus* (*N. crassus*) the crown was thicker at the base than that of *N. venticolus* and the lower end of the tooth was more recurved. It is thus apparent that the base of the upper canine crowns in males becomes thicker as we pass from lower to higher levels of the Eocene. In old animals the front face of the crown is flattened by the wear of the lower canine; in *N. crassus* (Amer. Mus. No. 11982) the lateral (external) face is marked by a deep vertical groove, flanked by a faint shallow groove in front and another behind. On the posterolingual side of the crown there is a deeper groove and near the root faint grooves or plications appear on all sides of the crown. This condition is foreshadowed in *N. venticolus.* The posterior cutting ridge of the canine is sharply defined in that species, less so in *N. crassus.*

In a supposed female (type of *N. osborni*, Amer. Mus. No. 11466) the upper canine is quite small, its crown having a length of only 4.5 mm., as compared with 10–12 mm. in a male *N. venticolus.* The crown is decidedly less caniniform and somewhat more premolariform than that of the male. It is essentially, however, a weak variant of the male canine, with a slightly recurved tip which differentiates it from the premolars. It is quite dissimilar to the upper incisors. In *Adapis* an analogous difference between the canines of supposed males and females has been observed by Stehlin (1912, p. 1171).

The *lower canines* of males are more slender at the base of the crown than the corresponding upper canines. The root is very massive and is more or less strongly recurved. As noted above it crowds the roots for the incisors. In *N. venticolus* and *N. tenebrosus* the crown is convex labially and flattened to concave on the lingual side. Posteriorly it is flattened and worn where it works against the upper canine. It has a faint anterior ridge, homologous with that of the

Fig. 31. Fragment of the left premaxilla, nasal and maxilla, with incisors and canine of *Notharctus venticolus.* Amer. Mus. No. 14656. Lower Eocene, Lost Cabin beds, Wind River Basin, Wyoming. Twice natural size. Lateral, inferior and medial aspects.

premolars. In *N. crassus* and *N. pugnax* the crown of the lower canine is more obtusely conical.

The female lower canine is also a low-crowned delicate tooth, more premolariform than the upper canine. In *N. osborni* (Amer. Mus. No. 11466) it has a faint internal cingulum continuous with a curved anterior ridge, and it is differentiated from p_1 chiefly by its much greater size, straighter front edge and steeper, flatter posterior face. In *N. matthewi* (Amer. Mus. No. 11202) the lower canine, which may well be that of a female, is a small tooth with a vertical single fang; the crown is not caniniform but distantly resembles that of p_1; it is markedly asymmetrical, flattened on the inner face, with a very obtuse, gently recurved tip. In an older species *N. nunienus* (Amer. Mus. No. 12736) the female canine is less premolariform, with a higher, more pointed crown. In the large species of *Pelycodus* the canine was nearly as stout as it is in *Notharctus* but in the very small and primitive *P. ralstoni* the canine alveolus (Amer. Mus. No. 16093) shows that this tooth was slender. This may very well be a female character.

Fig. 32. Front end of lower jaw of *Notharctus pugnax*, showing all four incisors *in situ*. Viewed from above. Middle Eocene, Lower Bridger beds. $\times \frac{3}{1}$.

Taken by itself, the direct evidence is insufficient to decide whether in the Paleocene ancestors of the Notharctinæ the canines were stout and caniniform, or slender and with the crown remotely resembling that of p_1. The loss of the third lower incisors at a very early date, however, offers some evidence for the view that they were crowded out by the enlargement of the canines, and the presence in early members of the group of a fairly stout jaw and well-developed muscle crests is compatible with the view that originally the canines were at least much larger than the incisors and anterior premolars. This subject is discussed below, page 200.

In *Adapis* both the upper and lower canines have shorter, less caniniform crowns than those of male *Notharctus*. In *Adapis parisiensis* the canines are sub-premolariform with compressed and cutting rather than piercing crowns, and there is a marked tendency for incisors, canines and premolars to assume a more or less cutting type, with a closed tooth row (loss of diastemata). In *Adapis magnus* (cf. Stehlin, 1912, figs. on pp. 1240, 1243) the upper and lower canines distantly resemble those of the female *Notharctus* but are much thicker; the upper canines are also blunter; the lower canines have the short crown more sharply recurved and the root is very thick; a heavy internal cingulum is present. In *Adapis* *rütimeyeri* (cf. Stehlin, 1912, fig. on p. 1268) the lower canine resembles that of the female of *Notharctus matthewi* and *N. osborni* save that the tooth is more recurved, the internal and external cingula are heavier and end posteriorly at the junction with the crista posterior in a low projection. This tooth is also intermediate in structure between that of the more specialized *Adapis parisiensis* and the primitive type preserved in the American representatives of the family.

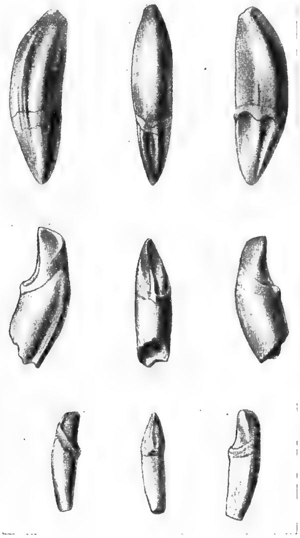

Fig. 33. Upper and lower canines of *Adapis*. $\times \frac{3}{2}$. After Stehlin.

Top row: *Adapis magnus*. Left upper canine: buccal, anterior (mesial), lingual.
Middle row: *Adapis magnus*. Left lower canine: lingual, posterior and buccal views.
Bottom row: *Adapis rütimeyeri*. Right lower canine: lingual, posterior and buccal views.

Premolars

The premolars of *Notharctus* may be divided into three categories: first the very small and simple $\mathrm{p}\frac{1}{1}$, which are never replaced, erupt with the deciduous teeth, and may be homologous with them; in the upper jaw p^1 has only a single root; in the lower jaw p_1 has either a single root, e. g., *Pelycodus trigonodus, N. osborni, tyrannus, pugnax, crassus*, or there is a faint external groove, showing an incipient tendency to divide the root into anterior and posterior moieties (*N. venticolus*). Second, the intermediate group $\mathrm{p}\frac{2}{2}$, $\mathrm{p}\frac{3}{3}$, of which $\mathrm{p}\frac{2}{2}$ are more simple and but little advanced beyond $\mathrm{p}\frac{1}{1}$, while $\mathrm{p}\frac{3}{3}$ are very distinctly more advanced toward the pattern of $\mathrm{p}\frac{4}{4}$; both $\mathrm{p}\frac{2}{2}$ and $\mathrm{p}\frac{3}{3}$ have two *principal* roots arranged anteroposteriorly and homologous with the two primary roots of the molars[1]; p^3 has also an internal root beneath the inwardly projecting protocone,[2] while p_3 shows a transverse widening of the posterior part of the crown

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[1] On the homologies of these roots, see Gregory, 1916, Bull. Amer. Mus. Nat. Hist., XXXV, p. 246.

[2] I apply the name protocone to the main lingual cusp of the premolars for the reasons given in Part I of this series, 1916, Bull. Amer. Mus. Nat. Hist., XXXV, pp. 242–245.

which may indicate that the root is becoming divided into external and internal moieties; third, p$\frac{4}{4}$, which become progressively submolariform in the later types but never attain the complete molar pattern; p^4 has three complete roots; the main anterior and posterior roots are more or less grooved or divided into

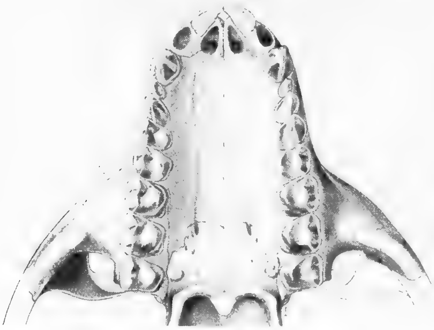

Fig. 34. Upper dental arch of *Adapis magnus*. After Stehlin. × $\frac{1}{1}$.

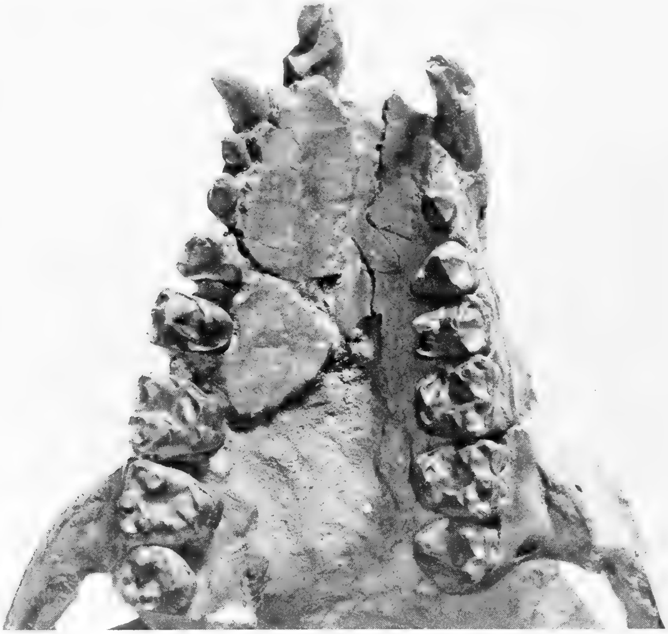

Fig. 35. Upper dental arch of *Notharctus osborni*. Amer. Mus. No. 11466. × $\frac{2}{1}$. The right side is distorted, but the left side is well preserved.

buccal and lingual branches. There is a rapid increase in size and especially in transverse diameter as we pass from p^1 to p^4, p^1 being a very small tooth, while p^4 in progressive species is nearly as wide as m^1.

This general description of the premolars and their roots applies equally well not only to *Pelycodus* but to all the most primitive Eocene carnivores and ungulates. *Pelycodus* and *Notharctus* thus retained a very primitive general plan of the premolars.

In *Adapis parisiensis,* the whole premolar series is evidently more specialized than in the more primitive forms of the Notharctinæ and in a somewhat different direction; for, while p^4 has become almost molariform, p^3, p^2, p^1 are becoming like each other and like the canine, all having a compressed, sharp-edged crown with a single tip and a strong internal cingulum. In *Adapis magnus,* p^4 has likewise become submolariform, but there is much more of the primitive difference between p^3, p^2, and p^1, this species being less specialized in this respect as in many others. In general, the lower premolars conform in appropriate manner to the above described characters of the upper premolars. *Adapis rütimeyeri* (Stehlin, 1916, Taf. XXI.) is even more primitive than *A. magnus,* but already shows some disposition for p_2, p_3 to become like each other and different from p_4.

First Upper Premolar

Text Fig. 35

More in detail, p^1 is known in very few specimens of the Notharctinæ. In the type of *N. osborni* it is a very small simple tooth with an asymmetrical crown, strongly convex externally, with a short anterior ridge (crista anterior), a conical tip, a long posterior ridge (crista posterior) and an obliquely sweeping cingulum, which is confluent in front with the crista anterior and in the rear with the crista posterior; on the anterolingual face there is a very faint suggestion of a flattening or concavity, serially homologous with the anterolingual face of the paracone of succeeding teeth. It is well separated both from the canine and from p^2 by equal diastemata of about one millimeter in length. This equal spacing of the first premolar is found also in the lower jaw in *Notharctus tyrannus, N. venticolus, N. nunienus, Pelycodus relictus* and apparently also in the primitive *P. trigonodus,* but not in *P. ralstoni.* It may be reminiscent of a primitive condition in which the simple conical upper premolars were separated by equal intervals for the accommodation of the simple lower teeth. In connection with the enlargement of the premolars in the later species the diastemata are more or less abbreviated, that between p_1 and p_2 and p^1, p^2 being lost in *N. pugnax* and *N. crassus;* the large size of the upper canines, however, necessitates the retention of the diastema in front of p_1.

P^1 in *N. osborni* does not articulate with p_1, its anterior edge being some distance behind that tooth when the jaw is closed; but its posterolingual face shears past the anterolabial surface of p_2 after the fashion of the homologous surface of the succeeding premolars. The concavities on the lingual surfaces of p^1, p^2, c, i^2, i^1 may all be adapted rather to the surface of the tongue, which in modern lemurs presses against them, than to the action of the opposing lower teeth.

In *Adapis parisiensis* (Stehlin, p. 1168) p^1 is more compressed, with sharp anterior and posterior cristæ. In *Adapis magnus* (p. 1254) it is very small and less compressed; in either case its form is readily derivable from the more primitive type preserved in *Notharctus.*

First Lower Premolar

Plates XXXVI, XXXVII

The first lower premolar (p_1) is somewhat similar to p^1 but more compressed; it shows in a very incipient stage the tendency to become differentiated into an anterior moiety, or trigonid, and a posterior moiety, or talonid; the trigonid is represented by the conical tip (protoconid), by the crista anterior, which faces rather inward than forward, and by the flattened posterolingual face of the protoconid, foreshadowing the posterior face of the trigonid; the talonid basin is represented by the shallow fossa at the posterolingual base, while the posterior valley is represented by a still fainter fossa on the posterolabial slope; the whole posterior V of the molar type is represented by the slight swelling at the posterobasal tip of the crista posterior. These indications are very faint in *N. osborni*, as well as in *Pelycodus relictus;* but they are more distinct both in the progressive *N. pugnax* and in the primitive *Notharctus venticolus*, which also shows a slight grooving of the root. In *Pelycodus ralstoni* p_1, to judge from its alveolus, must have been a very simple tooth, which is perhaps correlated with the crowding together of c, p_1 and p_2 in that otherwise primitive species.

The evidence, then, by no means indicates that there was a stage in the remote ancestry of *Notharctus* in which p_1 had two distinct roots and a more premolariform crown; to the present writer, indeed, it seems more likely that in a pre-*Pelycodus* stage there was some variation in form both of the canines and of p_1, and that both were always somewhat different from each other and from p_2. This would be partly conditioned by their different distances from the fulcrum of the jaw, partly by the fact that the upper canine, with which the lower articulated, was always the first tooth behind the premaxillo-maxillary suture and therefore subject to conditions of use and growth that were considerably different from those affecting p^1 and p_1; thirdly, these last named teeth appear to be serially homologous rather with the deciduous canines, deciduous molars and true molars than with the permanent canines and premolars. For these reasons I infer that in the unknown Paleocene ancestors of the Notharctinæ $p\frac{1}{1}$ were simple teeth with only a bare suggestion of true premolariform character.

In *N. osborni*, p_1 articulated by its anterior crest with the posterior edge of the upper canine; it barely touched p_2. In *N. venticolus*, p_1 articulated both with the upper canine and apparently also with p^2.

P_1 in *Adapis parisiensis* (Amer. Mus. No. 10006) is a low-crowned, sharp-edged tooth of asymmetrical form with an incipient talonid at the base of the posterolingual fossa. It has all the elements in a barely incipient stage of the typical premolariform crown, namely sharp external and internal cingula, incipient differentiation into trigonid and talonid and incipient metaconid ridge. In the opinion of the writer it is more a specialized tooth than p_1 in the earliest Notharctinæ. In *A. magnus* p_1 is more compressed with a smaller internal basal extension. In *Adapis sciureus* (Stehlin, 1916, p. 1515, fig. 369) p_1 is less extended transversely than in *A. parisiensis* or even than in *A. magnus;* its internal cingulum is more pronounced than in *Notharctus.*

Second Upper Premolar

Text Fig. 35

P^2 is likewise known in very few specimens of the Notharctinæ. In the type of *N. osborni* it is a conical tooth about 2.5 mm. in length by 2 in breadth, at the base of the crown; it is supported by two roots of which the posterior is the wider transversely, the anterior root being decidedly smaller. Like p^1 it lacks an internal extension, but on the whole it represents a slight advance toward the true premolar shape. Its apex corresponds with the paracone of succeeding teeth; its crista posterior corresponds with the paracone-metastyle ridge of p^3; the slight depression or fossa on the posterolingual base, guarded by the posterointernal cingulum, is all that represents the internal spur or ledge. In an old male of *Notharctus venticolus* p^2 is much larger than in *N. osborni;* its crown is compressed and the two large and nearly subequal roots are widely separated. This is very possibly a more primitive condition than that observed in *N. osborni.* In *Adapis parisiensis* p^2 is more compressed and swollen than in *Notharctus* and has a sharp cutting edge; in *A. magnus* it is wider and more like p^3. In *Adapis rütimeyeri* (Stehlin, 1916, Taf. XXI, fig. 18) the premolars are all relatively primitive, but not so much so as in the Notharctinæ. P^2 suggests that of *A. magnus* in that it is less compressed than in *A. parisiensis.*

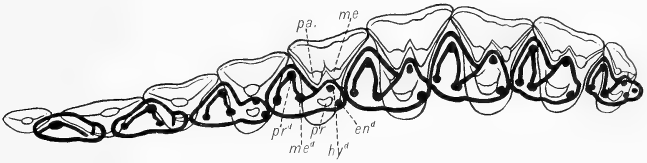

Fig. 36. Diagram illustrating progressive complication of the premolar-molar series and the interlocking relations of the upper and lower teeth in a generalized mammal. The crown pattern of the lower teeth is shown in heavy black lines.

According to the view adopted provisionally by the author the protocone of the upper molars arose from a lingual extension from the basal cingulum, as it did later in the premolars, the primitive tip of the crown being represented by the para + metacone. The para- and metacones probably became separated *pari passu* with the transverse widening of the talonid and the upgrowth of the hypoconid.

Second Lower Premolar

Plates XXXVI, XXXVII

P_2 exhibits considerable variation in form in the Notharctinæ; in the more progressive larger species *N. rostratus, N. pugnax, N. crassus* it is quite different from p_3, being much smaller and simpler, with a tendency toward the fusion of the roots. This character is marked also in *N. osborni* and *N. matthewi.* On the other hand in *N. venticolus, N. nunienus, P. trigonodus,* and *P. ralstoni* there is a more even gradation in form as we pass from p_2 to p_3; this has every appearance of being the primitive condition seen in Eocene carnivores and taken in connection with other evidence it suggests that the simple character of p^2_2 in *N. osborni* and of p_2 in *Pelycodus relictus* is partly retrogressive.

The anterolabial crest (crista anterior) of p_2 articulates with the posterolingual crest and surface of p^1. Its posterolingual surface probably articulated with the anterolabial surface of p^2. In *N. venticolus* the crista anterior of p_2 is partly worn, probably by articulation with p^2. In *Adapis parisiensis* (Amer. Mus. No. 10006) p_2 is more compressed and elongate than p_1, and shows all the premolariform characters more distinctly. It is obviously much more specialized than the corresponding tooth in *Pelycodus trigonodus* (Amer. Mus. No. 16843). In *Adapis magnus* (Stehlin, 1912, p. 1242, fig. 270) p_3 is thicker transversely than in *A. parisiensis* and far thicker than in primitive Notharctinæ. In *Adapis sciureus* (Stehlin, 1916, p. 1515, fig. 369) p_3 is more primitive than in either of the other species, but is essentially adapine in its low, obliquely placed crown. In *A. rütimeyeri* this tooth retains an incipient hypoconid.

Third Upper Premolar

Plate XXXV; Text Fig. 35

P^3 in *N. venticolus, N. osborni,* and *N. crassus* shows a distinct advance toward the pattern of p^4. It is roundly triangular in section, the rounded apex of the triangle forming a low internal projection or protocone supported by a stout root; there is a single main cusp homologous with the paracone of the molars, with a crista anterior and a crista posterior; the anterolingual and posterolingual faces are flattened, the latter being much the larger. The external cingulum rises anteriorly into a low parastyle and posteriorly into a prominent metastyle. The anterolabial surface is slightly convex but the posterolabial surface is gently concave. Thus the chief features of p^4 are foreshadowed in p^3, the main difference being in the small size and low position of the protocone or internal cusp, and the feeble development of the parastyle. In *N. osborni* the protocone is extremely small, narrow, and located more to the rear; this is possibly a conservative condition; in the progressive *N. crassus* the protocone region is wider and the crown is approaching the general form of p^4.

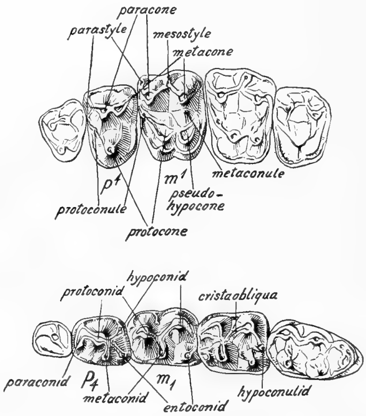

Fig. 37. Diagram of the left upper and right lower molars and last two premolars of *Notharctus*, showing the names of the principal cusps and crests.

With regard to its functional relations with the lower teeth, the outer side view in *N. venticolus* shows the simple conical paracone, articulating by its anterior slope with the posterior slope of the conical p_2 in a very primitive fashion. Its posterior slope articulates with the anterior slope (crista anterior) of p_4, its protocone spur partly with the talonid of p_3 and partly with the paraconid of p_4. Similar relations are observed in *N. crassus*. In *N. osborni* the small size and backward displacement of the protocone results in its articulating solely with the trigonid of p_4 and not at all with the talonid of p_3. This is possibly a retrogressive condition.

P^3 is not well known in the earlier species of the Notharctinæ. In *Pelycodus jarrovii* it appears to be similar to that of *N. venticolus*.

In *Adapis parisiensis* p^3 is less like p^4 than it is in *Notharctus;* it is biconvex with a heavy internal cingulum, representing the reduced protocone spur. In *Adapis magnus* on the other hand p^3 is a wide tooth with a large protocone and an almost bicuspid general contour. Thus, in the characters of p^3, both these divergent phyla of the Adapinæ are obviously more specialized than the primitive members of the Notharctinæ in which p^3 approximates the primitive placental type which is seen in many Eocene carnivores and insectivores. In the primitive *Adapis rütimeyeri* (Stehlin, 1916, Taf. xxi, fig. 18) p^3 is more primitive than that of *A. magnus*, its protocone being less expanded and the contour of the crown view more oblique.

Third Lower Premolar

Plates XXXVI, XXXVII

The most ancient and primitive p_3 known in the Notharctinæ is that of *Pelycodus ralstoni* from the Sand Coulée horizon at the base of the Lower Eocene (Amer. Mus. No. 16093). It has a compressed, slightly recurved crown with sharp anterior and posterior cristæ and distinct internal cingulum, the latter rising on the middle of the inner surface of the protoconid into a slight projection. The stout posterior cingulum rises in the middle into a low cusp which is probably homologous with the entoconid of the molars and is continuous with the crista posterior; lateral to the crista posterior and supposed entoconid is a slight depression which seems to represent the central external valley of the molars; medial (lingual) to the above named crest is another and slightly deeper fossa which appears to represent the talonid basin. The talonid as a whole, though small, is well marked; it is supported by a root which on the inner side is much larger than the one beneath the potential trigonid.

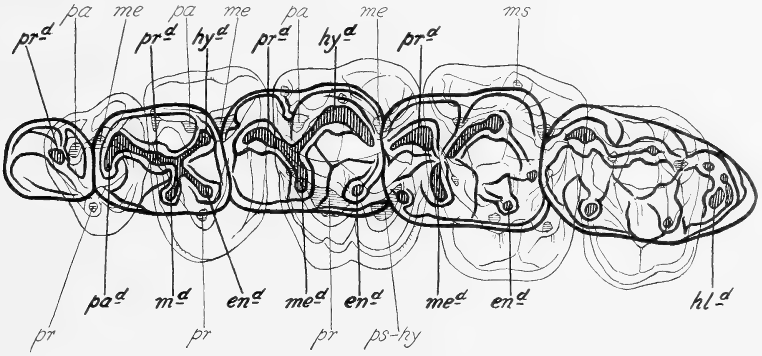

Fig. 38. Occlusal relations of the upper and lower cheek teeth of *Notharctus crassus* at the moment of maximum lateral displacement of the mandible. Amer. Mus. No. 11982.

The protoconids (pr^d) fit between two upper molars, the hypoconids (hy^d) fit between the para- (*pa*) and metacones (*me*); the protoconid-paraconid crest shears past the metacone-metastyle crest. The metaconid (me^d) articulates between the pseudohypocone (*ps-hy*) and the protoconule. The entoconid (en^d) articulates between the protocone and the pseudohypocone. As the mandible is closed it passes linguad, bringing the protocones into the central fossæ, or basins, of the talonids and the pseudohypocones into contact with the paraconid region.

In *Pelycodus trigonodus* (Amer. Mus. Nos. 16843, 15017) p_3 is somewhat more compressed and elongate and the internal cingulum is somewhat less sharply defined. In *P. jarrovii*, which is one of the larger species of the genus, the crown of p_3 becomes thicker transversely; the crista posterior gives rise to a medial branch ending below in a slight swelling or ridge, which appears to be prophetic of the metaconid. In *Notharctus venticolus* the tip of the tooth is lower, the supposed metaconid ridge is barely perceptible; in *N. tyrannus* (paratype, Amer. Mus. No. 11478) the metaconid swelling is clearly indicated and the whole crown is thicker and lower; this tendency culminates in *N. pugnax* and *N. crassus*, which have the crown of p_3 quite swollen transversely, with the metaconid swelling now conspicuous. This extremely gradual evolution of the metaconid on p_3 is analogous with the similarly slow appearance of the mesostyles and pseudohypocones of the upper molars.

In *N. venticolus* (Amer. Mus. No. 14655) the posterior flattened slope of the potential trigonid of p_3

articulates with the anterior face of p^3, the tip of the protoconid articulating with the parastyle of p^3 It will be shown below that one side of the upper and lower jaws could be pivoted upon $m\frac{3}{3}$ and when this happened p_3 could be swept transversely across p^3, so as to produce the worn surface on the posterior face of the former and on the anterior surface of the latter. Similar articulating relations of $p\frac{3}{3}$ are very well shown also in *N. osborni* (left side of type) and in *N. crassus* (Amer. Mus. No. 11982).

In *Adapis parisiensis* p_3 was a much compressed and low-crowned, sharp-edged tooth, with sharp internal and external cingula, a small talonid and a low metaconid ridge. It is much more specialized than the corresponding tooth of the oldest members of the Notharctinæ. In the later Notharctinæ this tooth has become widened transversely. In *Adapis magnus* p_3 is not as compressed as it is in *A. parisiensis*, but is otherwise similar. In p_3 of *Adapis sciureus* (Stehlin, 1916, fig. on p. 1515) we have apparently a more primitive form of the adapine type which is, however, obviously not as primitive as that of *Pelycodus trigonodus*. In *A. rütimeyeri* (Stehlin, 1916, Taf. XXI, fig. 24) p_3 is as little like p_4 as it is in *A. magnus*. It has a compressed oval crown somewhat obliquely placed, with a large protoconid, a stout paraconid, no metaconid and a low hypoconid.

Fourth Upper Premolar

Plates XXXV, XLI; Text Fig. 40

P^4 in the oldest and most primitive Notharctinæ (*P. ralstoni*, Amer. Mus. No. 16089) has an undivided pointed paracone with sharp anterior and posterior cristæ; the external cingulum is barely continued across the paracones; it rises into a distinct parastyle and an incipient metastyle; the protocone spur is relatively narrower than in later types so that the contour of the crown is slightly constricted in the middle between the paracone and the protocone. From the tip of the protocone runs outward and forward a sharp low crest which, after giving rise to an incipient protoconule, is continued outward to its junc-

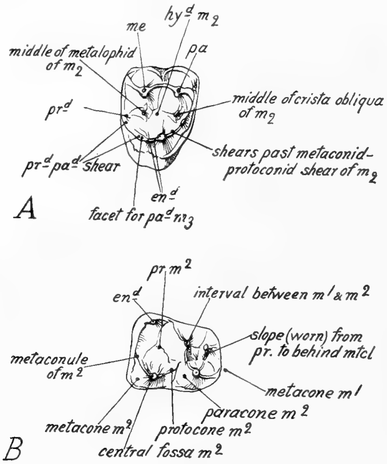

Fig. 39. Diagram: occlusal relations of the right m^2 and m_2 in the most primitive species of *Pelycodus*. See page 149.

A. *Pelycodus ralstoni*. Second right upper molar. Amer. Mus. No. 16089. $\times \frac{3}{1}$.

B. *Pelycodus ralstoni*. Second right lower molar. Amer. Mus. No. 16093. $\times \frac{3}{1}$. "Protocone m^2" should read "protoconule m^2."

tion with the parastyle; it is thus homologous with the protoloph of the molars. Behind the protoloph and incipient protoconule there is a small depression corresponding with the central fossa of the molar crown and guarded posteriorly by a low transverse papillate ridge which foreshadows the metaconule. Behind the ridge in question and on a lower level lies the posterior cingulum.

In *Pelycodus trigonodus* (Amer. Mus. Nos. 15017, 16089, etc.) p^4 is not materially different from that of *P. ralstoni*, save that the protocone is perhaps a little larger. Old individuals show the tip of the paracone worn by the hypoconid of p_4, the tip of the protocone worn by the talonid of p_4, and a worn ovoid area in the fossa between the protocone and the posterior cingulum; this was probably worn by the prominent paraconid of m_1. In an old individual of *Notharctus venticolus* (Amer. Mus. No. 14655) the center of the ovoid area above mentioned is worn through so as to expose the dentine, which appears as a subcircular spot surrounded by a worn strip of enamel; so that the whole assumes the appearance of a worn down "tetartocone" or pseudohypocone, like that of the molars. In *Notharctus nunienus* (Amer. Mus. No. 4735), from the Wind River formation, the slightly worn tip of the paracone is just beginning to become constricted on its posterior ridge and to give rise to an incipient metacone. This indication is confirmed by the presence of a very faint groove running down on the lingual slope of the paracone from the point of cleavage of the para- and metacones; this groove is the beginning of the external valley between the paracone and the metacone. In *Notharctus matthewi*, a conservative species of the Lower Bridger, there is extremely little suggestion of the cleavage of the para- and metacones but in all the other Lower Bridger species this separation is more or less marked, especially in *N. pugnax* (Amer. Mus. No. 14567) where the cleft and groove are very pronounced, as they are also in the immediately succeeding species *N. crassus* of the Upper Bridger. In these later types p^4 becomes nearly as wide transversely as the molars, the protocone widens anteroposteriorly and the middle of the crown loses the constricted appearance of the earlier types, the anterior and posterior borders becoming more nearly parallel. But even at this stage p^4 is by no means molariform, although all the principal elements of the molar crown are more or less distinctly indicated especially in the worn condition.

In *Adapis parisiensis* p^4 is very nearly molariform, having two widely separated external cusps and a sharp oblique protoloph (protocone-parastyle ridge); it has, however, no hypocone. It is more elongate anteroposteriorly than that of the Notharctinæ and these two have evidently evolved along quite divergent paths. In *Adapis magnus* p^4 is less molariform than that of *A. parisiensis;* it is wider transversely and less elongate anteroposteriorly, but the subfamily affiliation is evident. A more primitive stage of p^4 is shown in *A. rütimeyeri* (Stehlin, 1916, Taf. XXI, figs. 27, 29) but even in this p^4 has two very distinct external cusps, which are much more distinct and separate than those even of the latest of the Notharctinæ. In *Adapis sciureus* p^4 is not known, but the very retarded condition of the hypoconid of p_4 gives reason to believe that p^4 either had but one external cusp or that the metacone was connate with the paracone.

Fourth Lower Premolar

Plates XXXVI–XLI; Text Fig. 38

P_4 in its most primitive form is found in *Pelycodus ralstoni* and *P. trigonodus,* where the cusps of the incipient trigonid have the sharp pricking character which was so common among Paleocene and Eocene insectivorous mammals.

P_4 is distinguished from p_3 by the following characters: it has a distinct paraconid (at the front end of the crista anterior); the large thorn-like metaconid is an outgrowth of the "metaconid ridge" which was but faintly foreshadowed in p^3; it is connected with the protoconid by a small oblique crest forming the short posterior limb of the potential anterior V or summit of the trigonid, of which the crista anterior and paraconid form the anterior limb; the potential trigonid, as in most primitive insectivorous types, projects far above the level of the low potential talonid; its posterior wall, culminating above in the proto-metaconid ridge, descends steeply to the talonid; it shears past the crista anterior and flat antero-lingual face of the paracone of p^4. The basin of the talonid is represented by a fossa in the postero-lingual half of the talonid; this fossa is separated from a smaller fossa, situated on the labial side of the talonid and representing the central external valley, by a sharp crest which represents the lower end of the primitive crista posterior and will give rise in later types to the crista obliqua or anterior limb of the posterior Λ of the tooth. The hypoconid is represented by a low median cusp at the junction of

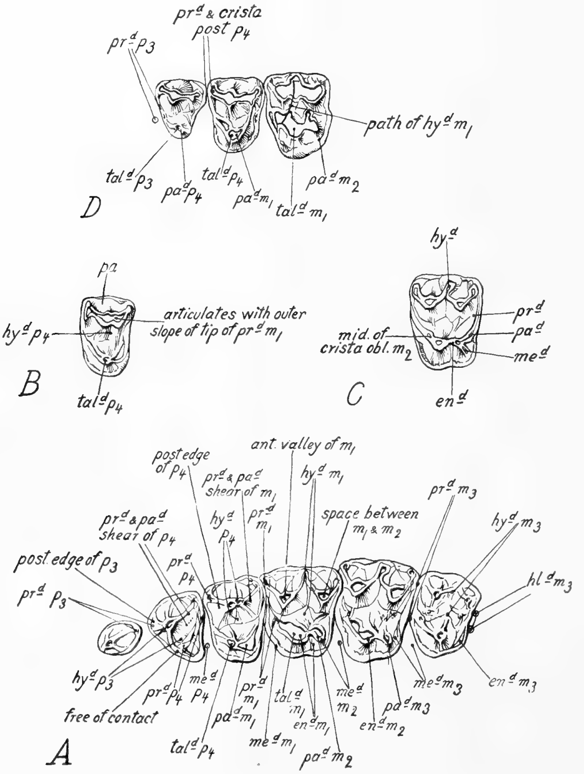

Fig. 40. Diagram: occlusal relations of left upper and lower cheek teeth in *Notharctus*. Compare Fig. 38.

A. *Notharctus osborni*. Amer. Mus. No. 11466. × $\frac{3}{1}$.
B. *Notharctus crassus*. Amer. Mus. No. 11982. × $\frac{3}{1}$.
C. *Notharctus crassus*. Amer. Mus. No. 11982. × $\frac{3}{1}$.
D. *Notharctus venticolus*. Amer. Mus. No. 14655. × $\frac{3}{1}$.

the crista obliqua with the raised posterior cingulum, which is potentially the posterior limb of the posterior Λ.

In *Pelycodus jarrovii* the crown of p_4 shows some degree of advance, for the tooth is now wider transversely, the trigonid crown is lower and the cusps have lost their thorn-like character. This transverse thickening and blunting of p_4 is emphasized in *N. venticolus* of the Wind River formation and culminates in *N. pugnax* and *N. crassus* of the Bridger. In these species p_4 is very coarse and thick and in the much worn condition shows a considerable advance toward the molar pattern. The evolution of p_4 like that of all the teeth is thus traceable through a considerable series of small gradations, extending from the base of the Lower Eocene to the top of the Middle Eocene. (Plates XXXVI, XXXVII.)

The articulation of p_4 with p^3 and p^4 has been intensively studied chiefly in *Notharctus venticolus*, *N. osborni* and *N. crassus* and less fully in *Pelycodus trigonodus*. The potential trigonid of p_4 was wedged between p^3 and p^4; its sharp metaconid did not oppose any part of the upper teeth, but as it pressed into the interval between the protocone of p^3 and that of p^4 it would pierce and break the food, and, on the transverse movement of the jaw, it would tend to tear the food apart. In a subvertical movement of the mandible the cutting protoconid-metaconid edge of p_4 and the steep wall below it, when shearing past the parastyle-paracone blade and associated wall of p^4, would cut the food; in a transverse movement of the mandible it would tend to tear it apart. The talonid crest, pressing against the protocone tip, would also assist in cutting and breaking the food. Repeated examination of the interlocking relations of the teeth and of the construction of the glenoid and condyle shows that in the later species there was a very considerable transverse motion of the mandible, great pressure being exerted first on the outer side of the upper and lower teeth, where the principal cutting action took place and where the food was firmly gripped by the main external cusps; as the teeth were pushed further into place the lower tooth row moved inward, over a wider arc in the front part of the tooth row than in the rear, so that the food was finally pressed between the protocones and the talonids of p^4–m^3. In the later forms with more transverse excursion of the mandible the wider fourth premolars were more effective in cutting, crushing and tearing apart the food; while in the small earlier types a more direct chopping motion was sufficient to cut and break up the brittle insect food. (Plate XLI; Fig. 38.)

In *Adapis parisiensis* p_4 is almost molariform. The anterior and posterior V's are complete, although the anterior one is still widely open. Even a distinct entoconid was present and the prominent metaconid ridge was nearly of the molar type. In *Adapis magnus* p_4 is even more molariform. On the posterolingual slope of the metaconid ridge it bears a small accessory cusp (metacristid) homologous with that of the molars. The summit of the protoconid-metaconid crest is sharp and obliquely placed; it sheared past the sharp oblique protoloph of p^4. This sharp oblique development of the protoloph of p^4 and of the protoconid metaconid ridge of p_4 is characteristic of the Adapinæ and is associated with a lesser transverse excursion of the mandible, and with a flattened convex condyle. It is evident that the food of the Adapinæ was of tougher fiber, requiring great muscular power of the jaws, exerted more vertically than in the Notharctinæ.

In *Adapis rütimeyeri* (1916, Taf. XXI, fig. 24) p_4 suggests that of *A. magnus*, but has not yet acquired a metacristid; the entoconid is low, the protoconid-metaconid crest is more transverse. In *Adapis priscus* (1916, p. 1511) p_4 is nearly molariform with a well defined trigonid and talonid, including a fairly large entoconid. The tooth is not compressed and elongate as it is in the specialized *A. parisiensis*. It differs from p_4 in all the Notharctinæ in the relatively large size and advanced condition of the talonid, including the hypoconid and the entoconid.

First and Second Upper Molars

Plates XXXV, XLI; Text Figs. 38–40

The oldest and most primitive member of the family *Pelycodus ralstoni* from the Sand Coulée beds, Clark's Fork Basin, has tritubercular upper molars with only a faint suggestion of the pseudohypocone on the posterior ridge of the protocone of m^1 and m^2. The external cingulum of m^1, m^2 rises into a faintly incipient mesostyle; the crowns are relatively wider transversely than in later species, that of m^2 being notably wide in proportion to its anteroposterior diameter. The proto- and metaconules bear transverse crests that run from the flattened labial slope of the protocone to the lingual slopes of the para- and metacones; the tip of the protoconule lies in the oblique protoloph ridge that runs obliquely from the protocone outwards and downward toward the parastyle; the outer half of this ridge, beyond the tip of the protoconule, may be regarded as the anterior limb of the protoconule V, of which the posterior limb is the transverse protoconule crest mentioned above. The whole crown is surrounded by a cingulum which is crenulate opposite the protocone. M^2 shows the following more or less worn facets for articulation with the lower molars: the tip of the paracone fitted into the external valley of m_2, the metacone into the valley between m_2 and m_3; past the crista anterior of the paracone of m^2 sheared the posteroexternal slope of the trigonid of m_2; past its crista posterior sheared the anteroexternal slope of the hypoconid of m_2; past the crista anterior of the metacone sheared the posteroexternal slope of the hypoconid of m_2; past the crista posterior of the metacone sheared the anteroexternal crest of the trigonid of m_3. The crest running from the parastyle tip is worn by the protoconid of m_2; the protocone-protoconule crest (protoloph) and the anterior fork of the protoconule are worn by the protoconid-metaconid crest (protolophid) of m_2; the tip of the protoconule is worn by the anterior tip of the crista obliqua of m_2; the tip of the metaconule is worn by the middle of the posterior limb of the posterior V of m_2. The tip of the protocone of m^2 fitted into the talonid basin of m_2, immediately behind the tip of the protocone and on its lingual slope is a worn groove or facet, which is especially well shown in No. 15681, which is caused by the tip of the entoconid; on the posterolabial slope of the protocone, immediately external to the facet last described, is a worn streak or path running obliquely posterolabially, which has been worn by the tip of the paraconid of m_3. Thus the region of the pseudohypocone, or posterointernal cusp, which is here only in an incipient stage, is bounded lingually by the groove or facet for the entoconid of m_2 and labially by the groove for the paraconid of m_3. (Fig. 39.)

The detailed characters of the wearing-facets of the upper molars, as well as the general form of the whole dentition, indicate that in this oldest and presumably most primitive member of the family (*Pelycodus ralstoni*) the motion of the mandible was more vertical and less transverse than in the later species; also that the small wide molars with fewer cusps gave relatively greater piercing power and less grinding and cutting action; this in turn suggests that the ancestral Notharctinæ were probably insectivorous, a conclusion that is supported by considerable collateral evidence.

In *Pelycodus trigonodus*, the succeeding stage, from the lower part of the Gray Bull horizon, m^1, m^2 are of distinctly larger size and their relative width is less in proportion to their anteroposterior diameter; the incipient mesostyles are more distinct and the pseudohypocones are sometimes better developed, although they are at most only an obtuse swelling on the posterior slope of the protocone. *Pelycodus frugivorus*, as defined by Matthew (1915, p. 439), from the Upper Gray Bull beds, is more advanced than *P. trigonodus;* one specimen referred to *P. frugivorus* (Amer. Mus. No. 15022) shows a well-developed pseudohypocone on m^1 and a small one on m^2; the contour of m^2, however, is less quadrate than in later types. (Plate XXXV.)

P. jarrovii from the Upper Gray Bull beds (Amer. Mus. Nos. 4174, 15041) is considerably larger; the pseudohypocone of m^1 wears into small round cusps connected by a short neck with the protocone, and the contour of the crown is becoming more or less quadrate; although it is less elongate anteroposteriorly than in the later stages the mesostyle is more (Amer. Mus. No. 15041) or less (4174) distinct, so that on the whole this species approaches *Notharctus*. (Plate XXXV.)

The most primitive species of *Notharctus*, *N. nunienus* (Amer. Mus. No. 4735) from the Lost Cabin formation of the Wind River Basin, differs from *Pelycodus jarrovii* in having the pseudohypocones of m^1 and m^2 slightly more advanced; the mesostyles though small are distinct bead-like cusps and m^2 is possibly a little less wide transversely in proportion to its anteroposterior diameter. (Plate XXXV.)

Notharctus venticolus from the Lost Cabin beds, Wind River Basin, is a large and relatively progressive species with large and distinct pseudohypocones, quadrate molars and large mesostyles (Amer. Mus. Nos. 14637, 14655), so that it foreshadows the still larger and more progressive species of the Bridger (*N. pugnax*, *N. crassus*). A primitive character, however, is the greater relative width of m^2 and the relatively smaller anteroposterior diameter of m^1, m^2. Other parts of the crown are more advanced, as compared with earlier species in the following details: the protoconule is now associated almost exclusively with the protoloph and has nearly lost the posterior limb of its originally V-shaped crown. The metaconule of m^1 is relatively large and is of truncate pyramidal shape. The cingulum is fairly heavy all around the tooth, except opposite the protocone of m^1. The pseudohypocone in m^1 is roundly conical and the neck that joins it with the protocone is narrow. A deep fissure on the labial side separates it from the protocone. In m^2 the pseudohypocone is a little less advanced than in m^1. (Plate XXXV.)

No. 14637 shows the wearing facets little worn and No. 14655 shows them greatly worn, and is moreover associated with the lower jaw; so that a careful study of the movement of the jaw and articulating relations of the teeth was made possible. The parastyle and labial part of the anterior cingulum of m^1 was worn by the protoconid of m_1; the mesostyle by the hypoconid of m_1, which also slid down into the central fossa, leaving in No. 14655 a wide groove extending from the mesostyle inward and forward to the back of the protoconule (Fig. 40) and showing that in this stage a markedly transverse excursion of the mandible had become established. In the little-worn state the constriction between the protocone and the pseudohypocone bore on its lingual side a groove for the entoconid; in the old stage the labial slope of the pseudohypocone of m^1 is scarred by the paraconid of m_2. In the young stage there was perhaps more vertical and less transverse movement of the mandible than in the old stage.

Accordingly, the Notharctinæ of the Bridger formation show a considerable range of variation in the pattern of m^1, m^2. In the conservative *Pelycodus relictus* these teeth are as small as they are in *Pelycodus trigonodus*, but are narrower; the pseudohypocones are small, but the mesostyles are distinct and the contour of the crown is more quadrate than in any true *Pelycodus*. In *Notharctus osborni* (Amer. Mus. No. 11466) m^1, m^2 are notably longer in anteroposterior diameter than in the species of *Pelycodus;* m^2 is not greatly wider than m^1, the mesostyles are large and the contour of the crown is subquadrate. But the pseudohypocones do not project upon the labial border of the tooth. The internal cingulum is delicate. The articulating relations of m^1, m^2 have been closely studied and are indicated in Figs. 39, 40. In m^1 and m^2 the constriction between the protocone and the pseudohypocone and the valley that marks this separation on the lingual border of the crown engage the entoconids of the lower molars m_2, m_3. The tip of the pseudohypocone articulates with the paraconid; the posterolingual slope is pressed by the metaconid.

In the very progressive *N. pugnax* (Amer. Mus. No. 14567) the pseudohypocone of m^1 is worn into a large circular surface which fills the whole posterolingual corner of the crown; the mesostyle is displaced posteriorly, so that the distance from the mesostyle to the metastyle is decidedly less than the distance from the mesostyle to the prominent parastyle; in correlation with this backward position of the mesostyle the sharp groove for the hypoconid runs obliquely inward and forward; the metastyle is prominent, at least in little-worn teeth; the metaconule is low and inconspicuous, more so on m^2 than on m^1. (Plate XXXV.)

In *N. crassus*, the largest and latest known member of the subfamily, from the Upper Bridger formation, m^1, m^2 have increased their anteroposterior diameter and the mesostyles, paracones, metacones, and pseudohypocones are a little larger; but otherwise these molars resemble those of *N. pugnax*. (Plate XXXV.)

To recapitulate the evolution of m^1 m^2 in the Notharctinæ, the earliest forms had tritubercular molars, wide transversely and with a bare suggestion of the mesostyle and pseudohypocones. These evolve by small gradations, through the ascending levels of the Lower and Middle Eocene into the large subquadrate molars of *Notharctus crassus*, with large mesostyles and large pseudohypocones. The pseudohypocones appear in a region which articulates lingually with the entoconids, labially with the paraconids and posteriorly with the metaconids of the lower molars. The excursion of the mandible in the earlier forms was somewhat more vertical, in the later forms it was somewhat more transverse.

In *Adapis parisiensis*, m^1 and m^2 are very different from the corresponding teeth in any known member of the Notharctinæ. Not only do they lack the mesostyle and the pseudohypocone and possess a true hypocone derived from the cingulum, but they are distinctly more elongate anteroposteriorly, the para- and metacones are widely separated, the ectoloph is flatter and obliquely placed, the metaconule is reduced or absent, the protocone is high and the oblique protocone-parastyle crest is prominent and sharp.

In *Adapis magnus* (Amer. Mus. No. 10511) the fundamental pattern is the same as in *Adapis parisiensis* but the molars are relatively wider. The sharp protocone-parastyle crest is opposed by the protoconid-metaconid ridge of the lower molars; the rounded hypocone projected above the trigonid but did not fit into it; the large central fossa received the hypoconid while the meta- and paracones opposed the middle valley and lower molar intervalley respectively. The upper molars of *Adapis sciureus* (Stehlin, 1916, p. 1514, fig. 368) were much more primitive with the crown less elongate anteroposteriorly, the para- and metacones less separated and more conical, the proto- and metaconule large and the trigonid of the crown distinctly tritubercular; the hypocone is a prominent upgrowth from the cingulum. As first noted by Stehlin (1912, p. 1289) the latter character sharply separates this species from all the Notharctinæ. In *Adapis rütimeyeri* (Stehlin, 1916, Taf. XXI, figs. 27–31) m^1 and m^2 in pattern suggest those of *A. magnus* but they are relatively wider and when little worn have more of the tritubercular stamp even though the hypocone is larger. The metaconule in the specimen illustrated in Taf. XXI, fig. 31 is better developed than in others referred to the same species. Even at this early

Fig. 41. Upper and lower teeth of *Adapis rütimeyeri*. After Stehlin. × $\frac{3}{2}$.

1. P^3, p^2 and alveolus of p^1, right side.
2. P^4, m^1, right.
3. M^1–m^3, right.
4. P^4, m^1, m^2, left.
5. P_2, p_3, p_4, m_1, right; alveoli of c and p_1.

stage the true adapine characters are already more or less clearly indicated in m^1, m^2, just as the true notharctine characters are foreshadowed even in the corresponding teeth of the oldest known *Pelycodus*.

First and Second Lower Molars

Plates XXXVI–XXXVIII, XLI; Text Fig. 39

In *Pelycodus ralstoni* the construction of m_1, m_2 approaches that of the more primitive Eocene Insectivores and Creodonts; the trigonid comprises a small triad of rather delicate more or less pointed cusps, followed on a much lower level by the wide talonid, which consists of a large projecting hypoconid, bearing the posterior cutting V and a small low entoconid, which projects gently on the lingual border. The anterior and posterior roots are not subdivided longitudinally. The paraconid on m_1 juts forward; that on m_2 is near the metaconid. The crown as a whole is relatively narrow; m_2 is notably larger than m_1. The external cingulum is irregularly arranged and does not extend across both talonid and trigonid as a sharp ridge. (Plate XXXVI.)

In the latest and most progressive members of the subfamily m_1, m_2 are of large size, low crowned, with swollen cusps; the trigonid decidedly less elevated above the level of the talonid; the crown as a whole is shorter, wider and rounder as seen from above; the paraconid on m_1 is small, on m_2 it is reduced or wanting; the metaconid more nearly internal to the protoconid; the proto-paraconid crest short and inconspicuous; the entoconid is notably larger and more in line with the metaconid; a small hypoconulid has appeared at the junction of the posterior V with the posterior cingulum. The sharp external cingulum is continued across both talonid and trigonid. The main anterior and posterior roots are subdivided longitudinally with the inner and outer branches more or less divergent, especially in old animals. Between these two extremes in the construction of m_1, m_2 in the earliest and latest types there are several successive stages from ascending horizons of the Lower Eocene, passing from *Pelycodus ralstoni* to *P. trigonodus* and *P. frugivorus* and thence on the one hand to *P. jarrovii* and perhaps to *Notharctus venticolus*, *N. pugnax*, *N. crassus*, and on the other hand to *Notharctus nunienus* and perhaps *N. osborni*. (Plate XXXVI.)

The general articulating relations of m_2 in the Notharctinæ are shown in Figs. 38, 40; Plate XLI; they are essentially the same as in all primitive mammals with tuberculosectorial lower molars. In the oldest forms the motion of the lower jaw and the consequent impact of the lower molars seem to have been somewhat more vertical and less transverse than in the latest types. The molars of the early forms accordingly seem to be adapted to a more or less insectivorous diet, those of the later members rather for vegetable food, especially leaves and fruits, perhaps more or less varied with insects, eggs, etc.

In *Adapis parisiensis* m_1, m_2 show a certain analogy with the corresponding teeth of primitive perissodactyls and other ungulates, inasmuch as they bear two cross crests, corresponding to the protolophid and metalophid; the paraconid also is absent, and the crista obliqua (interior limb of the posterior V) joins the protolophid half way between the protoconid and the metaconid; a metacristid (not metastylid, since it does not arise from a fissuring of the metaconid tip) is present on the slope leading down from the metaconid to the talonid; the talonid fossa is continued labially as a deep notch between the metacristid and the low entoconid; into this notch fitted the labial face of the protocone; the crown as seen from above does not bulge sharply in the rear but the trigonid is nearly as wide as the talonid. These teeth are of small size and comparatively narrow in proportion to the size of the jaw and to the great strength of the jaw muscles and must have been very effective in cutting tough vegetable fibre. The protolophid is obliquely placed, and its edge is worn posteriorly from shearing past the sharp protocone-protoconule crest of the upper molar. The chief difference from the molar pattern of such Eocene perissodactyls as *Lambdotherium* and *Telmatherium* is that the anterior limb of the anterior V is nearly lacking, the protoconid lies nearer the anterior end of the crown and the protolophid points more obliquely backward.

More in detail the articulating relations of m_1, m_2 with m^1, m^2, as shown in American Museum specimens (Nos. 10001–10017) are as follows: the small trigonid fossa came opposite to but did not touch the jutting hypocone of the upper molar; this is the normal primitive mammalian relation of the trigonid fossa and contrasts with the relations of the trigonid fossa in the Notharctinæ, which articulated quite behind the pseudohypocone. The sharp protoconid was received into a small fossa immediately behind the metacone of the preceding upper molar and in front of the anteroexternal part of the protoloph crest of the corresponding upper molar. The high metaconid sheared in front of the protocone and its tip was received in a shallow fossa between the protocone and the anteroexternal corner of the internal cingulum.[1] The metacristid ridge is the continuation of the protolophid and shears past the labial slope of the protocone; the lingual slope of the large hypoconid articulates with the labial slope of the wide protocone; the low small entoconid comes opposite the notch between the protocone and the low hypocone; the notch between the entoconid and the metacristid as above noted is lingual to the tip of the protocone. The anterior slope of the metalophid (hypoconid–entoconid crest) articulates with the posterior slope of the protocone. (Plates XXXVIII, XXXIX, XLI.)

In *Adapis magnus* (Amer. Mus. No. 10511) the general plan of m_1, m_2 is identical with that in *A. parisiensis* but the crowns are relatively wider and much larger; the cristids are very prominent and the sharp protoloph crest is wider; the entoconids are low. The articulating relations with the upper teeth are identical with those described above in *A. parisiensis*.

In the very primitive *Adapis rütimeyeri* (Stehlin, 1916, Taf. XXI) the anterior limb of the anterior V is still present although the paraconids have already been lost; the protolophid is less oblique and the metacristid has not yet developed. The notch between the metaconid and the entoconid is not so deep. But the interlocking relations, as may be seen by comparison with the upper molars, already foreshadowed the adapine conditions. The lower molars of *Adapis rütimeyeri* together with those of *Adapis sciureus* represent early stages of the adapine phylum which might readily be derived from a much more primitive pattern that is preserved in most respects in *Pronycticebus* (Fig. 80, p. 231).

Third Upper Molar

Plates XXXV, XLI

M^3 in *Pelycodus ralstoni* has a small wide asymmetrical tritubercular crown, the paracone higher than the metacone, the protoloph sharp; while there is no trace of a pseudohypocone the posterior slope of the protocone is worn flat by the entoconid of m_3. Parastyle and metastyle not present, mesostyle incipient; cristæ of conical paracone and metacone arranged anteroposteriorly and with very little tendency to form a V. Metacone without crista posterior. Internal and posterior cingula well marked; no hypocone on cingulum. Lingual face of paracone pyramidal rather than conical, proto- and metaconules with blunt transverse crests.

In the latest of the phylum, *N. crassus*, m^3 is relatively larger, more symmetrical, subquadrate with an increased anteroposterior diameter, a large mesostyle, low roundly conical para- and metacones, blunt

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[1] A somewhat analogous fossa is present in the *lower* molars of opossums on the anteroexternal wall of the trigonid, for the tip of the enlarged metacone.

protoloph and obscurely defined protoconule. Posterior cingulum very thick, giving rise to a hypocone. All cusps coarse, para- and metacones conic, their cristæ tending to form a W.

Between these extremes the species from ascending horizons furnish a series of intermediate conditions. The interlocking relations of m^3 will be discussed below.

In *Adapis parisiensis* (Amer. Mus. No. 10005) m^3 differs from m^2 as described above (p. 140) chiefly in the absence of a hypocone, in the somewhat smaller size of the crown, which is less extended anteroposteriorly; protoloph sharp and high, metacone smaller than in m^2; internal cingulum delicate; no metaconule. In some of the varieties of *A. parisiensis* as figured by Stehlin (1912) m^3 has a low hypocone-cingulum. In *Adapis magnus* (Amer. Mus. No. 10511) m^3 is tritubercular with barely incipient hypocone, with conical para- and metacones, and a prominent sharp protoloph, which is, however, less elevated than in *A. parisiensis*. The crown is less elongate anteroposteriorly than in that species. *Adapis rütimeyeri* (Stehlin, 1916, Taf. XXI, fig. 31) has a very primitive m^3, which approaches those of *Pronycticebus* and *Pelycodus ralstoni*. The crown is wide transversely, the paracone much larger than the metacone, the protoloph low and interrupted by the large protoconule; the hypocone swelling of the cingulum is much more distinct than in either *A. magnus* or *A. parisiensis*.

Third Lower Molar

Plates XXXVI, XXXVII

M_3 in *Pelycodus ralstoni* (Amer. Mus. No. 16096) is elongate anteroposteriorly with a wide trigonid and a long tapering talonid; paraconid small, near the metaconid, protoconid-metaconid crest low, entoconid very small, hypoconulid small; hypoconid crests not forming a distinct V. (Plate XXXVI.)

This very primitive form of m_3 which recalls that of *Pronycticebus*, leads through the intermediate species to the pattern of m_3 in *N. crassus*, which is as follows: talonid as wide as trigonid, entoconid large, paraconid reduced; anterior cingulum thick, hypoconulid large, hypoconid crests forming a widely open V; one or more small accessory cusps on the ridge connecting the hypoconulid with the entoconid; all cusps with very thick enamel.

The occlusion of m_3 with the upper teeth has been studied in *Pelycodus trigonodus* (Amer. Mus. No. 15017), *N. venticolus* (14655), *N. osborni* (11466) and *N. crassus*. The small size and peculiar character of m^3 and m_3 are doubtless conditioned by the fact that they lie nearer to the fulcrum than the other teeth, which enables them to exert great pressure, the smaller size further increasing their penetrating power. The narrow hypoconulid of m_3 would be well adapted for piercing or breaking resistant objects; together with the entoconid it presses against the posterior slope of the protocone of m^3. The remaining parts of $m\frac{3}{3}$ articulate much as they do in the other molars. (Plate XLI; Figs. 39, 40.)

In this subfamily the subcrescentic shape of the para- and metacones and many other features are connected with the lateral sweep of the lower molars across the upper. In the later Notharctinæ $m\frac{3}{3}$ could apparently be used as a pivot for this lateral motion. The animals could exert great pressure on one side or the other by pressing together the outer parts of the teeth and then pushing the lower teeth up the slopes of the upper teeth as the mandible passed inward. This motion was essentially the same as it was in *Lambdotherium*, *Tapirus* and many other mammals investigated by the writer.

In *Adapis magnus* (Amer. Mus. No. 10511) the pattern is essentially similar but the tooth is wider; the entoconid is absent; metacristid very prominent. In *Adapis sciureus* (Stehlin, 1916, p. 1515, fig. 368) the protolophid is small, metacristid absent, entoconid distinct, hypoconulid short and narrow. In

Adapis priscus (Stehlin, 1916, p. 1511, fig. 366) the protolophid is narrow transversely, the talonid broad, the hypoconid very large, entoconid large, hypoconulid short. M_3 in *Adapis rütimeyeri* (idem, Taf. XXI) suggests *A. magnus* but lacks the metacristid; hypoconulid very small, entoconid low.

Thus, all the Adapinæ differ from the Notharctinæ in the oblique position and progressive prominence of the protolophid, in the progressive development of a metacristid, in the relatively large size of the hypoconid, reduction of the entoconid and narrowness of the hypoconulid.

In the Adapinæ the interlocking relations of $m\frac{3}{3}$ have been studied from specimens Nos. 10001–10017 (*Adapis parisiensis*) and 10511 (*A. magnus*). There was evidently less transverse movement of the mandible than in the Notharctinæ. The principal cutting was done by the sharp protoloph and protolophid; the sharp cones and crests easily pierced the relatively tough vegetation. (Plate XXXIX.)

The final summary of the evolution of the dentition in the Notharctinæ and in the Adapinæ may be deferred until after the mandible has been described.

MANDIBLE

Plates XXXVI–XLII; Text Figs. 42–45

The lower jaw in the Notharctinæ is fairly stout, but of slight to moderate depth. No very marked differences are apparent between the earlier and the later types, except that in the later species of *Notharctus* the opposite rami coalesce at the symphysis in old animals, leaving, however, a visible suture on the lower border of the chin. There is a wide range of variation in the depth of the ramus, which in *N. venticolus* (old male), *N. osborni, N. tyrannus* is relatively deep, in *N. affinis, N. pugnax, N. crassus* quite shallow. The chin also is sometimes very shallow (*N. rostratus*), sometimes deep (*N. osborni*), and it is not apparent that these differences are either sexual or specific; for both shallow and deep jaws are sometimes assigned to the same species (e. g., *N. tyrannus*) on account of the close agreement in the teeth, and again

Fig. 42. Comparative figures: mandibular condyles of *Notharctus* and *Adapis*. Rear view. Twice natural size.

1. *Notharctus osborni*. Amer. Mus. No. 11466.
2. *Notharctus crassus*. Amer. Mus. No. 12588.
3. *Adapis parisiensis*. Amer. Mus. No. 10007.

some of the deep jaws (*N. osborni*) have small canines and appear to belong to females while other deep jaws (*N. venticolus*) bear large canines and apparently belonged to males.

The condyle is best preserved in *N. osborni* (Amer. Mus. No. 11466), *N. tyrannus* (Yale Univ. Mus. No. 12151), and *N. crassus* (Amer. Mus. No. 12588). As seen from above it is bean-shaped, with the concave side turned backward; the inner end is produced downward and backward and in *N. crassus* this downward prolongation is very pronounced, so that much of the articular surface may be seen from the rear; the whole condyle is broadly convex both transversely and anteroposteriorly. This shape of the condyle is correlated with the shape of the glenoid cavity and postglenoid process (see below, p. 159). The mandible was capable of very free motion in the glenoid fossa (as may be seen in the type of *N. osborni* and in *N. crassus*) and could be shifted forward, when special pressure was exerted upon the canines, incisors and premolars, as well as inward or outward, as in lateral movements of the mandible (see below, p. 148).

The condyle of *Adapis parisiensis* (Amer. Mus. No. 10007) differs from that of *Notharctus* in being extended transversely, without the backward and downward turning of the inner moiety; it is also flatter above. It is more analogous with that of *Lemur* and was probably less freely displaced laterally and anteroposteriorly. (Plate XXXIX.)

The coronoid process is well preserved only in *N. pugnax* (Amer. Mus. No. 11480) and *N. tenebrosus* (Yale Univ. Mus. No. 12151). It is very large and high with a strong anterior border, defining the insertion area of the temporal muscle, and a nearly straight and vertical posterior border. It differs from that of *Adapis* in not being sharply recumbent and in having the posterior border straight instead of concave. The temporal insertion areas on the inner and outer sides of the coronoid process were consequently not so wide inferiorly as in *Adapis* but were more extended vertically. The areas for the masseter internus and masseter externus, on the side of the ascending portion below the temporal area were, on the whole, much less extensive than in *Adapis parisiensis*, since the whole region of the angle was less expanded. The masseter fossa is sharply defined anteriorly by the ridge that runs down from the coronoid process. As in other mammals with stout malars the masseter doubtless bulged prominently below, and pressed the border of the jaw inward, this causing the characteristic concavity of the lower border behind the swollen middle part of the ramus, which is seen in many Eocene mammals and some modern carnivores and insectivores. This peculiar concavity of the lower border is even more pronounced in *Adapis* which doubtless had a much swollen masseter. The lower border and adjacent inner surface of the jaw in front of the concavity above mentioned is slightly roughened in some specimens; this may very well mark the insertion area of the digastric muscle, which in *Propithecus*, *Lemur* and many other mammals is inserted in this region.[1] In *Adapis* a fossa on the inner side of the jaw above and in front of the masseter concavity is provisionally identified by Leche and by Stehlin (1912, p. 1221) as probably for the insertion of the mylohyoid, but to the present writer this area, by comparison with *Propithecus*, seems much more likely to mark the insertion of the digastric, the mylohyoid area being probably above it. (Plate XLI.)

The angle of the jaw is well preserved only in *N. venticolus* (Amer. Mus. No. 14655). It was not widely expanded as in *Adapis*, but was of primitive lemuroid form, though wider than in most lemurs. Externally it bears the lower part of the masseter area and internally it bears the well-defined lower fossa for the internal pterygoid muscle, flanked by a sharp crest above and by the rounded inturned border below. It was the broken section of this partly inturned border, which is conditioned by the

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[1] See the dissections in Milne Edwards and Grandidier (1875) and in Cuvier and Laurillard "Planches de Myologie."

bulging of the masseter and by the insinking of the pterygoid fossa, which misled Marsh into attributing an "inflected angle" to the jaw. But the inflection, such as it is, is widely different from that which is characteristic of the marsupials. In *Adapis* the lower fossa for the internal pterygoid is not fundamentally dissimilar to that described for *Notharctus*, but is wider dorsoventrally and less produced backward.

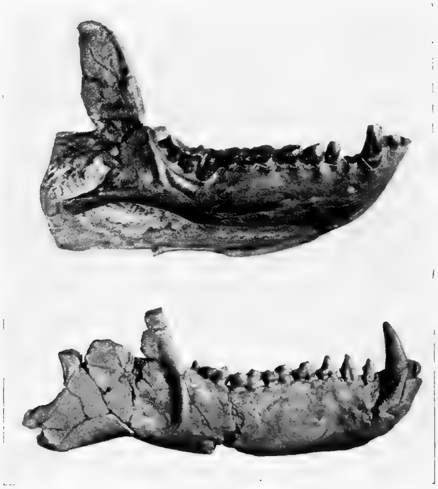

Fig. 43. Lower jaws of *Notharctus pugnax*. Amer. Mus. No. 11480, Middle Eocene (Upper Bridger), and *N. venticolus*, Amer. Mus. No. 14655, Lower Eocene (Wind River). Lateral view. Natural size.

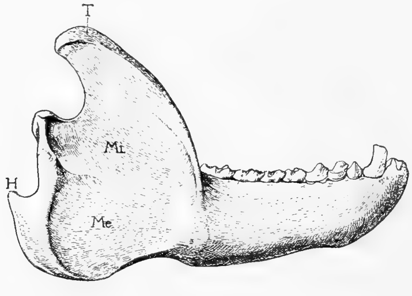

Fig. 44. Lower jaw of *Adapis parisiensis*. After Stehlin. Natural size.

The upper fossa for the internal pterygoid in both *Notharctus* and *Adapis* lies below the ridge forming the lower border of the temporal area. The inturning of the lower border of the jaws, beneath the lower internal pterygoid fossa, is very pronounced in certain old individuals of *A. parisiensis* (Amer. Mus. Nos. 10014, 10010, 10012). Such an inturned border has been acquired independently in many placental mammals and is quite different in form from the true inflected angle of the marsupials.

The external pterygoid muscle of *Notharctus* was probably inserted in a small fossa just below and in front of the posterior extension of the condyle. (Plate XXXVI.) The alveolar foramen is well shown in *N. venticolus* (Amer. Mus. No. 14655). (Fig. 45.) The foramen is located about 7 mm. behind m_3 and about 5 mm. below the ridge that bounds the temporal area below. From the foramen a straight groove leads upward and backward, marking the course of the inferior dental nerve and vessels. This groove is clearly defined in certain specimens of *Adapis* (Amer. Mus. No. 10007). (Plate XLI.)

Behind the symphysis and immediately above the lower border is a pair of shallow pits which probably mark the insertion of the geniohyoid muscles. (Fig. 45.) The corresponding pits in *Adapis parisiensis* (Amer. Mus. Nos. 10007, 10013) are defined below by a sharp rim. (Plate XLI.)

Fig. 45. Left mandibular ramus of *Notharctus venticolus*. Amer. Mus. No. 14655. Lower Eocene (Lost Cabin beds), Wyoming. Medial aspect. Natural size.

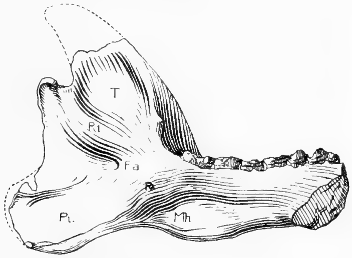

Fig. 46. Left mandibular ramus of *Adapis parisiensis*. After Stehlin. Medial aspect. Natural size.

Mental Foramina

The position of the "mental foramina" has been examined in the following specimens of Notharctinæ and Adapinæ:

Pelycodus	*ralstoni*	A. M. N. H. No.	16093
"	*trigonodus*	" "	15036
"	*frugivorus*	" "	16852
"	*jarrovii*	" "	15624
Notharctus	*nunienus*	" "	12736
"	*venticolus*	" "	14655
"	*matthewi*	" "	42011
"	"	" "	13030
"	*osborni*	" "	11466rt.
"	"	" "	" l.
"	*tenebrosus*	U. S. N. M.	
"	*rostratus*	A. M. N. H. rt.	
Notharctus	*rostratus*	A. M. N. H. l.	
"	*pugnax*	A. M. N. H. No.	11461
"	"	" "	11482
"	"	" "	12575
"	*crassus*	" "	12581
Adapis	*sciureus*	(Stehlin, 1916, p. 1515)	
"	*parisiensis*	A. M. N. H. No.	10008
"	"	" "	10006
"	"	" "	10007
"	"	" "	10013
"	*magnus*	" "	10511

In the Adapidæ as a whole there are usually three mental foramina, which may be called the first (I), second (II) and third (III) mental foramina respectively; typically the first foramen is beneath p_1, the second beneath p_3, and the third beneath p_4. In the Notharctinæ the first foramen is occasionally beneath the canine or between the canine and p_1, and the second beneath p_2. In some of the later Notharctinæ (*N. pugnax*) there is a fourth foramen (IV) beneath m_1, or in one extreme case beneath m_2. In the Adapinæ also there are usually three mental foramina, of somewhat variable position, but perhaps more typically beneath p_1, p_3 and m_1. Possibly the posterior foramen may represent No. IV of the Notharctinæ, while No. III may often be absent.

Action of the Jaw Muscles

From a study of the areas of origin and insertion and the consequent direction of the jaw muscles in the skull and jaw of *N. osborni* the following inferences appear highly probable.

(1) The jaw was pulled forward and upward by the combined action of the masseters, pterygoidei internus and externus; after the jaw was pulled forward these muscles, together with the temporals, could exert strong pressure in the region of the canines and premolars.

(2) The jaw was pulled upward and backward by the temporals; acting with the pterygoids this would give a powerful vertical pressure on the molars.

(3) The jaw was tilted toward the outer side by the combined action of both divisions of the masseter and the temporal, possibly assisted by the pterygoids of the opposite side.

(4) Oblique and lateral movements of the mandible were probably effected by alternate and selective tension and relaxation of muscles on opposite sides. For example, the ental movement of the right mandible in mastication (see page 139 above) was probably executed as follows:

- (a) tension of the left external pterygoid, the other muscles being relaxed, this pulling the left condyle forward and inward, forcing the right condyle back against the postglenoid process and swinging the whole jaw on the right condyle as a pivot toward the right; the right temporal and the right masseter co-operate by slightly tilting the right ramus outward, the right condyle being the pivot; this slightly depresses the left condyle, and brings the outer cusps (protoconid, hypoconid) of the right lower cheek teeth nearly opposite the outer cusps (para- and mesostyles) of the right upper teeth;
- (b) a maximum tension of the right temporal, right masseter and right internal pterygoid, producing great vertical pressure on the cheek teeth;
- (c) increasing tension of the left temporal, left masseter and left internal pterygoid, relaxation of the left external pterygoid, all tending to pull the whole jaw toward the left side and causing the lower teeth to sweep across the upper teeth from right to left, that is from the outer side inward (ental);
- (d) relaxation of the temporals, masseters and internal pterygoids of both sides, combined with
- (e) tension of the digastric of both sides, lowering the jaw, and tension of the right external pterygoid pulling the right condyle forward and inward and swinging the right ramus toward the left.

In *Adapis* the motion of the jaw was probably more orthal and less ental. The huge development of the masseters, as indicated by the great size of the malar, and of the internal pterygoids, as indicated by the expansion of the pterygoid fossæ of the jaw, suggests that great force could be exerted by vertical pressure of the sharp-edged canines, incisors and premolars; the sharp protolophs and protolophids also would be effective in chiefly vertical but slightly transverse movements of the mandible.

Summary of Occlusal Relations of the Upper and Lower Teeth

Referring to the writer's conclusions (1915, pp. 422, 423) regarding the supposed correlation between differences in the excursion of the mandible and concomitant differences in the upper and lower molars Dr. Stehlin asserts (*op. cit.*, p. 1538) that: "Gregory nimmt in sehr zuversichtlicher Weise Stellung zu diesen Fragen." He also said in this connection that: "Im übrigen scheinen mir die Ausführungen Gregorys nicht nur rein hypothetisch, sondern sehr anfechtbar zu sein" (p. 1539).

In reply, it may be proper to state that the conclusions under consideration, although perhaps too briefly stated, were not hasty outgivings of the moment but were one of the incidental results of long continued study on the mechanical interrelations of the parts of the upper and lower teeth in many recent and fossil mammals, on the areas and attachments of the jaw muscles, and on the movements of the mandible in mastication, it having been found by experience that all these facts were closely interrelated and that they often contribute to a better understanding of the probable origin and evolution of the dentition and of the skull as a whole. In view of the abundant material described and figured in the present paper and summarized above (pages 133–148) the following may be taken not as theoretical deductions but as literal facts.

(1) In the earlier Notharctinæ, between the protocone and the incipient pseudohypocone of the upper molars, there is often a notch-like facet of wear, caused by the attrition of the entoconid of a lower molar. (Fig. 39.)

(2) On the posterointernal face of the incipient pseudohypocone of these forms there is an extended facet of wear caused by the attrition of the paraconid of a lower molar. (Fig. 39.)

(3) The pseudohypocones of the upper molars and the entoconids of the upper molars are but poorly developed in the earliest Notharctinæ, become gradually larger in those of intermediate age and culminate in the very large pseudohypocones and entoconids of the latest and most progressive species *Notharctus crassus.* (Fig. 38.)

(4) A precisely analogous case is supplied by the Eocene and Oligocene titanotheres, in which the posterointernal cusp of the upper premolars develops *pari passu* with the entoconid of the lower premolars; the tip of the entoconid likewise sweeps across the lingual face of the upper tooth in the region of the constriction separating the "pseudohypocone" from the protocone (1915, p. 423).

(5) In *Adapis parisiensis,* on the contrary, the posterointernal cusp (true hypocone), which is an upgrowth of the cingulum, has no direct relation at all with the entoconids of the lower molars; it rather protrudes into the space between adjacent upper teeth and above the basin of the trigonids of the lower molars, as it does in all normal mammalian dentitions (Plate XLI).

(6) The generally retarded and internally placed entoconids in the Adapinæ do not articulate with the region of the pseudohypocone which never develops; they have, on the contrary, a functional relation with the whole of the posterointernal slope of the protocones of the upper molars since they help to press the food against them (Plate XLI).

(7) As a result of the foregoing facts it follows that Dr. Stehlin's citation (p. 1539) of the variable development of the true hypocones and of the entoconids in the Adapinæ by no means disproves the thesis of the writer that a high pseudohypocone in the Notharctinæ was correlated with a progressive entoconid (or vice versa), a fact which can be determined by actually "fitting the upper and lower teeth together," as originally stated (1915, p. 422).

(8) The writer's original statement (1915, p. 423) that in the Notharctinæ "the progressive development of the mesostyle is also correlated with a partly transverse excursion of the mandible and with the V-like modification of the para- and metacones," can now hardly be questioned in the light of all the evidence cited in this paper and of the analogous cases among other groups of mammals (e. g., *Lambdotherium*, *Propithecus*, *Moropus*, etc.) which the writer has investigated.

(9) No less decisive is the evidence cited above (pages 137, 142, 144, 159) that in the Adapinæ the motion of the jaw was more orthal than it was in the Notharctinæ and that this more orthal movement is found in association with the lack of V-shaped para- and metacones, the total absence of mesostyles, the emphasis of the protoloph and of the protolophid (protoconid-metaconid crest).

In reference to the writer's statement (1915, pp. 422, 423) to the effect that by fitting the upper and lower teeth together it was observed that the movement of the mandible must be more transverse in *Notharctus* and more vertical in *Adapis*, Dr. Stehlin (1916, p. 1539) says: "Da ich keine Gelegenheit gehabt habe, das Kiefergelenk von Notharctiden zu untersuchen, kann ich mich nicht zu der Frage äussern, ob eine solche Differenz in Kaumechanismus besteht oder nicht."

The appended photographs (Fig. 42, p. 144) of the condylar region of *Notharctus* and of *Adapis* may partly supply this need, although it must be stated that there is nothing so demonstrative on this point as the fitting together of specimens and the study of the actual movements of the lower teeth when they are pressed against the upper teeth in their natural positions. These may readily be determined by fitting the protocone of the first upper molar into the talonid basin of the first lower molar. When this is done the remaining parts of the teeth will exhibit the spatial relations which were summarized by the writer in 1910.[1]

DECIDUOUS DENTITION

Plate XLII

The upper milk molars of *Notharctus* cf. *tyrannus* are preserved in Amer. Mus. No. 13025, from the Bridger Basin, Horizon B. This specimen shows the alveolus of p^1, and the well-preserved dp^2, dp^3, dp^4 followed by m^1, m^2 all in place. P^4 lies in the bone beneath the last milk molar (dp^4), while p^3 lies beneath dp^3; impression made by p^2 against the maxillary is shown beneath dm^1. The alveolus of p^1 (which, as in most mammals, appeared with the deciduous molars) is at the intersection of lines drawn through the base of the crowns of the milk series and through the permanent series of premolars beneath them. It thus may be possible that p^1 originally belongs with the permanent series, but has been forced into association with the deciduous set through the early eruption of the permanent canine, and that the deciduous predecessors of p^1 have been lost. M^3 is also present; it is just beginning to erupt and must have been nearly covered by bone. The specimen thus shows that m^1, m^2 were fully in place and that m^3 was also on the point of erupting while the deciduous molars were firmly in place. (Plate XLII, figs. 7, 8.)

As usual among mammals the last milk molar (dp^4) was much more molariform than p^4. It has two widely separated external cusps, with a distinct mesostyle; it also has a small but distinct pseudohypocone. Its protoloph is very oblique, and the protocone is low. (Stehlin, 1912, p. 1178, fig. 248). Except that it has both pseudohypocone and mesostyle it is much like the corresponding deciduous tooth in *Adapis parisiensis*, whereas the tooth that succeeds it (p^4) is quite unlike that of *Adapis*. (Plate XLII, figs. 6–8.)

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[1] Bull. Amer. Mus. Nat. Hist., XXVII, pp. 190, 191.

The second milk molar (dp^3) is much simpler in form; it is widely triangular in section with a long outer side supported by two widely separated roots, and a low internal protocone spur, supported by a single but large root. It has only a single, high external cusp (paracone), low para- and metastyles and an incipient oblique protoloph-cingulum. The posterolingual face of the tooth is worn by the high protoconid face of dm$_3$. The crown of p^3 is pushing itself between the inner and the outer roots of dp^3, while the crown of p^4 lies between the roots of dp^3 and dp^4. Dp^3 distantly resembles that of *Adapis* in its triangular contour; it has, however, but one external cusp while that of *Adapis* has two; and its protocone and protoloph are much less developed. Dp^2 is an extremely simple tooth, somewhat resembling the first permanent premolar (p^1) but with a shorter crown. It is asymmetrical in all views, with a very short crista anterior, a long crista posterior and a slightly recurved tip. Its anterolingual face foreshadows the corresponding face of the paracone; its larger posterolingual face is flattened or concave; its external face strongly convex. The anterointernal cingulum faintly foreshadows the protoloph and ends anteriorly in a barely perceptible parastyle; the posterointernal cingulum is homologous with the posterior cingulum of succeeding teeth and ends externally in a low metastyle. The corresponding tooth of *Adapis parisiensis* has a compressed oval crown, with but little differentiation of parts. (Plate XLII, figs. 6, 7.)

The lower deciduous cheek teeth are partly preserved in *Notharctus tyrannus?* Amer. Mus. No. 13029, from the Bridger Basin, Horizon B$_2$. Unfortunately the surfaces of the crowns are mostly broken off; but the lower parts of the crowns and the roots remain, and beneath them lie the unerupted p$_4$, p$_3$, p$_2$. Behind the deciduous series m$_1$, m$_2$ are fully in place, while m$_3$ is nearly up. P$_2$ lies nearer to the surface than p$_3$, p$_4$ and would erupt before them. (Plate XLII, figs. 9, 10.)

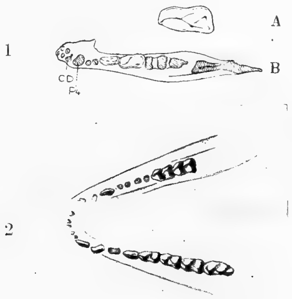

Fig. 47. Lower jaw with deciduous and permanent teeth of *Adapis parisiensis*. After Stehlin.

1. *A*. Second right lower deciduous molar. Natural size.
   B. Left mandibular ramus with alveoli of both the deciduous and the permanent incisors, of the deciduous canine, of the first permanent premolar ("P_4"), of the last deciduous molar and first true molar. The other two deciduous molars are *in situ*.
2. Lower jaw of *Adapis parisiensis*, showing all three true molars in place, along with the deciduous molars, the deciduous canine and the first premolar.

The last deciduous molar (dp$_4$) was much more molariform than the tooth which replaced it (p$_4$), since its talonid was larger than its trigonid, whereas the reverse is the case in p$_4$. The posterointernal root of dm$_3$ rests in the small talonid basin of p$_4$, while its anterointernal root was apparently in process of resorption. The other deciduous molars (dp$_3$, dp$_2$) were likewise elongate anteroposteriorly, their posterointernal roots having somewhat similar relations to the potential talonids and trigonids of p_3, p_2. (Plate XLII, fig. 10.)

In *Adapis parisiensis* (Stehlin, 1912, figs. on pp. 1180, 1181) the last deciduous lower molar (dp_4) was fully molariform, but more compressed than m_1. Comparison of the crown with that of *Notharctus* is not possible. (Fig. 47.)

Succession of the Teeth

Stehlin (1912, pp. 1183–1188) has shown that in *Adapis* the probable order of replacement after the eruption of the deciduous teeth was as follows.

1. $M\frac{1}{1}$ and $p\frac{1}{1}$ appear.
2. $M\frac{2}{2}$ appear.
3. $M\frac{3}{3}$ appear. Replacement of deciduous incisors by permanent incisors ($i\frac{1}{1}$ being somewhat ahead of $i\frac{2}{2}$). Deciduous canines drop out and permanent canines begin to come in.
4. Replacement of $dp\frac{4}{4}$, $dp\frac{3}{3}$ by $p\frac{4}{4}$, $p\frac{3}{3}$.
5. Replacement of $dp\frac{2}{2}$ by $p\frac{2}{2}$. Canines assume final position; earlier in females than in males.

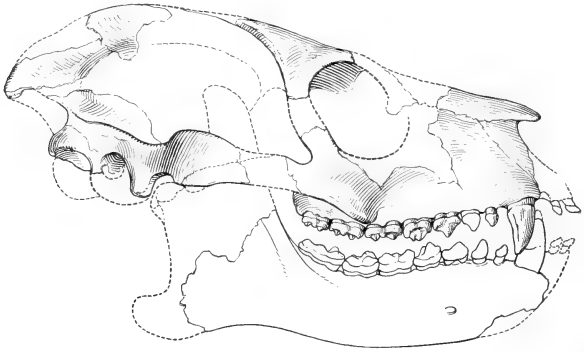

Fig. 48. Skull of *Notharctus crassus*. Reconstruction based on Amer. Mus. No. 12567. Middle Eocene (Upper Bridger), Wyoming. Natural size.

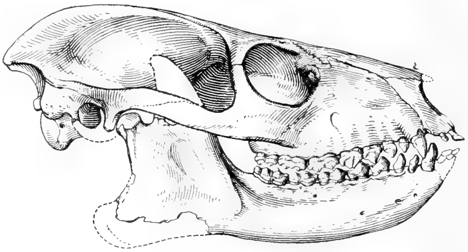

Fig. 49. Skull of *Notharctus osborni*. Type, Amer. Mus. No. 11466. Middle Eocene (Lower Bridger), Wyoming. Lacrymal region restored from other specimens. Natural size.

The evidence is incomplete in the case of *Notharctus,* especially with regard to the incisors and canines, but so far as it goes it indicates that the order of replacement was not dissimilar to that of *Adapis*. From two of the specimens above noted (Amer. Mus. Nos. 13029, 12578) it is established that the third lower

Fig. 50. Skulls of *Adapis*. Natural size.

1. *Adapis parisiensis*. After Filhol.
2. *Adapis magnus*. After Grandidier.
3. *Adapis magnus*. After Stehlin.

molar came in before the deciduous molars were shed as in *Adapis* and the modern lemurs, while in the New World and Old World monkeys m_3 is delayed until after the deciduous molars have been replaced by the premolars.

From the relations of m^3 and m_3 and the other teeth it appears that Amer. Mus. specimen No. 13025 (Plate XLII, figs. 7, 8) is in a stage between 2 and 3 of *Adapis* as defined by Stehlin, since p^1, m^1, m^2 and all the deciduous molars are in place but m^3 is not yet up. The first lower jaw (Amer. Mus. No. 13029) is at the beginning of stage 3, since m_3 is just coming in, and the second lower jaw (No. 12578) is perhaps in the middle of stage 3, since the permanent canine is beginning to come in. Possibly the permanent incisors were already in place as apparently indicated by the presence of a pit in front of the canine tip, but the evidence is not altogether clear; p_4 is quite close to the surface preparing to push out dp_4. (Plate XLII, figs. 9, 10.)

THE SKULL AND BRAIN CAST OF *NOTHARCTUS*; COMPARISON WITH *ADAPIS*

Skull

Text Figs. 48, 49, 51, 52, 56, 58, 62

The general form of the skull in the two subfamilies is summarized below (page 185). The detailed description of the parts is as follows:

The face of *Notharctus osborni*, measured on the line joining the postorbital process of the frontals to the projection of the premaxillary, is about as long as the brain-case, while in *Adapis*, although varying in different species, it is distinctly shorter than the brain-case. The orbit is larger than it is in *Adapis magnus* or *A. parisiensis* and the malar is smaller. The postorbital constriction in *Notharctus osborni* is much less pronounced than in *Adapis*, but in the older *Notharctus venticolus* the sharper postorbital constriction recalls that of *Adapis magnus leenhardti* (Stehlin, 1912, p. 1278, fig. 286). The sagittal and lambdoidal crests of *Notharctus* are less elevated than those of *Adapis*. The greatest difference is in the lower jaw, which has a strongly expanded angle in *Adapis* and a very primitive projecting angle in the Notharctinæ. The horizontal ramus of the mandible is also much deeper in *Adapis* in proportion to its length. These differences, as well as the heavy zygoma and prominent masseter tubercle of *Adapis*, are correlated with its more voluminous temporal, masseter and internal pterygoid muscles. (Figs. 48–50.)

Very little is known of the structure of the skull in the older Notharctinæ. Fragments of the maxillary preserved in *Pelycodus ralstoni*, *P. trigonodus* and *P. jarrovii* (Amer. Mus. No. 4174) indicate that, at least in the females, the malar below the orbit was not as deep as it is in *Notharctus;* probably in these smaller forms of *Pelycodus*, the orbits were a little larger, with more slender postorbital rims (*P. trigonodus*, No. 15017). The opposite rows of cheek teeth converged more toward the midline than in the later forms with heavy canines and the muzzle was probably somewhat shorter and narrower. This is a step backward toward the hypothetical stem form of the Notharctinæ and Adapinæ, which presumably had fairly large orbits, a more delicate muzzle and less developed muscular crests.

Premaxillæ

Text Figs. 52, 58

Except for their palatal processes these elements are preserved in *Notharctus venticolus* (No. 14656) and in *N. osborni* (No. 11466). (Fig. 52.) They are strikingly like those of *Adapis* and have similar relations with the nasals and maxillaries. The gentle inclination of the opposite premaxillaries toward the midline was probably similar to that of *Adapis parisiensis* var. *bruni* (Stehlin, 1912, p. 1201, fig. 259).

Nasals

Text Figs. 52, 54

The nasals of *Notharctus venticolus* and *N. osborni* spread at the proximal end, where they have wide contacts with the frontal and maxillary; they are decurved and taper toward the distal end, where each ends in a short pointed tip. In *N. crassus* the distal end seems to have been heavier than in the others. In *Adapis magnus* (Stehlin, 1912, pp. 1248, 1249, figs. 275, 276), on the other hand, the nasals are narrow proximally and swell more or less widely toward the distal end. Even the primitive *Adapis magnus* var. *leenhardti* (Stehlin, 1912, p. 1278, fig. 286) shows a beginning of this tendency, but in *A. parisiensis* it is less pronounced, the proximal ends in the variety *bruni* (Stehlin, 1912, p. 1192) approaching the conditions in *Notharctus;* the distal end, however, is wider. The inferior border of the proximal part of the nasal in *N. venticolus* (Amer. Mus. No. 14656), where it meets the ascending plate of the maxilla, was produced inward as a prominent crest.

Maxillæ

Text Figs. 49, 58

In *Notharctus* the maxillary is essentially similar to that of *Adapis* but appears to be somewhat longer anteroposteriorly that of *Adapis* tending to become short and deep. The posterosuperior extension of the maxillary is in contact with the frontal and the lacrymal as in *Adapis*. A shallow fossa on the side of the maxilla in front of the lacrymal is present also in *Adapis* and probably lodged the orbicularis palpebrarum muscle (Stehlin). The infraorbital canal and foramen are best seen in a young fragmentary skull of *N. osborni* (Amer. Mus. No. 12569); the foramen is about two millimeters in height; it opens about four millimeters above the anterior end of p^4. Stehlin's figures (pp. 1196, 1197, 1251) show that in *Adapis* the infraorbital foramen was sometimes double and opened above p^4 or between p^3 and p^4. The tubercle for the anterior tendon of the masseter is located on the maxilla immediately below the junction with the malar as in *Adapis*. (Fig. 58.) The palatal shelves of the maxillæ are long and narrow transversely. There is considerable variation in the relative width of these elements in different forms of *Adapis* as shown in Stehlin's reconstructions. (Figs. 59–61.)

Lacrymals

Text Figs. 49, 51, 52

This element is preserved in *Notharctus tenebrosus* (?) Yale Museum, No. 12151; its relations with surrounding elements are partly indicated in *N. venticolus*, American Museum No. 14656, and in *N. osborni* No. 11466). It formed a prominent protuberance on the extreme anterior limit of the orbit above the anteroinferior orbital rim (crista anterior), which was formed by the malar. The lacrymal did not extend in front of this rim, at least as seen from the outside, and hence there was no exposed pars facialis. The lacrymal foramen was located at the extreme anterior corner of the lacrymal and immediately behind the upper part of the crista anterior. The foramen may have been partly surrounded by the lacrymal, partly by the maxilla and perhaps partly by the jugal; at least it lies at or very near the meeting place of these elements. The limits of the orbital part of the lacrymal are not shown. The protuberant portion (crista posterior) articulated above with the frontal. It was separated from the nasal by the fronto-maxillary contact. The upper part of the crista anterior near the foramen may have been formed exclusively by the maxilla rather than by the lacrymal, and if this is true then the malar did not quite reach to the lacrymal. But at most there was only a narrow strip formed by the maxilla between the malar and the lacrymal.

The lacrymal of *Notharctus* very nearly resembles that of *Adapis*, especially *Adapis magnus*, as described by Stehlin (1912, pp. 1251, 1252). In that form, however, the malar was solidly in contact with the lacrymal, but in the specimen of *Adapis parisiensis* described by Forsyth Major (1901, pp. 134–135) the malar was separated from the lacrymal by a narrow strip of the maxillary. In the same specimen the foramen is a little further forward than in *Notharctus tenebrosus*, since it sharply notches the maxilla. In *Adapis magnus*, on the other hand, the foramen was chiefly surrounded by the lacrymal and malar. Thus the whole lacrymal region of *Adapis*, with all its contacts, differs only in minor details from that of *Notharctus*. (Fig. 53).

Fig. 51. Skull of *Notharctus tenebrosus* (?). Yale University No. 12151. Middle Eocene (Lower Bridger), Wyoming. Right and left sides. × 1.

The right side shows the lacrymal protuberance, the lacrymal foramen just in front of the orbit and the contact or close proximity of the malar and the lacrymal. The left side shows the lacrymal protuberance.

Fig. 53. Lacrymal region of *Adapis magnus*. After Forsyth Major.

Fig. 52. Part of facial region, *Notharctus venticolus*. Amer. Mus. No. 14656. Lower Eocene (Lost Cabin), Wyoming. × 1.

Shows the region of the fronto-lacrymal and fronto-maxillary contacts.

Malars

Text Figs. 49, 58

This element in *Notharctus* is not nearly so wide below the orbits as it is in *Adapis*, and it was narrower in the early species of *Pelycodus*. The postorbital process was not as heavy as in *Adapis*. The orbital rim of the malar is sometimes pierced by a foramen as it is in *Adapis* (*N. venticolus*, Amer. Mus. No. 11465). The outer suture between the malar and the zygomatic process of the maxilla, as well shown in *N. matthewi*, Amer. Mus. No. 13030, passes above the tubercle for the anterior tendon of the masseter and runs obliquely upward, forward and inward toward the lacrymal, as in *Adapis*. The lower part of the malar was deeply cleft into inner and outer laminæ which embraced the thin zygomatic process of the maxilla (Amer. Mus. No. 13030). The posterior zygomatic part of the malar is not known, but it probably did not extend back to the glenoid (p. 159 below).

Frontals

Text Fig. 54

The frontals of *Notharctus osborni* are distinctly wider across the forehead than those of *Adapis* and the orbits are larger. In *Notharctus venticolus* (Amer. Mus. No. 14656), however, the frontals are very much narrower. The superior surface of the frontal, above the orbit, shows in *N. venticolus* a moderate swelling (above the fore part of the frontal sinus), behind which is a wide shallow depression. This condition is suggested in *N. osborni*, and seems to be indicated in varying degrees in different skulls of *Adapis* figured by Stehlin. The temporal crests of the frontals behind the orbits are further separated in *Notharctus osborni* than in most forms of *Adapis*, but in *N. venticolus* this part of the skull is narrower. The frontal sinus was well developed (*N. venticolus*); the opening for the cribriform plate was large. As in *Adapis* the frontals did not extend far back over the top of the brain (*N. venticolus*). The sides of the interfrontal suture on the cerebral surface are raised into a low ridge corresponding in position with the interfrontal sinus. The lower border of the frontal has a wide contact with the lacrymal. The orbital

Fig. 54. Skull of *Notharctus osborni*. Amer. Mus. No. 11466. Natural size.

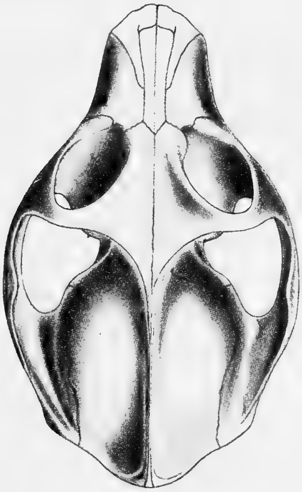

Fig. 55. Skull of *Adapis magnus* var. *leenhardti*. After Stehlin. Natural size.

lamina of the frontal (*N. osborni*) was in contact with the orbital plates of the palatine and of the orbitosphenoid, and probably also with the alisphenoid. It was apparently excluded from contact with the squamosal by the parieto-alisphenoid contact. Similar relations of the frontal were observed by Stehlin in *Adapis magnus* (1912, p. 1252).

Parietals

Text Fig. 54

The coronal suture is not clearly defined except in a skull fragment referred to *N. osborni* (Amer. Mus. No. 11474), where enough of the fronto-parietal suture is preserved to show that the fore part of the parietals were overlapped by the constricted interorbital part of the frontals, as they are in *Adapis.* The mid-parietal expansion is much more pronounced in the female skull of *N. osborni* (Amer. Mus. No. 11466) than in the old male of *N. venticolus* (Amer. Mus. No. 14655) which has a very narrow brain-case and a long high sagittal crest. In *N. crassus* this crest becomes very high. This is less convex antero-posteriorly than in *Adapis.* As in *Adapis* the parietal crest and the parietal itself are continued back to the occiput, the supraoccipital not being exposed on the top of the skull. Anteriorly, at the back of the orbit, the parietal appears to be in contact with the frontal, orbitosphenoid and alisphenoid. The sides of the parietal in *N. osborni* are swollen, but much less so in *N. venticolus* and *N. crassus.* By reason of the relatively small size of the brain the parietal convexity of *Notharctus,* as well as of *Adapis,* is some distance behind the postorbital rim and there is consequently little if any tendency to close the orbit by a posterior partition. Laterally the parietal is bounded by the long irregular parieto-squamosal suture which begins near the parieto-alisphenoid contact and ends at the lambdoidal crest, after passing through the parieto-squamosal foramen, as in *Adapis.*

Squamosals

Text Figs. 48, 49, 54, 58

This element is known chiefly from the type of *N. osborni* and from a large fragmentary skull of *N. crassus* (Amer. Mus. No. 12567). Its general relations are the same as in *Adapis* and many other primitive primates. On the anterior part of the squamosal there is a sharp horizontal ridge which is continuous with the anterior edge of the glenoid region; this ridge separates the area of the temporal muscle from that of the external pterygoid. Stehlin (1912, p. 1200) states that in *Adapis* this ridge extends forward across the alisphenoid to the orbitosphenoid and the same is true in *Notharctus* (*N. osborni*). There is a wide difference in the glenoid region between the female skull of *N. osborni* and the large male skull of *N. crassus* (Amer. Mus. No. 12567). In the former the glenoid fossa is shallow, the postglenoid process is delicate and the entoglenoid process is low. In the latter the glenoid fossa is deeply concave, the postglenoid process is robust and the entoglenoid process is represented by a sharp ridge. Again in *N. osborni* the entoglenoid process and the pterygoid flange of the alisphenoid were separated only by a narrow fissure, while in *N. crassus* these parts, except in the rear, were separated by a portion of the squamosal which is about 5 mm. wide at the front end. In *Adapis* the glenoid region is flatter and there is little indication of the entoglenoid ridge; this region, however, is in contact with the pterygoid flange of the alisphenoid as in *N. osborni.* The tip of the postglenoid process is roughened in *Notharctus* as well as in *Adapis,* probably by the posterior slip of the masseter externus.[1] In both *N. osborni*

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[1] See the dissection of *Propithecus diadema* in the Memoir of Grandidier and Milne Edwards. (Hist. Physique Nat. et Politique de Madagascar, IX, Tome IV, Atlas, Pl. LV.)

and *N. crassus* the glenoid region permitted all the motions of the mandibular condyle which have been described above (p. 148). The back part of the glenoid fossa and the postglenoid process articulated with the downwardly produced posterior extension of the condyle; the smooth side of the entoglenoid process articulated with the internal convexity of the condyle, while the deepest concave portion of the glenoid fossa articulated with the convex summit of the condyle. The anteroposterior extension of the glenoid fossa and glenoid ridge permitted a marked anterior displacement of the mandible. In *Adapis* the flattened glenoid region permitted some anterior displacement but was apparently not so favorable for the tilting and transverse movements of the mandible.

The zygomatic process of the squamosal in *N. osborni* was evidently slender; in *N. crassus*, although massive, it was surpassed by that of *Adapis*. The dorsal root of the zygomatic process is continued above the external auditory meatus as a strong crest which bounds the area of the temporal muscle externally and is continued upward into the lambdoidal crest, as in *Adapis*. In *N. crassus* the lower ridge of the zygomatic process is roughened for the attachment of the masseter. Apparently the posterior extension of the malar did not extend back to the glenoid region of the zygoma as it does in *Adapis* but was limited to the middle of the zygoma. On the posterior slope of the postglenoid process is the prominent postglenoid foramen as in *Adapis*. The external auditory meatus is bordered above by a rim of the squamosal, which forms an obliquely warped arch opening outward and backward. In *N. osborni* this passage is wider than in *N. crassus*. It is fundamentally similar to that of *Adapis*. The post-tympanic process is small and fused with the anterior part of the mastoid region.

Occiput

Text Fig. 56

The occiput is almost perfectly preserved in the type of *N. osborni* and partly preserved in *N. crassus* (Amer. Mus. No. 12567). Its general aspect is similar to that of *Adapis parisiensis* (Stehlin, 1912, p. 1199), but in the female skull of *N. osborni* the occiput is not so wide, the superior extension of the mastoid is narrow, the foramen magnum is deeper and the articular facets of the condyles are flatter, more vertical and more extended dorsally. In the male skull (*N. crassus*) the lambdoidal and sagittal crests are much higher, the general outline of the occiput being almost triangular, suggesting rather the occiput of a carnivore, except for its greater width at the base. The median superior tip of the occiput (inion) is produced somewhat backward and ends in a tubercle for the ligamentum nuchæ, not dissimilar to that of *Adapis;* beneath this a sharp median crest separates the neck muscles of the right and left side. The lateral extension of the exoccipital was apparently separated from the wide supraoccipital by the horizontal fissure mentioned below (p. 160). The interparietal and supraoccipital are coalesced, so that their limits could not be determined, but it is not likely that they extended forward on top of the skull as they do in lemurs.

The back of the occiput and of the lambdoidal crests served for the attachment of muscles which were probably arranged essentially as they are in modern lemurs[1] and indrisines.[2] Attached immediately beneath the rim of the lambdoidal crests was a series of layers of muscles, the outermost two layers, namely, trapezius, rhomboideus, being connected with the fore limb; the next layer included the complexus series (dorsal) and the splenius (lateral), representing the anterior continuation of the spinal series.

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[1] Cuvier and Laurillard, Planches de Myologie.

[2] Grandidier and Milne Edwards, 1870, Pls. XXXVI and XXXVII.

The fossæ on the surface of the occiput below the lambdoidal crest probably mark the insertion of the deep muscles which run to the spine of the axis and raise the head, namely, the rectus capitis posticus major; while to the region above the foramen magnum may have been attached the atloido-occipitalis, which arose from the stout arch of the atlas. The large and protuberant mastoids probably gave attachment dorsally to the trachelo-mastoid (running along the side of the neck vertebræ), to the cleido-mastoid, sterno-mastoid and digastric. Above the mastoid and below the lambdoid crest the obliquus capitis superior was probably attached. From the sharply ridged character of the occiput even in the female *Notharctus* it seems likely that although these neck muscles were less thick transversely than in *Adapis* they were yet vigorously developed. (Figs. 56, 57.)

Fig. 57. Neck muscles of *Propithecus*, after the removal of the rhomboideus and trapezius, showing the complexus (*K*, *L*) and the rectus capitis posticus major.

Fig. 56. Occipital view of skull. Natural size.

Notharctus osborni. Amer. Mus. No. 11466.
Adapis parisiensis. After Stehlin.
Adapis parisiensis. After Stehlin.

J, jugal; *P.gl.*, postglenoid process; *T.h.*, tympano-hyal insertion; *Ex*, exoccipital; *M.*, mastoid; *Au*, auricular meatus; *F.p.*, postglenoid foramen; *B*, audital bulla; *Gr.*, fossa for neck muscle, leading to "foramen arteriæ meningeæ posterioris" ?

The mastoid process is much larger and more protuberant in the male *N. crassus* than in the female *N. osborni;* as compared with that of *Adapis,* it is more swollen below and tapers rapidly to a dorsal point while in *Adapis* it extends dorsally as a wide strip. The jugular or paroccipital process of the exoccipital embraces the inner side of the mastoid as it does in *Adapis.* Above the exoccipital is a slit or foramen at the bottom of the fossa for the rectus capitis posticus major (?), which recalls the similarly located foramen in *Adapis.* Stehlin (1912, p. 1200) suggests that this foramen may have served to give entrance to the "Arteria meningea posterior," a branch of the occipital artery.[1] The mastoid foramen near the posterior border of the mastoid is prominent. It is not located between the mastoid and the exoccipital

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[1] Not to be confused with the posterior meningeal branch of the pharyngeal artery.

but, as shown in Amer. Mus. No. 12569, it lies at the bottom of a deep fissure which is closed at the top, as if the vein transmitted by the foramen had sunk deeply into the mastoid after passing above it in the embryo. Stehlin does not describe the mastoid foramen in *Adapis*. The mastoid has a deep fossa on its ventral surface as in *Adapis*. Possibly this fossa may have given attachment to the digastric. The S-shaped groove described by Stehlin in *Adapis* (1912, p. 1201) on the lower surface of the mastoid was not recognized in *Notharctus*. The interior of the mastoid (Amer. Mus. No. 12569) was pneumatic. The stylomastoid foramen opens on the ventral surface of the mastoid behind the carotid foramen (see p. 178 below); it leads into a bony canal which traverses the periotic anteroposteriorly and receives the stapedial canal (see p. 178 below) and which is therefore the Aqueduct of Fallopius. (Plate XLIV; Figs. 58–62.)

Occipital Condyles

Text Figs. 56, 58, 62

The posterior face of the condyles is flattened and vertically extended, while the ventral surfaces are more extended transversely and less produced anteroposteriorly than in *Adapis*. The median part of the basioccipital between the condyles shows a faint articular facet for the ventral rim of the axis in flexion of the head; while the deeply concave intercondylic rim is facetted for the stout odontoid process. The general form of the condyles indicates that the atlas had a relatively deep and narrow cotylar facet, that motion of the skull upon the atlas was more nearly transverse and less oblique than in *Adapis* and probably that the inclination of the skull to the atlas-axis complex was less than in that genus.

Basioccipital

Text Figs. 58, 62

As the whole skull is longer and less widened than that of *Adapis* the same is true also of the basioccipital. The basioccipital-basisphenoid suture ends anteriorly on a line with the anterior extension of the bullæ, while in *Adapis* this suture is considerably behind the front ends of the bullæ (Stehlin, 1912, pp. 1168, 1255, figs. 244, 280). The median ridge of the basioccipital is quite pronounced, as well as the fossæ on either side of it, which gave insertion to the stout recti capitis antici (major and minor) muscles. The lateral border of the basioccipital is raised into recurved alæ overlapping the medial base of the bullæ after the fashion of the tympanic processes of the basioccipital of Insectivores. In *Adapis*, on the other hand, these flanges are absent (Stehlin, 1912, pp. 1254, 1255, figs. 279, 280) or but faintly indicated (idem, p. 1168, fig. 244). The condylar foramen is continued forward into the foramen lacerum posterius as it is in *Adapis magnus* var. *leenhardti* (Stehlin, 1912, p. 1279, fig. 287), but the jugular foramen is distinct. In *A. parisiensis* var. *bruni* (Stehlin, p. 1201, fig. 259) the foramen lacerum posterius is well separated from the condylar foramen. The encephalic surface of the basioccipital is not known.

Auditory Region

Plate XLIV; Text Figs. 58, 62

This region is remarkably well preserved in the type of *N. osborni*, and, thanks to the skill of Mr. A. E. Anderson, it reveals for the first time the intricate anatomy of the internal ear and auditory ossicles of an Eocene mammal. The cochlea auris and ossicula of *Adapis* not being known for comparison, the description of these parts in *Notharctus* will be given in another section of this paper (pp. 160, 170 below); but the region of the tympanic cavity may be compared with that of *Adapis*, which has been fully described by Stehlin (1912, p. 1203–1215). The general plan of construction of the tympanic region in these genera is that common to the existing Malagasy lemurs and has been very thoroughly investigated by Forsyth Major (1899), van Kampen, Stehlin and others. In all these forms the bulla consists of a greatly expanded bubble or shell of bone surrounding a diverticulum (sinus hypotympanicus) of the true tympanic cavity which in turn is a dilatation of the tubo-tympanal duct; the bony shell in question apparently does not arise from a separate center like the os bullæ (entotympanic) of many mammals, but is derived solely from the periotic and represents perhaps what was once merely a rim of the periotic, overlapping the membranous hypotympanic cavity; the beginnings of such a rim are shown in certain insectivores, as suggested by van Kampen (see also Fig. 66). This periotic shell or rim doubtless gradually grew over

Fig. 58. Norma basalis of skull of *Notharctus osborni*. Amer. Mus. No. 11466. Middle Eocene (Lower Bridger), Wyoming. Twice natural size.

the membranous hypotympanic cavity. Beneath and to the outer side of this bulla lay the tympanic ring (bearing the tympanic membrane) in a nearly horizontal position.

Forsyth Major (1899, pp. 987) described the ontogenetic development of the bulla of the Malagasy lemurs as follows:

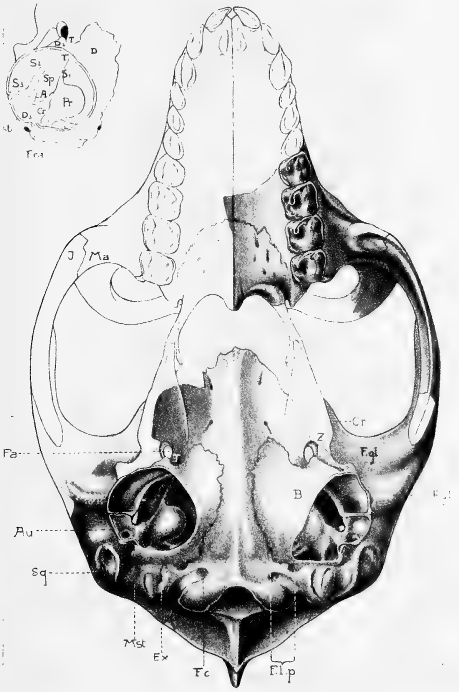

Fig. 59. Norma basalis of skull of *Adapis parisiensis.* Enlarged. After Stehlin.

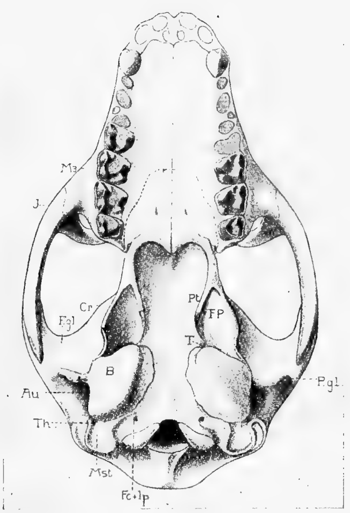

Fig. 60. Norma basalis of skull of *Adapis magnus* var. *leenhardti.* Natural size. After Stehlin.

In the youngest stage available to me for examination, the fœtus of a *Chiromys*, there is no trace of an osseous bulla; the completely ossified annulus lies almost horizontally underneath the periotic. In a second stage (*Lepidolemur*) ossification begins to be developed from the lower sharp margin of the periotic, which adjoins the annulus. In a third stage (*Lepidolemur*) this outgrowth appears increased, and has a shell-like shape, with the concavity turned outward; the annulus is gradually being uplifted by it. In a fourth stage (*Lemur rubriventer*) the shell-like ossification is still more increased, and begins to cover the median part of the annulus; and this state of things is still more increased in the fifth (*Lepidolemur*) and sixth stage (*Avahis laniger*), with the result that first the median part, and eventually the remainder of the annulus becomes invisible when viewed from below, being shut by the periotic. In the adult (as will be seen by the skull of an adult *Lemur rubriventer* which I exhibit) the annulus is represented by a bony ring — the size is scarcely larger than in the youngest stages — which hangs freely in the tympanic cavity, being coalesced with the *squamosum* only in one part, viz. anteriorly to the stylomastoid foramen. Ontogeny thus teaches us that the annulus of the adult is not a secondarily detached part of the bulla."

At the same time Dr. Major stated the important fact "that in the Tertiary *Adapis* the annulus tympanicus is a free ring, independent of the bulla [but lying within it], absolutely as in the Malagasy lemurs."

If, as is commonly supposed, this ontogenetic process in lemurs gives a clue to the actual course of evolution, it is evident that in all the Malagasy lemurs, in *Adapis* and *Notharctus*, the hypotympanic shell of bone has extended outward beyond the tympanic ring so as to conceal it completely from the ventral view. Continuing to grow laterally and anteriorly it gained contact with the pterygoid wing of the alisphenoid and with the adjacent entoglenoid process of the squamosal; posteriorly its expansion was limited by the exoccipitals and internally by the basioccipital.

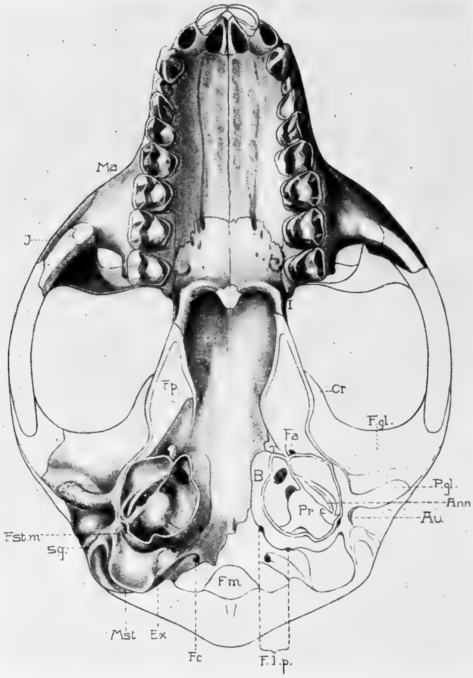

Fig. 61. Norma basalis of skull of *Adapis magnus*. Natural size. After Stehlin.

Fig. 62. Norma basalis of skull of *Notharctus crassus*. Amer. Mus. No. 12567. Middle Eocene (Upper Bridger), Wyoming. Natural size.

The hypotympanic sinus still communicates with the true tympanic cavity by a more or less widely open fissure, lying between the tympanic annulus and the auditory prominence and called the pneumatic foramen. The sinus hypotympanicus, or cavity of the bulla, lying beneath the cochlea, an essential organ of hearing, probably acts as a resonating chamber and possibly may have incidental advantages in regulating the pressure on either side of the tympanic membrane. The tympanic annulus itself in all these forms remains as a simple ring, incomplete above, fastened posteriorly to the periotic, in front of the carotid foramen described below, and anteriorly to the squamosal behind the entoglenoid process. The true tympanic cavity lies between the tympanic ring, the auditory prominence, or cochlea, and the sinus hypotympanicus. The tympanic cavity is continued forward to the Eustachian foramen (ostium tubæ). Above the tympanic cavity and above the auditory ossicles a membranous diverticulum in the periotic roof of the tympanic cavity near the squamosal is the recessus epitympanicus.

The cochlea, or promontory, bears on its outer surface a long bony canal, for the main internal carotid artery, which enters at the posteroexternal angle of the bulla in front of the stylomastoid foramen, runs forward and inward over the cochlea to the anterior end of the hypotympanic sinus, medial to the Eustachian foramen; here it pierces the back part of the basisphenoid and tunneling this bone emerges beneath the cerebrum on either side of the sella turcica. Soon after entering the hypotympanic cavity it gives off a stout branch, the stapedial canal which pierces the stapes and enters the periotic.

Both *Adapis*, as described by Major and by Stehlin, and *Notharctus*, as shown in the type of *N. osborni*, conform in every detail to the foregoing description of the tympanic region, except that in *N. osborni* the very delicate tympanic ring is not preserved. By comparison with *Adapis*, *Lemur* and *Propithecus*, however, there can be no doubt whatever that the position of the ring was substantially the same as it is in those genera: namely, that it was attached posteriorly to the junction of the post-tympanic process of the squamosal with the outer wall of the bony carotid canal, at the postero-external angle of the bulla, anteriorly to the posterior wall of the entoglenoid region of the squamosal, internal to the postglenoid foramen. Nor can there be any doubt that the bulla covered the tympanic ring. Direct evidence in favor of this view is given by a specimen of *N. venticolus* (Amer. Mus. No. 14655); the surface of the bulla in this specimen is completely preserved and extends laterally to the auditory meatus as it does in *Lemur;* as there is no possibility that the tympanic annulus was external to this edge it must have been inside the bulla. Indirect evidence for the same view is that in the type of *N. osborni* the broken edges of the bulla show the contact of the expanded portion of the bulla on the inner side of the entoglenoid region as in *Lemur* and *Propithecus* and that on account of the close agreement with *Lemur* in the portion of the bulla that is preserved, the roof of the bulla must have extended from this point of contact with the entoglenoid to the entrance of the carotid canal, and must therefore have covered the ring from below. But it is impossible to convey briefly in words the full force of the evidence for this immediate deduction from the facts, which appears inevitable after repeated study of the specimens. Additional indirect evidence that the ring in *Notharctus* was not outside the bulla results from a comparison with the tympanic region of the South American monkeys. For in these (Plate XLIX) the great widening of the brain-case, as compared with that of *Notharctus*, has evidently caused a relative displacement *outward* of the bony auditory meatus and of the attached ring, and *inward* of the bulla itself: the ring being thus drawn to the outer side of the bulla, and increasing greatly in size, yet retains its ancient contact with the entoglenoid region, while the bulla itself, not relatively reduced in size, has lost that contact; meanwhile the opening of the carotid canal retains its old place behind the ring, but is now also internal to it and presents inward or inward and backward rather than outward and backward; moreover the wide ring has now gained contact with the mastoid, while in the Eocene *Notharctus* and *Adapis* it was separated from it by the carotid canal. In brief, comparison with the conditions in the South American monkeys emphasizes the fact that in both the Eocene lemuroid genera named above the relations of the parts of the tympanic region were fundamentally the same as in modern Lemuridæ and Indrisidæ. (Plate XLIX.)

Along with this fundamental identity of plan there are minor differences in detail. The bullæ of *N. venticolus* were but little inflated as compared with those of *Adapis;* those of *N. crassus* were probably wider and more inflated than in *N. venticolus;* the conditions in *N. osborni* were intermediate. There were also considerable differences in shape and proportion of the bullæ in different forms of *Adapis* as figured by Stehlin, some being very wide (*Adapis parisiensis* var. *Schlosseri,* Stehlin, 1912, p. 1208, fig. 261, p. 1168, fig. 244), others narrower (*Adapis magnus,* p. 1255, fig.) and smaller (*A. magnus* var. *leenhardti,* p. 1279, fig. 287). The latter, which is one of the older varieties of *Adapis,* approaches *Notharctus* in the general appearance of the auditory region. There were also differences in the width of the contact between the entoglenoid ridge and the bulla, which was very wide in *A. parisiensis Schlosseri* (p. 1168) and narrow in *A. magnus leenhardti.* In both *A. parisiensis* and *A. magnus* the tympanic ring was more or less enwrapped in its ventral half by a thin sheet of bone, which seems to represent an infolded part of the wall of the hypotympanic sinus, where it has grown over the tympanic ring.[1] As this portion of the bulla is broken away in the type of *Notharctus osborni* we cannot be sure that a similar structure was absent in the Notharctinæ.

In the type of *Notharctus osborni* the foramen ovale opens more in front of and less to the outer side of the Eustachian foramen than it does in *Adapis* and the lemurs (cf. Stehlin, 1912, p. 1205) and the bone between these foramina was not produced downward into a delicate septum. Leading from the foramen ovale is a groove for the ramus mandibularis of the fifth nerve, running outward and forward and opening on the outer side of the pterygoid wing of the alisphenoid; below the groove in question there was a large foramen pterygospinosum near the junction of the pterygoid wing with the entoglenoid region of the squamosal; so that, as in *Adapis,* the foramen ovale may be seen from the outer side through the foramen pterygospinosum. According to Stehlin (p. 1205) this foramen probably transmitted a branch of the internal maxillary artery to the internal pterygoid muscle as in *Lemur.*

The anterointernal extensions of the bullæ are closely appressed to the hinder edges of the basisphenoid and true pterygoids and there are no foramina lacera media, the carotids entering the braincase by another route described above (p. 178).

Basisphenoid

Text Fig. 58

The middle of the lower surface of the basisphenoid bears a convex ridge which gradually bifurcates both posteriorly and anteriorly. The posterior forks are continued onto the basioccipital along the internal wall of the bullæ; the anterior forks run forward and outward toward the palatines. In *Adapis* there is some variation in the form of the median basicranial ridge, which sometimes extends from the vomer to the foramen magnum but never shows the doubly bifurcating pattern which is characteristic of *Notharctus.*

The VOMER is not preserved.

The posterior part of the PRESPHENOID is preserved, but is covered by the vertical plates of the palatines.

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[1] Dr. Stehlin (1912, p. 1294) refers to "die Verknöcherung der Annulus membran" and states (p. 1213) "das [in *Adapis*] sich das Septum an der vordern Aussenwand der Bulla S_2 [of *Lemur*] nach hinten zu bedeutend vergrössert hat durch totale Verknöcherung der zum Annulus hinüber gespannten Membran." Though a little uncertain as to Dr. Stehlin's meaning, I infer from the illustrations that the ossified membrane in question is not the true membrana tympani but a fold of the hypotympanic region of the bulla surrounding the pneumatic foramen.

Pterygoids

Text Fig. 58

Although the sutural limits of these elements are ill defined, it is evident that they articulated anteriorly with the vertical plate of the palatine and covered the inner side of the descending plate of the alisphenoid, against which they were tightly appressed, the pterygoid fossæ being only small slits between the lower border of the true pterygoids and of the alisphenoid; in *Adapis*, on the contrary, the pterygoids are separated below from the alisphenoids by a wide pterygoid fossa, the large size of which was doubtless correlated with the expansion of the fossa for the insertion of the internal pterygoid muscle on the medial surface of the angle of the mandible. The hamular process of the pterygoid is broken off near the base, but it evidently extended backward in the normal lemuroid manner. The hamular process is continuous above with a low ridge which runs posterodorsally along the inner side of the pterygoid. No such ridge is shown in *Adapis*.

Palatine

Text Fig. 58

But little of the horizontal plate of the palatine is preserved; the palato-maxillary suture extended forward to near the posterior part of m^1 (Amer. Mus. No. 11466, 12569); the palate was narrower than in *Adapis parisiensis* and the horizontal plates of the palatines were probably even narrower than in the primitive *Adapis magnus* var. *leenhardti.* The position of the posterior palatine grooves and foramina and the characters of the posterior palatine ridges are not known. The vertical plate of the palatine is preserved in the type of *N. osborni*; its stout lower rim as in *Adapis* was separated from the alveolar region of the maxillary by a notch for the posterior palatine artery, as in *Adapis* (cf. Stehlin, 1912, p. 1202) and *Cænopithecus*, while in modern later Primates this notch, which becomes more or less united with the true posterior palatine foramen, is closed by the union of the palatine and maxillary below it. The inner surface of the "vertical" plate of the palatine slopes obliquely inward and upward toward the presphenoid; it bears a prominent convex ridge running posterointernally and slightly dorsally toward the midline, where with its fellow of the opposite side it joins the median ridge of the basisphenoid described above (p. 166). Anterointernal to this ridge the basicranial floor was gently concave, on either side of the midline. Here were the posterosuperior limits of the internal nares. In *Adapis* this region appears to be wide and flat. The palatine was in contact with the pterygoid, the pterygoid and temporal plates of the alisphenoid, the maxillary, the lacrymal, the frontal and the orbitosphenoid, but the sutures separating it from these elements are not visible. The vertical plate of the palatine passes dorsosuperiorly into the large orbital plate which overlaps the descending wall of the frontal. The contact with the lacrymal is not shown. This is pierced by the sphenopalatine foramen (for the nerve of the same name) and from this a groove leads back toward the foramen rotundum or foramen lacerum anterius, whichever it may be. The limits of the orbitosphenoid and of the orbital part of the alisphenoid are not visible. The foramina at the back of the orbit are poorly shown.

BRAIN CAST

Text Fig. 63

A natural cast of the cranial cavity is partly exposed in *Notharctus tyrannus,* Amer. Mus. No. 11478. It affords a general but imperfect outline of the brain-cavity as seen from above. Certain details of the brain-cavity are shown in several fragmentary skulls, especially *Notharctus venticolus*, Amer. Mus. No. 14656, *N. osborni*, No. 12569, and *N. matthewi*, No. 13030.

As compared with the endocranial casts of *Lemur varius*, *L. jullyi*,[1] *Propithecus* and *Alouatta*, the brain of *Notharctus* had very small, narrow cerebra, with poor frontal lobes. Such feeble sulci of the cerebra as were present did not show through the membranes enough to leave any well-marked grooves on the cast, although the superior longitudinal sinus is indicated by a prominent median crest; and there seem to be vague indications of the sulcus intraparietalis. The median lobe of the cerebellum was exposed above, as in *Lemur*. The lateral lobe, filling the small subarcuate fossa in the periotic was also

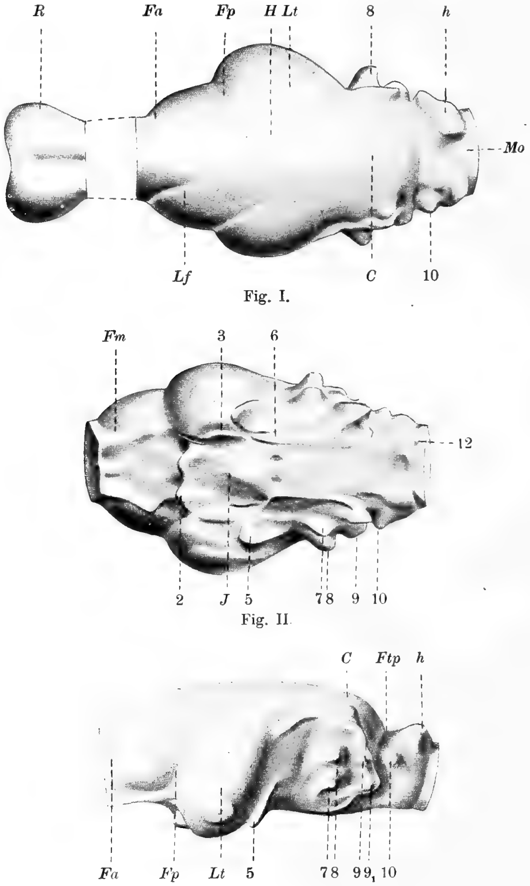

Fig. I.

Fig. II.

Fig. III.

Fig. 63. Endocranial cast of *Adapis parisiensis*. After Neumayer. Twice natural size.
8, fossa subarcuata

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[1] Cf. Elliot Smith, 1908, Trans. Zool. Soc. London, XVIII, part 2, p. 165, fig.

small; while the small size of the dorsoposterior part of the periotic and the total exclusion of the mastoid from all share in the cranial cavity, together with the relative narrowness of the base of the occiput, all reflect the small size of the cerebellum as a whole.

The olfactory fossa of the cranial cavity and its contained olfactory lobes were larger than those of *Propithecus coquerelli*, but not quite as large as those of a large *Lemur varius*. In proportion to the width of the frontal lobes, however, the olfactory lobes of *Notharctus* were much larger than those of recent lemuroids, so that it may be classed as macrosmatic. There was a sharp constriction between the olfactory and frontal lobes, corresponding to a high ridge on the endocranial surface of the frontals. The width of both frontal and parietal lobes was considerably greater in the progressive *N. osborni* than in the conservative *N. venticolus*.

As compared with the brain cast of *Adapis* figured by L. Neumayer[1] that of *Notharctus* is obviously of the same general type, save that in *Adapis* the temporal lobes are more expanded transversely, and project more prominently downward and forward behind the Sylvian fissure, both progressive characters pointing in the direction of the modern Lemuroidea. The floccular process of the cerebellum, which was lodged in the subarcuate fossa, in *Adapis* was larger than in *Notharctus*, another progressive feature. This fossa is wrongly indicated by the number "8" in Neumayer's figures, as there is no reason to doubt that the eighth nerve (marked "7") passed into the internal auditory meatus in the usual manner. The surface of the cerebrum shows no sulci.

THE COCHLEA AURIS AND OSSICULA OF *NOTHARCTUS*; COMPARISON WITH OTHER PRIMATES

Cochlea

Plate XLV

Under the delicate manipulation of Mr. Anderson the type skull of *Notharctus osborni* (Amer. Mus. No. 11466) has yielded not only a complete record of the anatomy of the interior of the bulla, but even a section of the bony cochlea, together with the auditory ossicles of the right side. Mr. Anderson and the writer have also made for comparison with *Notharctus* a series of preparations of the bony auditory region of other primates, some of which are illustrated in Plates XLIII–XLVII. A second specimen of *N. osborni*, Amer. Mus. No. 13030, includes the greater part of the periotic of both sides, showing the internal auditory meatus, the subarcuate fossa, a section of the cochlea, and other details.

As already noted, the general construction of the auditory region of *Notharctus* is identical with that of *Lemur* and *Propithecus*, the chief difference being that in the Eocene genus the bullæ are somewhat smaller and less extended anterointernally. The course of the internal carotid canal and its stapedial branch and the course of the Fallopian aqueduct also conform to the lemuriform type. Another important resemblance to the Lemuriformes is that the fenestra cochleæ (f. rotunda) is concealed from a view through the tympanic ring by the posttympanic process of the squamosal near its junction with the carotid canal, whereas in *Loris*, *Periodicticus*, and *Galago*, representing the Lorisiformes, and in the Platyrrhini, the f. rotunda is visible through the tympanic ring in the dried skull, after the removal of the tympanic membrane, lying immediately below and somewhat behind the fenestra ovalis.

Behind the fenestra cochleæ and separated from it by the ventral surface of the cochlea lies the posterior extension of the hypotympanic sinus, which is less expanded than in *Lemur*. The cochlea as

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[1] 1906, Ueber das Gehirn von Adapis parisiensis Cuv., Neues Jahrb. f. Min. etc., II, pp. 100–104, Pl. v.

seen in section from below is smaller than that of a large *Lemur varius*. It consists of two coils, a much larger medial coil, extending from the fenestra cochleæ inward, downward and forward, and then upward, outward and backward, and a smaller lateral coil, surrounding the apical portion of the osseous core or modiolus. A natural cast of these two coils is preserved in Amer. Mus. No. 12569 (*N. osborni*). It shows that there was little if any part of a third turn at the apex, indeed it is very doubtful whether even two turns of the spiral were entirely completed, while in *Lemur* a very small septum near the apex indicates part of a third turn. Between the coils in *Notharctus* three septa were represented as we pass from behind forward: a thick medial septum separating the outer coil of the cochlea from the hypotympanic sinus, a middle septum, springing from the region of the carotid canal and passing inward, and an outer septum, coiled around the spiral tip of the modiolus. The lamina spiralis ossea is represented by a low ridge seen on the posteromedial concavity of the middle septum; it is less developed than in *Propithecus* (Plate XLVI).

In general, the cochlea of *Notharctus*, like that of *Lemur*, if considered as a coil resting on its base, seems to have a smaller base in proportion to the height of its axis; while in *Propithecus* and still more so in *Ateles*, representing the Platyrrhini, the base is much wider in proportion to its height. This gives the latter the appearance of a flatter, more closely wound coil, with a lower pitch. In *Ateles* also the lamina spiralis ossea is sharply defined, the apical portion of the coil is wider and better differentiated, so that the whole coil makes considerably more than two complete turns. The surroundings of the cochlea in *Ateles* are totally unlike those of *Notharctus*, *Lemur* and *Propithecus*, as the cochlea is covered below not by the hypotympanic sinus but by the cavum tympani. (Plate XLVI.)

The internal auditory meatus is shown in *N. osborni*, Amer. Mus. No. 12569, and *N. matthewi*, Amer. Mus. No. 13030. Its only noteworthy feature is that it is larger than that of *Lemur varius* and more extended transversely; the subarcuate fossa above it and behind it on the contrary is not as deeply excavated as in the modern *Lemur* and *Propithecus;* a slender canal in the posterodorsal wall of the subarcuate fossa seems to be the superior semicircular canal, as in *Lemur* and *Propithecus*, but the aperture of the fossa being smaller does not extend up to the canal as in those forms. The most noteworthy feature in this region is the primitive exclusion of the mastoid from the cranial cavity, owing to the lack of brain expansion in this region. Above and in front of the internal auditory meatus the cranial surface of the periotic forms an eminence, separating the anterior from the posterior parts of the brain and indicating the beginning of the crista petrosa of *Lemur* and *Propithecus*.

OSSICULA

Plate XLVII

The malleus, incus, and stapes were found in place in the attic, or epitympanic recess, of the right side. The head of the left malleus was also found *in situ*. The above named recess comprised a small posterior sinus, containing the malleus and incus, and a much larger anterosuperior sinus which extended dorsad between the squamosal and the periotic, exactly as in *Lemur*. Stereoscopic views of the ossicles, compared with those of *Ateles* and *Macacus*, are shown in Plate XLVII. A study of these specimens and of Doran's memoir on the "Morphology of the Mammalian Ossicula auditus" (1876) shows that they are of primate type, with no special affinities to those of insectivores.

The malleus of *Notharctus* on the whole more nearly resembles that of *Propithecus coquerelli*, with which it agrees in the massive and deeply notched articular surface, which contrasts with the wide but shallow articular surface in *Ateles*. It approaches *Ateles* in the marked subcircular expansion of the head as seen from above. On the neck of the malleus opposite the lower part of the articular facet is an osseous lamina, the base of the processus longus, which has been torn off. Behind the lamina on the inner or cranial aspect of the neck is a deep fossa. All this is essentially the same as in *Lemur* and *Propithecus* save that the fossa is deeper and the vertex of the head is not elevated. The manubrium is somewhat crushed but appears to be complete; it differs from that of all other Primates in being extremely short in proportion to the width of the neck; it was wider at the base than in *Propithecus* and more sharply bent upon the neck, as it is in *Lemur*. The processus brevis and processus muscularis were not recognized.

The incus much resembles that of *Propithecus* in the general form of the body and in the shape of the articular surface; it differs in its smaller size, in the shortness of both its processes and in their wide divergence from each other. The tip of the stapedial process (proc. longus) as preserved is pointed, an unusual character, which at first suggested that this pointed process was the processus brevis; but further comparison of the articular surface and the general form of all the parts confirmed the present interpretation. No trace was found of the os orbiculare, or lenticular disc, on the end of the stapedial process of the incus.

The neck and crura of the stapes were found *in situ*, surrounding the bony stapedial canal as in *Propithecus* and *Lemur*. The foot plate, however, was not found. The stapes was unfortunately lost after being successfully extracted from the matrix, but not before it was compared with the stapes of *Propithecus* and *Indris*,[1] with which it agreed in general characters. The crura were delicate in their middle part, but the neck was broad as in *Indris*.

Accordingly, the ossicles of *Notharctus* appear to be of a primitive lemuriform character, the malleus being somewhat coarser than that of *Propithecus* with heavier head and articular facets and probably with a stouter lamina and processus longus, the manubrium being extremely short and more bent upon the head.

A REVIEW OF THE COURSE OF THE INTERNAL CAROTID ARTERY AND OF ITS BRANCHES IN THE BASICRANIAL REGION OF PRIMATES[2]

The consideration of the foramina in the region of the auditory bulla of *Notharctus* has led to a general review of the course of the internal carotid artery and its branches in the primates, with special reference to the foramina which serve for the entrance and exit of these and other arteries. This subject has been treated by a number of authors, especially Mivart (1864), Winge (1895), Tandler (1899, 1901, 1902), Wortman (1903), van Kampen (1905), Stehlin (1912, pp. 1206, 1207, 1212), and Keibel and Mall (1912, II), whose observations and chief conclusions are considered below.

Insectivora

Text Fig. 65

In *Erinaceus*, according to the researches of Hyrtl, Tandler (1899, p. 749) and others (cf. van Kampen, p. 430), the internal carotid enters the bulla from the rear, through a foramen that is incompletely separated from the stylomastoid foramen. Inside the bulla the artery divides into the *arteria stapedia* and the *art. promontorii*, as in lemurs. The *art. stapedia* is of large size, and after piercing the stapes runs

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[1] Cf. Milne Edwards and Grandidier, 1875, Pl. LXXXV, fig. 10.

[2] A summary of the following section was presented before the Paleontological Society of America, December 31, 1914, and published in 1915. Bull. Geol. Soc. America, XXVI, pp. 426–432.

forward in a groove in the roof of the tympanic cavity issuing into the temporal fossa (van Kampen, p. 430) through a notch or foramen (which may be named foramen caroticum alisphenoidei, *f. c. al.*) in the tympanic process of the alisphenoid, posteroexternal to the foramen ovale; this branch of the art. stapedia constitutes the *ramus inferior* ("art. maxillaris interna Calori," Winge). After leaving the tympanic fossa the ramus inferior passes forward medial to the foramen ovale and enters a very short alisphenoid canal ("canalis pterygoideus") on the outer side of the pterygoid plate of the alisphenoid; in front of this alisphenoid canal the ramus inferior gives rise to the large art. temporalis profunda, the ramus orbitalis and other branches.

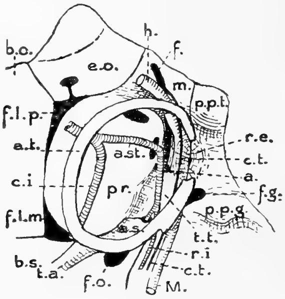

Fig. 64. Semidiagrammatic representation of the left tympanic region of a primitive mammal, after the removal of the ossicles and tympanic membrane. After Van Kampen.

a.t.	annulus tympanicus.
pr.	promontorium (cochlea).
c.i.	carotis interna ("art. promontorii").
a.st.	"arteria stapedia," passing across the fenestra ovalis (stapes omitted) and then running forward to divide into the ramus superior and ramus inferior (*r.i.*).
f.o.	foramen ovale.
f.l.m.	foramen lacerum medium.
f.l.p.	foramen lacerum posterius.
c.t.	chorda tympani.
f.	nervus facialis.
r.e.	recessus epitympanicus ("attic") (ossicles removed).
a.	apertura canalis facialis.
h.	tympanohyal.
m.	processus mastoideus.
p.p.t.	processus post-tympanicus.
p.p.g.	processus postglenoideus.
f.g.	foramen postglenoideum.
t.t.	tegmen tympani.
M.	cartilago Meckelii.
t.a.	tuba auditiva (Eustachii).

The fenestra cochleæ (rotunda) lies beneath the posterior part of the annulus (*a. t.*).

The second branch of the art. stapedia, called the *ramus superior,* springs from the main branch in the anterior part of the tympanic fossa, at a point about three millimeters medial to the postglenoid foramen. The ramus superior passes backward and upward, traversing the anterior margin of the petrosal, bending outward and issuing into the mid-cranial fossa near the outer angle; turning forward it gives off a small middle meningeal branch, and following the cerebral surface of the temporal it makes its exit into the orbit, through the cranio-orbital foramen where it anastomizes with the ophthalmic and ramus orbitalis [Tandler].

The *arteria promontorii,* as in *Lemur,* is given off from the common stem of the entocarotid near the posterior wall of the tympanic fossa; it bends over the cochlea, and passing forward and inward pierces the basisphenoid, passing obliquely forward and inward through a canal which may be named canalis caroticus basisphenoidei, and which is homologous with the carotid canal of Marsupials, *Centetes* and *Lemur*. Issuing in the mid-cranial fossa lateral to the sella turcica the art. promontorii joins the main cerebral trunk (art. communicans posterior, art. cerebri).

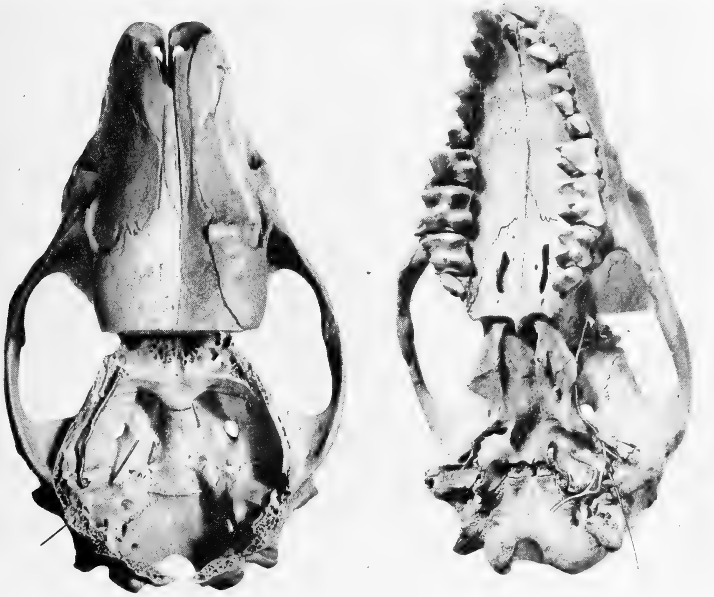

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Fig. 65. Course of the internal carotid and its branches in *Erinaceus*.

1. Oblique inferior aspect. The internal carotid (represented by a copper wire) enters the bulla on its posteromedial side and almost immediately divides into an arteria promontorii (medial fork) and an arteria stapedia (lateral fork). After traversing the stapes (not shown here) the arteria stapedia turns forward and gives rise to the ramus inferior, which runs forward to the orbit. Just before leaving the tympanic cavity the ramus inferior gives off the ramus superior. The bristle indicates the position of the canalis facialis (aqueductus Falopii).
2. Interior of brain-case, showing the course of the ramus superior along the medial surface of the endocranial wall, running forward through the foramen cranio-orbitale to the orbit. The bristle passes through the hiatus Falopii into the facial canal.

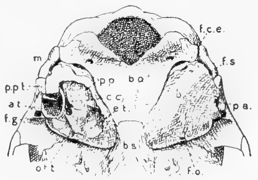

Fig. 66. Auditory region of *Tupaia*. After Van Kampen.

b, *bulla*, *e.t.*, entotympanicum, *m.*, pars mastoidea, *p.p.* pars petrosa, *a.t.*, annulus, *f.c.e.*, foramen caroticum posticum, *c.c.*, canalis caroticus.

In *Talpa*, which also represents the lipotyphlous insectivores, the course and distribution of the main branches of the entocarotid in general conform to the plan described above for *Erinaceus*. In *Tupaia*, representing the Menotyphla, which may well be allied to the Lemuroidea, the entocarotid likewise divides into two main branches — the art. promontorii and art. stapedia, which run in bony canals in the tympanic fossa (Hyrtl); according to Hyrtl's figure (*op. cit.*, Taf. II, fig. 15) the ramus inferior of the stapedial artery is large and issues from the tympanic cavity anteriorly as in *Erinaceus*.

LEMURINÆ

Lemur.— According to the collective results of Winge, Tandler, van Kampen (pp. 660, 661), and Stehlin (pp. 1207, 1202), here verified as far as possible in the dried skulls (Plates XLIII, XLIV, XLV), the entocarotid in *Lemur*, enters the bulla at its *posteroexternal* border medial to and below the stylomastoid foramen (*f. c. p.*).

Wortman (1903, p. 166) locates the carotid foramen in *Lemur catta* at the *posterointernal* angle of the bulla, between the bulla and the basioccipital in the region where it enters in many modern carnivores. But this interpretation is contrary to the statement of Tandler (1899, p. 761): "Dieses Gefäss, [arteria carotis interna], dessen Abgangsweise von der Carotis communis schon beschrieben wurde, zieht gerade cranialwärts und gelangt an die hintere Wand der mächtigen Bulla, zieht an dieser entlang und tritt in die Bulla selbst erst hoch ober, knapp unterhalb des Austrittes des Facialis ein." That is, it enters immediately below the stylomastoid foramen, as held also by Winge, van Kampen (p. 660) and Stehlin (1912, p. 1207). As may be seen in the dried skull, the opening which Dr. Wortman identifies as the carotid canal leads directly into the cranial cavity in the region of the posterior cranial nerves, and it is rightly regarded as a part of the foramen lacerum posterius by van Kampen (p. 658) and by Stehlin (1912, p. 1207).

The above described posterior carotid foramen (*f. c. p.*) on the posteroexternal wall of the bulla leads into a short carotid canal that runs forward, inward and upward to the external face of the auditory prominence or cochlea; the canal and its vessel then immediately divides into two branches named respectively (a) arteria stapedia and (b) arteria promontorii.

(a) The *arteria stapedia*, which is much the larger of the two branches, at first enclosed in a canal, turns sharply upward, bends outward and pierces the stapes; thence it enters the Fallopian aqueduct for the facial nerve (Winge) and following this canal part way through the petrosal it leaves it and emerges into the brain-cavity on the outer upper slope of the petrosal through a small foramen immediately posterointernal to the postglenoid foramen (Stehlin). It at once gives off the arteria meningea media, after which it turns forward, and running along a deep venous groove in the squamosal on the external basal corner of the brain-cavity, it emerges from the brain-case into the orbit, through the "cranio-orbital foramen" (Stehlin). This foramen is dorsolateral to the optic-sphenorbital-rotundum group and is near the dorsal border of the alisphenoid. After leaving the cranio-orbital foramen the stapedial artery crosses the orbit and joins the ophthalmic artery.

(b) The *arteria promontorii* (which is probably homologous with the main internal carotid of man) runs in a canal along the outer face of the cochlea (Plate XLV); it lies in *front* of the fenestra cochleæ (seu-rotunda) (contrast the Nycticebidæ, p. 180) and is parallel to the oblique septum that incompletely separates the hypotympanic from the true tympanic cavity. Continuing forward along the outer surface of this septum and immediately internal to the Eustachian foramen (ostium tubæ) the canal runs in the outer wall of the anterointernal extension of the bulla, gradually passing upward through the petrosal.

Issuing in the brain-cavity on the anterior slope of the petrosal (Plate L), the vessel follows a small groove, at the bottom of the channel for the trigeminus, forward and inward, piercing the cerebral surface of the basisphenoid and again issuing in a small foramen that is lateral to the sella turcica, immediately thereafter uniting with the ophthalmic artery (Stehlin). The arteria promontorii is very small, and both Tandler (p. 763) and Stehlin (p. 1207) found that in *Lemur* the chief supply for the cerebral arteries is furnished by the vertebral arteries.

INDRISINÆ

Plates XLVI, XLIX, L; Text Fig. 67

In a skull of *Propithecus* sp. (Amer. Mus. 31255) the foramina for the carotid are located as they are in *Lemur*. The posterior carotid foramen on the posteroexternal corner of the bulla leads into a prominent canal lying along the external face of the cochlea and no doubt carrying the arteria promontorii; the canal runs forward to the anteroexternal corner of the roof of the cavity of the bulla, pierces the basisphenoid and enters the brain-cavity through a very small foramen that is lateral to the sella turcica. The stapedial branch probably enters from the petrosal into the brain-cavity and follows the deep venous sulcus that runs along the base of the brain-case at its outer margin, thence emerging into the orbit through the prominent cranio-orbital foramen. The foramen lacerum posterius is divided into two distinct openings as in *Lemur*.

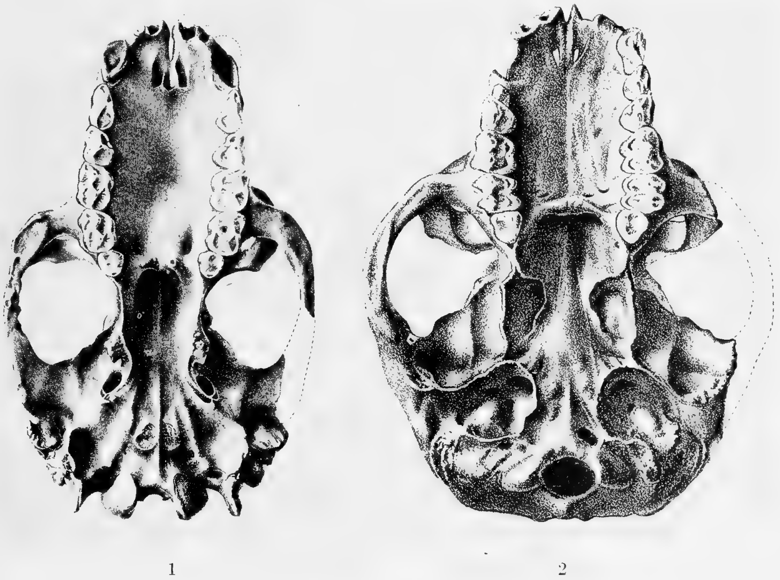

Fig. 67. Norma basalis of the skull of two subfossil indrisine lemurs from Ampasambzimba, Madagascar. After Standing.

(1) *Palæopropithecus maximus*, one-half natural size.
(2) *Mesopropithecus pithecoides*, natural size.

In *Mesopropithecus* the whole region of the bulla is essentially the same as in *Propithecus*. The foramen lacerum medium was closed and the canal for the art. promontorii ran along the outer margin of the cochlea. (Fig. 67.)

Indris is closely allied to *Propithecus* and no doubt agrees with it in the course of the carotid as it does in the form and relations of the bulla. The inside of the brain-cavity of *Indris* as beautifully figured by Edwards and Grandidier (1875, Pl. xxxv, fig. 1) is likewise essentially similar to that of *Propithecus*. The narrow slit marked *c* ("trou carotidien") is represented also in the dried *Propithecus* skull and appears to be merely a remnant of the space between the petrosal and the alisphenoid. Although no distinct foramina for the carotid lateral to the sella are shown in the figure, very probably in *Indris* the true carotid foramina (for the art. promontorii) were even smaller than they are in *Propithecus*, and the main supply for the cerebral arteries was drawn from the vertebral arteries as in *Lemur*. The venous sulcus in which runs the stapedial branch, on the laterobasal corner of the brain-cavity, is clearly figured (*op. cit.*, Pl. xxxv, fig. 2).

In *Lichanotus* (*Avahi*) a British Museum specimen shows the anterointernal process of the bulla covering the region of the foramen lacerum medium; the Eustachian opening, foramen ovale and stylomastoid are located as in *Propithecus;* a foramen at the posterior tip of the bulla is apparently the posterior carotid foramen.

In *Palæopropithecus* the collective characters of the skull, dentition and lower jaw prove that we have to do with an aberrant specialization of the *Indris*-type, as will be shown in a later part of this work. The whole basicranial region has been markedly altered from the *Indris* type, perhaps in correlation with the great increase in size of the areas of origin and attachment of the masseter, internal pterygoid and digastric muscles. The pterygoid plate of the alisphenoid no longer extends to the bulla, the bulla has become flattened, the thick membrane that lies external to the tympanic annulus has become irregularly ossified, so as to obstruct the opening of the external meatus. With all these changes it is not surprising that the foramina in the region of the bulla should be correspondingly modified. Hence, taking the normal Indrisidæ as a guide, I conceive the long oval opening that lies posteroexternal to the pterygoid process of the alisphenoid to be the foramen ovale and not the "foramen lacerum medium" as Standing has named it (1908, p. 81). More or less confluent with the foramen ovale in some skulls, but distinct from it in others, is the Eustachian passage, which, as observed by Standing (pp. 81, 82) leads backward into the shallow outer chamber of the bulla. A small opening between the foramen ovale and the Eustachian foramen, which is present in the skull figured in Plate x, figure 1, of Standing's memoir, is of doubtful character, but appears to represent a remnant of the space which once separated the outer expansion of the bulla from the entoglenoid process of the squamosal, i. e., of the true foramen lacerum medium. The foramen lacerum posterius, as in Indrisidæ, is represented by two foramina which are here separated by a considerable interval. The posterior carotid foramen was not located, but if the present interpretation of the other foramina be correct it seems highly probable that, as in other Indrisidæ, the whole entocarotid was reduced, entering perhaps through some inconspicuous foramen (in the posterior part of the bulla), which has hitherto escaped notice, and that the cerebra drew their arterial supply mainly from the vertebral arteries. (Fig. 67.)

ARCHÆOLEMURINÆ

A skull of *Archæolemur platyrhinus*, No. 834 in the British Museum collection, shows beautifully the interior of the bulla. It closely resembles that of *Propithecus*, save that it is wider. The canal for the arteria promontorii on the surface of the cochlea is very prominent and leads to the anterior end of the cavity, medial to the Eustachian opening, beneath the bulla. The whole region so closely resembles that of *Propithecus* that we may safely assume that the course of the entocarotid and its branches was essentially similar. The posterior carotid foramen lies at the posterior end of the bulla and the foramen lacerum medium is roofed over.

CHIROMYIDÆ

Text Fig. 68

Comparison of the researches of Zuckerkandl (1900, pp. 160–162) and Tandler (1899, p. 762) shows that the whole course of the art. promontorii and art. stapedia in *Chiromys* is similar to that of *Lemur* and *Propithecus*. The posterior carotid foramen lies at the posterior end of the bulla 3 mm. below the stylomastoid foramen (Zuckerkandl). Inside the bulla, van Kampen (1905, p. 664) found the carotid canal in its usual place on the cochlea. The art. promontorii is very small, but as in other Lemurs the stapedial branch is larger. The foramen lacerum medium is roofed over by the bulla and the art. promontorii enters the brain-cavity through the remnants of this foramen, namely a narrow slit, lying above the Eustachian foramen and lateral to the septum that divides the cavity of the bulla into medial and lateral moieties. The cerebral arteries draw their chief supply from the vertebral arteries.

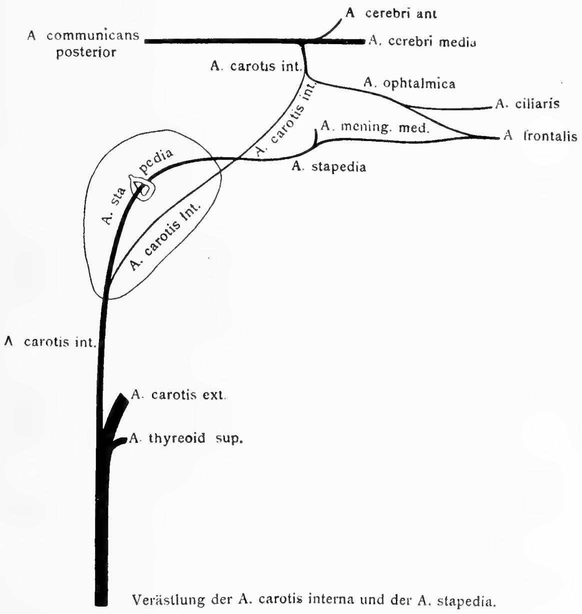

Fig. 68. Diagram showing the course of the internal carotid artery and its connections in *Chiromys*. After Zuckerkandl.

From the foregoing descriptions it will be seen that the course of the two main branches of the carotid and the locations of their several foramina are surprisingly uniform in the Lemurinæ, Indrisinæ, Archæolemurinæ and Chiromyidæ and that the conditions in *Palæopropithecus* may be interpreted as an aberrant derivative of the indrisine plan.

ADAPINÆ

Text Figs. 59, 61

From Stehlin's very thorough studies, first of the course of the entocarotid and its branches in an injected specimen of *Lemur varius* (1912, pp. 1207, 1211–1213), and secondly of well-preserved crania of *Adapis parisiensis* and *Adapis magnus*, he was able to show that *Adapis*, in the course of the entocarotid as well as in the whole architecture of the base of the cranium, is fundamentally similar to the Lemurinæ and Indrisinæ. The posterior carotid foramen lies at the posteroexternal corner of the bulla, below the stylomastoid foramen. The canal for the art. promontorii occupies its normal position on the anteroexternal face of the cochlea, and runs forward to the anterior end of the cavity of the bulla, medial to the Eustachian foramen, entering the cranium above this point. There was no foramen lacerum medium. The foramen lacerum posterius was divided into two well-separated foramina. The venous canal on the laterobasal corner of the brain-cavity, through which, in *Lemur*, runs the cranial portion of the stapedial artery, was likewise well developed in *Adapis* (p. 1216). This course of the entocarotid and its branches, together with the entire architecture of the skull, shows that *Adapis* is a member of the group that includes *Notharctus*, *Lemur* and *Indris*, and that in all probability the cerebra of *Adapis*, as in Lemurinæ, Indrisinæ, etc., received their main supply from the vertebral arteries by way of the art. communicans posterior or basilar artery.

NOTHARCTINÆ

Plates XLIV, XLV

The skull of *N. osborni*, Amer. Mus. No. 11466, (Plates XLIV, XLV) reveals the general course of the entocarotid and its branches within the bulla. The whole basicranial region is remarkably similar to that of *Lemur*, differing chiefly in the smaller size of the bulla. The anterointernal extensions of the bullæ, while not extending in front of the suture between the basioccipital and the basisphenoid as they do in *Lemur*, are joined to the posterior end of the basisphenoid so that there was no foramen lacerum medium. The anterior opening of the bony Eustachian canal is situated as in *Lemur*. The foramen ovale was external to the pterygoid plate of the alisphenoid. The cavity of the bulla was divided into external and medial parts by an incomplete septum running along the cochlea, the outer chamber being the true tympanic cavity, the inner being the hypotympanic sinus. The cochlea was about as large as in *Lemur mongoz* and bears on its outer face the bony canal for the arteria promontorii exactly as in *Lemur* and *Propithecus*, which runs forward and pierces the anterior wall of the roof of the bulla. The entrance to this canal for the art. promontorii is clearly seen in the posterior carotid foramen, on the posteroexternal angle of the bulla. Upon reaching the cochlea the carotid canal gives off a branch which carried the arteria stapedia. The canal for the stapedial branch is of somewhat wider diameter than that of *Lemur varius*. The stylomastoid foramen and the condylar foramen were located as in *Lemur* and apparently also the foramen lacerum posterius was divided into two separate openings. The postglenoid foramen was also identical in position with that of *Lemur*.

From all this, we may conclude with practical certainty, that the whole course of the internal carotid and its branches was essentially the same as in *Lemur*, and consequently that in *Notharctus*, as in *Adapis*, *Lemur, Propithecus*, and all other true lemurs except the Chirogaleinæ, the main internal carotid (art. promontorii) was small and the cerebra received their supply chiefly from the vertebral arteries; whereas, as noted by Tandler and by Wortman (1903, p. 175), in *Tarsius* and all the Anthropoidea (including New and Old World monkeys) the arteria promontorii or true entocarotid is greatly enlarged and supplies the chief arterial supply for the cerebra.

CHIROGALEINÆ

Plate LIV

In *Microcebus furcifer* of the Chirogaleinæ the observations of Mivart, Winge, Tandler and van Kampen (pp. 661, 662) collectively show that the main entocarotid branch runs through the widely open foramen lacerum medium and also pierces the basisphenoid (as in Marsupials); that the posterior carotid foramen (*f. c. e.*) is also present but small; as in *Chiromys* it lies near the foramen lacerum posterius, near the supposed junction of the bulla and the mastoid. Thus *Microcebus furcifer* agrees with the Nycticebidæ in that the main entocarotid branch enters through the foramen lacerum medium, while the posterior branch is small. In the other species of *Microcebus*, however, the foramen lacerum medium is said to be more or less roofed over by the anterointernal extension of the bulla (van Kampen). In *Chirogale* (Plate LIV) and *Atililemur* there are large carotid canals (*f. l. m.*) piercing the basisphenoid, but in *Myoxicebus* (Plate LIV), the skull of which appears to me to be related in structure to that of *Atililemur*, these openings are much reduced. According to the view here adopted provisionally, the branch which enters through the foramen lacerum medium and the basisphenoid in *Microcebus furcifer* is homologous with the arteria promontorii of *Lemur*, with the anterior branch in the Nycticebidæ and with the main internal carotid in man. The small posterior branch may be the art. stapedia.

In the cases where the foramen lacerum medium is partly roofed over by the bulla the art. promontorii may have passed through the bulla, entering the bulla by the posterior carotid foramen and entering the brain-cavity through the anterior part of the roof of the external chamber of the bulla.

The apparent shifting of the main carotid artery, which in most lemurs pierces the anterior wall of the tympanic cavity, but in Nycticebidæ and Chirogaleinæ enters through an anterior carotid foramen (*f. l. m.*) in front of the bulla, is explained by van Kampen (1905, p. 383) as follows:

> Wincza found in several placental mammals that ontogenetically the carotid, before it reaches the carotid foramen [*f.c. p.*] runs along the ventral side of the cochlear portion of the otic capsule. This fact explains the difference between adult placentals [of different groups], in which the artery either traverses the tympanic cavity, or remains medial to it, as in all monotremes and marsupials. This is connected especially with the origin of the ventral wall of the tympanic cavity. When it is formed from the bones of the basis cranii that are medial to the petrosal (namely, basioccipital, basisphenoid) then the carotid comes to lie inside the tympanic cavity (*Myrmecophaga*, most insectivores); in other cases it depends upon where the ventral wall of the tympanic cavity rises from the petrosal, whether the carotid shall run lateral to it and thus inside the cavity (*Tupaia*, most Prosimiæ and Simiæ), or medial to it (most *Xenarthra*, Carnivora, Ungulata, Lorisidæ, etc.). The course of the carotid may in this respect be different in nearly related animals (cf. among *Xenarthra*, Prosimiæ, Rodentia). [Translation.]

LORISIDÆ

Plate XLIX (*Perodicticus*)

In this family the divided "entocarotid" enters the brain-case by two widely separated routes.

(1) The largest branch enters in front of the bulla through the widely open foramen lacerum medium. Tandler regards this branch as homologous with the main internal carotid of man and with the "arteria

promontorii" of *Lemur*, a view which is adopted by Stehlin (1912, p. 1212). Winge's opposing view (cf. van Kampen, p. 672) that the main internal carotid in the Nycticebidæ is not homologous with the arteria promontorii of *Lemur*, appears to the present writer improbable, on account of the structurally transitional stages offered by the Chirogaleinæ (*vide supra*).

(2) The posterior branch (Plate XLIX), which is extremely small, enters the posterointernal region of the bulla immediately in front of the foramen lacerum posterius and passes over the cochlea, behind the fenestra cochleæ (rotunda). It is probably the "art. stapedia," but this identification lacks verification and is opposed by Winge, who held that it represented both the art. promontorii and the art. stapedia of *Lemur* (van Kampen, p. 672). At any rate, the Lorisidæ are characterized by the widely open foramen lacerum medium and by the reduced posterior carotid foramen (*f.c.p.*)

In *Necrolemur*, which in many respects combines characters of the Lorisidæ with others of the Tarsiidæ, there is a prominent foramen which is probably the internal carotid foramen located on the inner wall of the bulla immediately in front of the foramen lacerum posterius. In front of the bulla and lateral to the anteromedial protuberance there is a foramen which may be the opening of the eustachian tube since it strongly resembles that opening in the Nycticebidæ. This interpretation is based upon a skull of *Necrolemur antiquus* in the British Museum and upon another skull in the Peabody Museum at Yale University (Plate LI). It also accords with Dr. Stehlin's identification of the carotid foramen (1916, p. 1349). Thus, there was no foramen lacerum medium in *Necrolemur* and the carotid passed through the bulla, although its precise course is not known.

TARSIIDÆ

Plate LI

In *Tarsius* the internal carotid pierces the bulla, passing through an osseous canal located in the middle of the bulla and a little in front of the external auditory meatus. There is no foramen lacerum medium, this region being completely closed by the greatly inflated bulla, as it is in *Necrolemur*. Winge thought that there was a small opening for the stapedial artery in the posterior part of the bulla, but this was not confirmed by van Kampen (p. 676), who found a canal for the stapedial artery piercing the stapes, inside the bulla where it is given off from the canal for the main entocarotid artery or arteria promontorii; thus, according to van Kampen, the arrangement of the stapedial artery is fundamentally as it is in the Lemuridæ (see below). The stapedial canal is preserved in the specimen of *Tarsius* shown in Plate LI, but I was unable to observe its junction with the main canal. The vessel which traverses the main canal and gives off the stapedial artery is undoubtedly the homologue of the "internal carotid" of man; it is probably also homologous with the entocarotid of *Lemur* (which likewise divides into two branches inside the bulla).

In *Tetonius* ("*Anaptomorphus*") which is provisionally referred to the Tarsiidæ, the strong similarity of the parts of the bulla preserved to that of *Tarsius* suggests that the carotid likewise ran through a large bony canal, but no remains of this canal were recognized; very possibly it ran along the lateral face of the cochlea in the septum between the true tympanic and the hypotympanic cavity. (Plate LI.)

PLATYRRHINI

Plate XLIX (*Alouatta*)

In the New World monkeys the opening of the carotid canal faces posterointernally and it is generally near the posterior border of the bulla. The canal is much larger than in any of the Lemuriformes and lies deep in the petrosal; it thus avoids the tympanic cavity and does not pierce the basisphenoid; it emerges into the brain-cavity posteroexternal to the sella turcica (Plate L).

In *Nyctipithecus* (*Aotus*) and *Hapale*, as observed by Wortman (p. 168), there is a small canal, in front of the foramen lacerum posterius, lying partly between the bulla and the basioccipital and running through the latter into the cranial cavity. I have also observed the same arrangement in *Pithecia*. Dr. Wortman thinks that this small canal transmits an internal branch of the entocarotid and that it is homologous with a certain canal in *Lemur*, lettered cc. in his Fig. 101, p. 150; it probably is homologous with that canal in *Lemur*, but that it transmits a branch of the entocarotid is more than doubtful, as indicated above (p. 174); it more probably has nothing to do with the entocarotid but serves for the exit of one of the posterior cranial nerves.

The stapedial branch of the entocarotid is said to be wanting, at least in *Hapale penicillata* and *Ateles paniscus*, the forms examined by Tandler (van Kampen, pp. 684–688).

CATARRHINI

The foramen lacerum medium (foramen lacerum anterius of German writers) has not been developed either in the Old World or in the New World monkeys, since the bulla joins the alisphenoid and basisphenoid anteriorly; in the great apes this fissure between the tegmen tympani and the bones in front of it begins to develop but is more or less restricted; in man it is widely open, no doubt secondarily, and through it may be seen the entocarotid which passes across the upper part of the foramen on its way from the carotid canal into the cranial chamber; but it would be quite misleading to say that in man the internal carotid enters through the foramen lacerum medium; it enters through the carotid canal of the petrosal.

In the Hylobatidæ and the Simiidæ the course of the internal carotid is identical with that in man (van Kampen, p. 695); in the Cercopithecidæ it pierces the bulla more posteriorly, but its course is practically the same (van Kampen, p. 691).

In man the internal carotid artery ("entocarotid") broadly pierces the petrotympanic (or fused petrosal and tympanic) and, running through the carotid canal into the cranial chamber, gives rise to nine branches and numerous subdivisions (Cunningham, 1902, pp. 768–770). The three main branches are the ophthalmic artery and the anterior and middle cerebral arteries. One small branch, given off in the tympanic chamber, the stapedial artery,[1] in the embryo pierces the stapes, but later atrophies as it does also in the great apes and Old World monkeys (van Kampen, p. 691; Keibel and Mall, II, p. 628).

CONCLUSION

This review may be concluded by a summary of Tandler's general hypothesis as to the derivation of the various types of entocarotid distribution found in adult mammals. The internal and external carotid arteries are regarded by morphologists as having been derived phylogenetically from the afferent vessels of the branchial arches of the lower vertebrates (Keibel and Mall, II, p. 628). In mammals some of the minor branches belonging to adjacent arches tend to anastomose with each other, and when this happens, according to Tandler's theory, the terminal branches of the more anterior arches are captured, as it were, by the main trunks of the more posterior arches. In this way some of the minor branches

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[1] The stapedial artery in many mammals is connected with the internal maxillary and middle meningeal arteries. Although these two arteries appear to spring from it, their connection with it is nevertheless a secondary one; ontogenetically they are derivatives of the external carotid. The middle meningeal artery runs through the foramen spinosum, which is posteroexternal to the foramen ovale, and enters the cranial cavity.

in the orbit, which appear to have been supplied originally by the first visceral arch, are found in certain adult mammals to be supplied by the main vessel of the second visceral arch, which is the stapedial artery. Again the minor branches of the stapedial artery are often captured by the main trunk of the third visceral arch, which is the external carotid, and as a result of this capture the stapedial artery itself is often absent in the adult although present in the embryo.

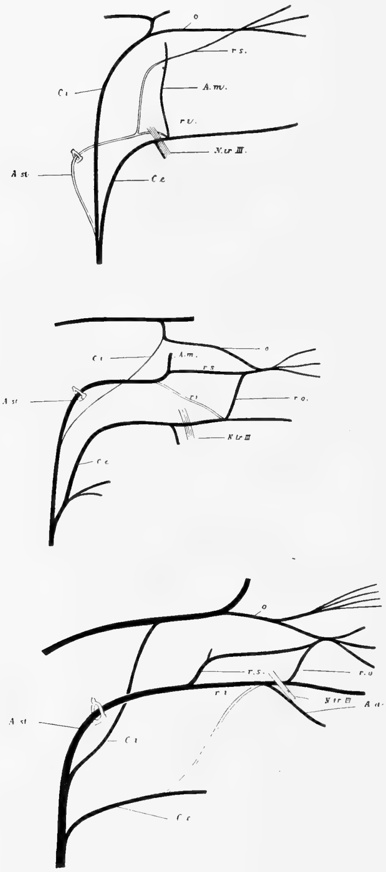

Fig. 69. Diagram showing the course and connections of the carotid arteries in (1) *Erinaceus,* (2) *Lemur,* (3) Man. After Tandler.

(1). *Erinaceus europæus.* The primitive pattern of the carotid system is nearly intact, save for the loss of a branch connecting the carotis externa (*c.e.*) with the ramus inferior (*r.i.*). The arteria stapedia (*A.st.*) retains both rami, superior (*r.s.*) and inferior (*r.i.*).

(2) *Lemur varius.* The external carotid (*c. e.*) has captured the vessels formerly supplied by the ramus inferior, which in the existing lemurs has disappeared. The true internal carotid (art. promontorii, *c. i.*) is reduced.

(3) Man. The external carotid has captured the whole system that was formerly supplied by the stapedial artery; the latter is lacking except in embryonic stages. The internal carotid (art. promontorii) becomes very large.

According to this theory the insectivores, as described above, have a more primitive type of entocarotid circulation than that of the lemurs, and the lemurs in turn are more primitive than the tarsioids and higher primates. In *Erinaceus,* as we have seen, the stapedial artery is fully developed and retains both its main branches, the ramus superior and ramus inferior with all their minor branches. In lemurs the arteria promontorii or true carotis interna is progressively reduced, the external carotid has "captured" the arteria maxillaris interna or orbital continuation of the ramus inferior, and the tympanic portion of the ramus inferior has been lost. The same condition is indicated in *Notharctus* and *Propithecus* by the total lack of a foramen caroticum alisphenoidei posterior in the anterior wall of the tympanic fossa. In the Lorisidæ and Tarsiidæ the whole stapedial artery is reduced or wanting but in these families the true internal carotid is enlarged, and, according to Tandler, in the Lorisidæ enters the cranium through the foramen lacerum medium, in front of the bulla, while in *Tarsius* it pierces the middle of the bulla. In man and other Platyrrhini (including both New World and Old World genera) according to Tandler, the arteria promontorii or true internal carotid is large, traversing the periotic through the carotid canal; the stapedial artery and the tympanic portion of the ramus inferior are usually reduced or wanting, while the distal branches of the ramus inferior are appropriated by the carotis externa.

From this review it appears that, if Tandler's observations and hypothesis are correct, the entocarotid distribution in *Notharctus* and other lemurs is structurally ancestral to those of higher primates, except that in Lemuridæ the arteria promontorii is reduced, while the Tarsiidæ resemble the Platyrrhini in the enlargement of the arteria promontorii and in the reduction of the arteria stapedia.

THE SYSTEMATIC POSITION OF *NOTHARCTUS*

The general systematic relationships of *Notharctus*, as understood by the writer, are as follows.

Order **PRIMATES**

Suborder **LEMUROIDEA**

Series **Lemuriformes** [1]

1. Postorbital process of malar joining postorbital process of frontal, but not extending inward as a partition separating orbit from temporal fossa.
2. Malar either touching lacrymal or barely separated from it by a narrow strip of the maxillary.
3. Mid-cranial region long or not greatly shortened; pterygoid plate of alisphenoid extended obliquely posteroexternally and joining glenoid and bulla; true pterygoid usually nearly in contact with bulla.
4. Expanded auditory bulla enclosing the tympanic membrane and tympanic annulus. Inflated portion of bullæ not greatly produced forward and inward toward the midline.
5. Main branch of internal carotid typically of small size, running in osseous carotid canal over the cochlea (except in Chirogaleinæ) and piercing the basisphenoid.
6. Pterygoid plate of alisphenoid pierced by "foramen pterygospinosum."
7. Dental formula primitively $I\frac{2}{2}\ C\frac{1}{1}\ P\frac{4}{4}\ M\frac{3}{3}$; variously reduced in specialized forms.
8. Molars typically erupting early: m^1, m^2, m^3, and m_1, m_2, m_3 in place with all the deciduous teeth.

Family **Adapidæ**

Eocene Lemuriformes of Europe and North America.

Dental formula: $I\frac{2}{2}\ C\frac{1}{1}\ P\frac{4}{4}\ M\frac{3}{3}$. Deciduous dental formula probably[2] $DI\frac{2}{2}\ DC\frac{1}{1}\ DP\frac{3}{3}$. Incisors and canines not abnormally modified (lower canine more or less caniniform or premolariform, not procumbent or styliform; second lower premolar not subcaniniform, not opposing upper canine). Central upper incisors (i^1) with compressed crowns. Lower incisors not sharply procumbent, with more or less truncate-spatulate crown. Protoconule of upper molars forming with the protocone a prominent oblique crest (protoloph). Metaconule, when distinct, tending to connect metacone and protocone. Upper molar cingula well marked. Hypoconulid of m_3 distinct. Brain-case small or not greatly expanded. A marked constriction of the skull behind the orbits. Orbits of moderate size. Lacrymal not expanded on face but lying within the orbit; lacrymal foramen marginal. Zygomatic arches stout; masseteric tubercle of malar well marked. Sagittal and lambdoidal crests typically high; occiput triangular. Mid-cranial region long; pterygoid plate of alisphenoid large. Mastoid forming a backwardly directed tuberosity, partly embraced by the paroccipital process of the exoccipital. Entrance of internal carotid at posteroexternal angle of bulla. Brain macrosmatic with large olfactory lobes, small frontal lobes and small cerebellum.

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[1] Gregory, W. K. 1915. On the classification and phylogeny of the Lemuroidea. Proc. Paleontol. Soc. Bull. Geol. Soc. America, XXVI, pp. 423–442.

[2] Only partially known in *Notharctus*.

Subfamily **Adapinæ**

Lower, Middle and Upper Eocene, Europe.

Upper molars tritubercular with cingulum-hypocone, no mesostyle; lower molars without paraconids and usually without hypoconulids (except m_3), talonids often enlarged; protolophid crest sharp, oblique. Fourth upper premolar early acquiring a posteroexternal cusp; fourth lower premolar with well developed talonid. Incisors typically wide-edged, trenchant; canines straight, dagger-like. Mandible typically short and very stout [1] with greatly expanded angle, condyle gently convex or flattened, coronoid recurved; symphysis coössified. Sagittal and lambdoidal crests high, pterygoid fossæ typically wide; mastoid exposure on occiput wide above.

Subfamily **Notharctinæ**

Lower and Middle Eocene, North America.

Posterointernal (pseudohypocone) cusps of upper molars progressively arising from a ridge connected with the protocone, cingulum-hypocone not developed (except rarely on m_3); m^1–m^3 progressively acquiring a mesostyle (incipient in earlier species). Fourth upper premolar with retarded evolution of the posteroexternal cusp; fourth lower premolar with retarded talonid; lower incisors small; canines progressively more or less caniniform, especially in males. Lower molars primitively with paraconids located immediately in front of the metaconids; these are frequently lost, while a central median cusp (pseudoparaconid) may be developed. Mandible elongate, angle forming a long backwardly produced apophysis; symphysis mandibuli primitively not coössified. Condyle transversely convex with a medial inferior prolongation; coronoid high, erect. Pterygoid, or hamular, fossæ narrow; mastoid exposure on occiput narrow above.

Genus **Pelycodus** Cope

Pseudohypocone (posterointernal cusp) of m^1, m^2 incipient or not well distinguished from protocone, contour of upper molars trigonal or not entirely quadrate; mesostyles incipient or small; symphysial suture of mandible distinct.

Genus **Notharctus** Leidy

Pseudohypocone of m^1, m^2 prominent, well distinguished from protocone and more or less nearly equal to it; mesostyle clearly distinct; symphysis of mandible co-ossified in old animals.

The species of *Notharctus* for the most part have been founded upon incomplete specimens of lower jaws and teeth; they have recently been revised for systematic purposes by Granger and Gregory,[2] and are considered rather from a morphological viewpoint in present memoir. They exhibit a fairly wide range of size and progressive emphasis of the generic characters. The older species from the Wind River Basin (summit of the Lower Eocene) connect *Notharctus* with the more primitive and ancestral genus *Pelycodus*. The latest species, *N. crassus*, from the Upper Bridger horizons (late Middle Eocene) is an advanced stage of evolution, in which the upper molars have large mesostyles and very distinct posterointernal cusps. The family is apparently represented in the Upper Eocene by the dwarfed and little-known form named ?*Notharctus uintanus*, which is the last known survivor of the race, unless, indeed, the South American primates were derived from this subfamily (see pages 217–221).

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[1] Except *Adapis sciureus*.

[2] 1917, Bull. Amer. Mus. Nat. Hist., XXXVII, pp. 841–859.

SUMMARY OF THE DIVERGENT EVOLUTION OF ADAPINÆ AND NOTHARCTINÆ

NOTHARCTINÆ	ADAPINÆ
Upper and lower incisors of insectivorous-frugivorous type.	All incisors with wide chisel-like edges (specialized frugivorous type, probably adapted for cutting off stems).
Canines caniniform, but rounder in section.	Canines dagger-like (adapted for piercing tough rinds?).
Premolars becoming wider transversely.	P^{1-3} becoming more or less compressed and trenchant (*A. parisiensis*).
Anterior external cusp of p^4 retarded; close to posterior cusp.	P^4 with two external cusps, the posterior well separated from the anterior cusp.
P_4 retarded, with small talonid.	P_4 progressive with large talonid.
Mesostyles, upper molars with V's.	No mesostyles, no V's on upper molars.
Pseudohypocones.	True hypocones.
Protolophs and protolophids less emphasized.	Protolophs and protolophids conspicuously developed as cutting crests.
Metacristids absent.	Metacristids typically developed.
Paraconids present in early types, usually reduced or absent.	Paraconids absent.
Entoconids progressive.	Entoconids retarded.
Excursion of mandible progressively ental.	Excursion of mandible more orthal.
Lower jaw elongate with large high coronoid.	Lower jaw short with greatly expanded angle and short deep ramus.
Condyle of jaw very convex with internal posterior extension.	Condyle of jaw flatter.
Skull mesocephalic.	Skull wide.
	Sagittal and lambdoidal crests very high.
Orbits larger.	Orbits smaller.
Malar less robust, not extending to glenoid.	Malar very stout, extending nearly to glenoid.
Pterygoid fossæ small, slit-like.	Pterygoid fossæ expanded.
Basicranial region less expanded transversely.	Basicranial region wider.
Condylar foramen remaining separate from foramen lacerum posterius.	Condylar foramen typically confluent with foramen lacerum posterius.

The evolution of the molar teeth in the Notharctinæ was outlined by Professor Osborn in 1902. In 1915 Dr. Matthew described the two oldest and most primitive species, *Pelycodus ralstoni*, from the base of the Lower Eocene, and its successor *P. trigonodus;* he hinted that the latter gave rise respectively to *P. frugivorus* and *P. jarrovii*, and that these two in turn passed into the two most ancient species of *Notharctus*, *N. nunienus*, and *N. venticolus* of the Wind River (Lost Cabin) formation. In 1917 Mr. Granger and the present writer, revising the species of *Notharctus*, were enabled to connect the most advanced stage, *N. crassus* of the Upper Bridger (formerly assigned to a separate genus *Telmatolestes*), with less advanced species of the Lower Bridger, through the newly described form *N. pugnax*. In the present work all the material has been closely restudied, with reference not only to phyletic relationships but chiefly for the purpose of tracing the evolution of the dentition as a whole and of following the detailed changes in the incisors, canines, premolars and molars. (Plates XXXV–XXXVII.)

With regard to phyletic relationships the conclusions above mentioned have seemed upon re-examination to be justified by the available evidence. The very progressive line culminating in *N. crassus* seems to be clearly foreshadowed in all its characters by the relatively progressive *N. venticolus* of the Wind River, while the smaller and more conservative species *N. osborni*, *N. matthewi*, if not representing the females of some of the larger forms, bear more resemblance to the primitive *N. nunienus*. The chief outstanding difficulty is to settle the precise relationships of those Lower Bridger forms which are of intermediate size; namely, *N. tyrannus*, *N. anceps*, *N. affinis*.

The evolution of the dentition as a whole appears to be as follows:

In the earliest forms, *Pelycodus ralstoni* and *P. trigonodus*, the dentition although not exclusively insectivorous in character retains many reminders of a generalized insectivorous type; the animals themselves were of very small size; the incisors and canines were small, the lower incisors gently procumbent, the premolars simple, the upper premolars tritubercular, the lower molars tuberculosectorial with low entoconids; the dentition lacked only the third upper and lower incisors of the primitive insectivorous Eutherian formula. The lower jaw in these primitive types was relatively slender and probably its motion was largely orthal. The latest form, *Notharctus crassus*, was nearly as large as a howler monkey; the canines are caniniform, with long thick fangs, the fourth and even the third premolars are becoming more molariform, the upper molars have two external V's, a large mesostyle and a large pseudohypocone; the lower molars have the paraconids reduced or absent and now have large entoconids; all the cusps were coarse and subcircular. The mandible could be displaced transversely from the outer side inward, this giving considerable cutting and grinding action to the molars.[1] The lower incisors were smaller than those of the Adapinæ with the crown less extended transversely; the central upper incisors were compressed and inclined toward the midline; the lateral incisors were behind them. On the whole the incisors were adapted rather for prehension than for cutting. Such a dentition seems to have been adapted largely to a diet of leaves and soft-rind fruits. As in other families of primates in which the canines progressively become caniniform the males of the robust species of Notharctinæ were probably more or less aggressive fighters.

The Adapinæ range in size from *Adapis sciureus* (Stehlin, 1916, p. 1515, fig.) which was smaller than the smallest known Notharctine (m_{1-3} measuring only about 9.3 mm., as compared with 11–14 in *Pelycodus ralstoni*) up to *Adapis magnus* in which m_{1-3} measures 23.5 (about the same as in *Notharctus crassus*). In *A. magnus*, and still more in *A. parisiensis*, the very massive jaws and muscle supports were much larger in proportion to the size of the cheek teeth than in any of the Notharctinæ. The incisors, canines and premolars all had sharp cutting edges; the incisors were wide and chisel-like, the canines more or less premolariform; the fourth premolars were almost molariform, the others more or less trenchant. The upper molars had a partly flattened ectoloph, rather delicate conical para- and metacones, and a sharp oblique protoloph; there were no mesostyles and no pseudohypocones but true cingulum hypocones. The low hypocones did not oppose the low entoconids, but jutted inward above the trigonids of the lower molars. The lower molars lacked paraconids, and had low entoconids; they bore a prominent oblique metalophid, ending lingually in a large metacristid and shearing past the protoloph of the upper molars. The motion of the jaw was more orthal and less ental than in the Notharctinæ, and the condyles show corresponding differences.

The dentition of the more specialized Adapinæ presents certain analogies to those of ungulates, especially Eocene perissodactyls with lophodont molars. On the other hand the persistence of the brachyodont condition and the conical sharp character of the para- and metacones, together with the more orthal movement of the mandible, suggest that the food was not ground but was merely pierced, cut, and pressed. The closest resemblances to *Adapis*, however, both in the patterns of the premolars and molars and in the interlocking relations between the upper and the lower teeth, are seen in the modern

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[1] This movement of the mandible from the outer side inward, pressure being exerted first on the outer side, is here called entad, as in the Century Dictionary *ental*, by analogy with proal and palinal, notwithstanding that Cope (Journ. of Morphol., 1889, p. 226) gave to ental and ectal meanings which were precisely the reverse of what one would have expected from their etymology.

Lepilemur. It thus seems likely that *Adapis parisiensis* lived upon some small fruit with a tough rind. The sharp chisel-like incisors would be adapted for cutting the fruit from the branches, the canines would pierce the rind and the premolars would cut it into large pieces; the conical cusps of the fourth premolars and the molars would break up the rind and the protoloph shear would cut it, the pestle and mortar action of the protocone, and other cusps, would press the pulp without grinding it. *Adapis magnus* with coarser teeth and relatively smaller muscular power may have fed upon larger fruit with a proportionately less resistant rind.

The account given in the preceding pages (137–139, 149) of the interlocking relations of the upper and lower teeth and of the motions of the mandible is based upon intensive and repeated study of a number of specimens in which it was possible to fit the lower and upper teeth together and to ascertain the exact topographic relations of the parts of the upper and lower teeth during successive stages of occlusion as well as the paths described by the mandible in its excursions. These studies seem to the writer to afford very definite evidence in favor of the following conclusions which were set forth in a preliminary way in 1915.[1]

(1) In the Notharctinæ the progressive development of mesostyles, pseudohypocones and entoconids are all more or less directly correlated with[2] the progressive development of an ental motion of the mandible in the act of "chewing on one side."

(2) In the Adapinæ the lack of mesostyles, the retarded or even retrogressive state of the entoconids, the normal relations of the true cingulum-hypocone to the trigonid and the progressive development of the metacristid and the emphasis of the protoloph and protolophid are all correlated with a more orthal motion of the mandible.

(3) In the early Notharctinæ the region of the future pseudohypocone suffers transverse attrition on the lingual side by the entoconid of the corresponding lower molar, and on the posterolabial side by the paraconid of the succeeding lower molar. In the final stage, *N. crassus*, the large entoconid tip opposes the cleft between the protocone and the pseudohypocone.

(4) In *Adapis parisiensis* and *A. magnus* the lower entoconid lies well to the inner side of the true hypocone and seems to have no very direct relations with it.

(5) The very retarded development of the second external cusp (metacone) of p^4 in the Notharctinæ is connected with the anteroposterior crowding of the premolars and the very retarded development of the hypoconid of p_4, while in the Adapinæ the early appearance of the metacone of p^4 is correlated with the precocious lengthening of the premolar series and the appearance of a well-developed hypoconid on p_4.

From the little that is known of the postcranial skeleton of the Adapinæ, it is evident that the limbs were fundamentally similar to those of *Notharctus* the chief difference being that the calcaneum, if correctly referred to *Adapis*, was shorter.

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[1] Bull. Geol. Soc. Amer., XXVI, pp. 422, 423.

[2] The words "correlated with," as used above do not mean "caused by." The divergent trends in the evolution of the patterns of the teeth in Notharctinæ and Adapinæ are *associated with* progressive differences in the functions and mechanical relations of the parts and with equal differences in the movements of the lower jaw; but for present purposes it is not necessary to decide whether the changes in function followed upon orthogenetic changes in dental pattern, whether diverging environmental conditions resulted in the selection of divergent functions and structural patterns, or whether both processes contributed to the objective results which alone are matters of observation.

Systematic Relations of the Notharctinæ with the Adapinæ and a Discussion of the Value of the "Family" in Classification. A Reply to Dr. Stehlin's Criticisms

In a paper read before the Paleontological Society of America, Dec. 31, 1914, and published in 1915,[1] the writer summarized briefly the general results of his studies on the Lemuroidea and his provisional conclusions of that date. On page 421 of that paper occurs this passage:

> Stehlin, in 1908, in his monographic revision of the European genus *Adapis*, which ranges from the Lower to the Upper Eocene of France, concluded from a comparison of the dentitions that the American *Notharctus* and its allies were not nearly related to *Adapis*, but that the two formed divergent contemporary families in Europe and America, which were not more nearly related to each other than to other families of Primates. Stehlin showed that the Adapidæ in the fundamental architecture of the skull were related to the modern Lemuridæ.

To this Dr. Stehlin in his "Nachträglichen Bemerkungen über das Verhältniss von Adapis zu den Notharctiden" (1916, p. 1518, footnote) objects as follows: "Gregory resumiert meine Darlegungen unrichtig, wenn er mich kurzweg sagen lässt 'that the Adapidæ and the Notharctidæ were rather widely separated families not more nearly related to each other than to other groups of Lemuroids.'"

Among the passages in his earlier memoir on *Adapis* (1912, pp. 1287–1290) which led the writer to that summary are the following:

> Von den Eigentümlichkeiten, in welchen die Notharctiden mit den Adapiden übereinstimmen, beweisen diejenigen, welche wir bei den Wurzelformen aller Primatenstämme erwarten müssen, sehr wenig für das Vorhandensein eines nähern Zusammenhangs; diejenigen, welche sich noch nicht mit Bestimmtheit als Differenzierungsmerkmale erwiesen haben, vorderhand kaum mehr. Zu den erstern gehört die Vollständigkeit der Praemolarreihe, die Existenz einer Berührung zwischen Alisphenoïd und Parietale,[2] das Fehlen eines knöchernen Gehörgangs und ziemlich sicher auch der transperiotische Verlauf der Carotis interna; zu den letztern glaube ich die Kleinheit des facialen Lacrymale und die intraorbitale Lage des Thränenloches rechnen zu sollen. Sehr wenig zu bedeuten hat ferner auch die Übereinstimmung in solchen Differenzierungsmerkmalen, welche, wie die starke Blähung der Bullae, die starke Entwicklung der Pterygoïdalflügel, die Preisgabe eines Incisivenpaares, unter niedrigen Primaten überhaupt verbreitet sind. Eher liesse sich Gewicht darauf legen, dass beide Gruppen ihr mandibulares Vordergebiss nicht nach Lemurenart, sondern mehr nach Affenart differenziert haben und dass beide die, unter Primaten seltene, Tendenz zeigen, die hintersten Praemolaren zu complicieren. Aber auch diese Specialisierungen sind nicht beweisend für einen nähern Zusammenhang, denn sie können separatim erworben sein, und dass sie es tatsächlich sind, ergiebt sich, wie ich glaube, mit Bestimmtheit aus der folgenden Reihe von Gebissdifferenzen wischen den beiden Gruppen, in der ich die fundamentaleren voranstelle.

After enumerating a highly important list of divergent characters in the dentition of the Notharctidæ and Adapidæ, Dr. Stehlin proceeds:

> Die Entwicklungsbahn der Notharctiden divergiert also stark von derjenigen der Adapiden und das Wasatchstadium derselben, Pelycodus, welches aus chronologischen Gründen allein allenfalls als Wurzelform der letztern in Betracht kommen könnte, zeigt sich schon so deutlich in dieser Bahn engagiert, dass es sich unmöglich mehr in der Richtung des europäischen Genus weiter entwickeln konnte.
>
> Ob Adapiden und Notharctiden überhaupt durch ein engeres Band als dasjenige, welches alle Primaten Verbindet, mit einander verbunden sind, halte ich für fraglich. Jedenfalls lässt sich die Berechtigung einer systematischen Categorie, welche die beiden Gruppen zusammenfasst, auf Grund unserer heutigen Kenntnisse nicht erweisen. Es erscheint vielmehr vorderhand ebensowohl möglich, dass diesselben schliesslich ihren Platz an ziemlich weit von einander entfernten Stellen des Primatensystems finden werden.
>
> Weit eher als zwischen Notharctiden und Adapis könnte sich eine nähere Verwandtschaft zwischen erstern und Protadapis herausstellen. . . . Jedenfalls liegt vorderhand mehr Grund vor, den Anschluss von Protadapis bei den Noth-

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[1] Bull. Geol. Soc. Amer., XXVI, pp. 419–446.

[2] Einzelne Notizen über den Schädelbau der Notharctiden giebt Wortmann, 1903, *loc. cit.*, 172–174.

> arctiden zu suchen als bei den Adapiden. Aber zur Formulierung eines zuverlässigen Schlusses bietet unsere gegenwärtige Kenntniss des Genus noch nicht hinlängliche Anhaltspunkte.
>
> Weder im europäischen noch im nordamericanischen Untereocaen ist also vorderhand die Wurzelgruppe der Adapiden zu finden; die Frage nach der Herkunft derselben bleibt bis auf weiteres unbeantwortet.

To the writer it appears that the general purport of Dr. Stehlin's views in 1912 was that the Adapidæ and Notharctidæ followed divergent trends of evolution in the dentition, that the common characters might well be primitive, inherited from the stem forms of all primate stocks and giving very little evidence for a near connection of these two families.

The writer's error in regarding *Protoadapis* as a primitive member of the Adapinæ (1915, p. 423) has been corrected by Dr. Stehlin (1916, p. 1520). He also shows (1912, p. 1286) that this puzzling genus in the structure of the fourth lower premolar and lower molars approaches *Pronycticebus Gaudryi*, which the writer regards as perhaps the most generalized of all the European Eocene primates: structurally allied on the one hand with the *Tarsius*-like group, in another direction with the Lorisidæ, and thirdly with the Adapidæ. Dr. Stehlin also shows (1912, p. 1289) that in the characters of its lower molars *Protoadapis* approaches the Notharctidæ rather than the Adapidæ.

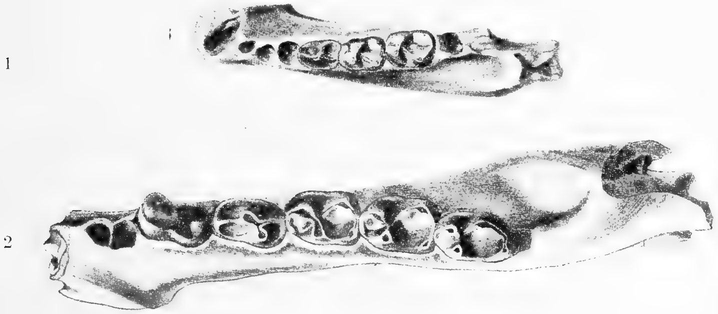

Fig. 70. Lower jaws and teeth of *Protoadapis*. After Stehlin.

1. Left ramus of the lower jaw of *Protoadapis brachyrhynchus*. Natural size. Phosphorites, Prajons (Lot). After Stehlin.
2. Right ramus of the lower jaw of *Protoadapis recticuspidens*. Lower Eocene (Yprésien), France. Three times natural size. After Stehlin.

The existence in the Eocene of Europe of other genera (e. g., *Plesiadapis*, *Anchomomys*) that exhibit structural affinities with the primates of the Eocene of America tend to support the hypothesis that these two "Entwicklungsherden" are divergent derivatives of a Paleocene or Upper Cretaceous common stock, of uncertain geographic location.

In another passage of the 1915 paper cited above, the writer said (p. 423): "The oldest forms of *Pelycodus*, which have recently been described by Doctor Matthew,[1] have extremely primitive tritubercular upper molars, without any posterointernal cusp, and they have a pattern which, according to accepted principles of dental evolution, is structurally ancestral to the two divergent lines seen in the Notharctinæ and Adapinæ."

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[1] 1915, Bull. Amer. Mus. Nat. Hist., XXXIV, pp. 429–483.

To this statement Dr. Stehlin very rightly replied in substance (p. 1519) that even in the oldest representatives of the Notharctidæ the peculiar family characteristics of the upper and of the lower molars were already present in an incipient stage which carried them out of the direct line of ancestry of the Adapidæ. While the justness of this criticism must be fully acknowledged it may be affirmed that the writer never regarded any known member of the Notharctidæ as genetically and directly ancestral to the Adapidæ. What the original passage intended and should have said was that the earliest members of the Notharctinæ had a pattern of the upper molars, which, according to accepted principles of evolution, *approached* the common structural ground-plan "of the two divergent lines seen in the Notharctinæ and Adapinæ." This common structural ground-plan, doubtless of Paleocene age, is also approached on the part of the European Eocene lemuroids by *Adapis rütimeyeri* (especially the specimen figured in Dr. Stehlin's Taf. XXI, fig. 31), and from another direction by *Anchomomys pygmæus* (*op. cit.*, Taf. XXII, fig. 11).

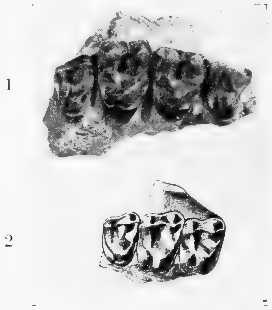

Fig. 71. Comparison of the upper molars of the oldest known American and European species of Adapidæ.

1. *Pelycodus ralstoni.* Amer. Mus. No. 16089. Lower Eocene Sand Coulée beds, Clark's Fork Basin, Wyoming. × $\frac{3}{1}$.
2. *Adapis rütimeyeri.* After Stehlin. Middle Eocene (Upper Lutétien), Egerkingen, Switzerland. × $\frac{3}{2}$.

It has been noted above (pp. 60, 149) that the writer in 1915 attempted to connect the divergent structural modifications in the dentition of the Adapidæ and the Notharctidæ with progressive differences in the methods of mastication, so that the primitive structural plan or heritage came to be disguised by adaptive or cænotelic differences. In commenting on this idea Dr. Stehlin says (1916, p. 1520):

> Gregory glaubt die Structurdivergenzen, welche zwischen dem Adapiden und dem Notharctidengebiss bestehen, beruhen auf Unterschieden im Kaumechanismus und meint, wenn ich mir hievon Rechenschaft gegeben hätte, wäre mein Urtheil über die Beziehungen von Adapis zu den Notharctiden anders ausgefallen. Diese Bemerkung meines geschätzten Critikers ist mir unverständlich. Welches auch der Grund jener Structurdivergenzen sein mag, sie sind nun einmal Thatsache, haben eine bestimmte Zeit gebraucht, um sich herauszubilden und sind bei der Reconstruction des Stammbaumes zu berücksichtigen. Die Divergenz der Stammlinien muss unter allen Umständen bis an den Zeitpunkt zurückgeschoben werden, wo die Divergenz der Gebissstructuren deutlich wird. Das ist die sehr einfache Logik meiner Ausführungen und ich denke kaum, dass sich dagegen etwas Stichhaltiges einwenden lässt. Auf Gregorys Ansichten über den Zusammenhang von Kaumechanismus und Gebissstructur werde ich unten noch zurückkommen.

The question as to the precise correlations between diverse methods of mastication and corresponding modifications of the dentition has already been discussed (p. 149). With regard to the divergence of the two groups in question, the fact remains that in the Viverridæ, Mustelidæ, Procyonidæ, Canidæ, we have examples of families, each of which preserves a characteristic ground-plan of skull structure, more or less divergently modified in accordance with considerable differences in the jaws and in the muscle areas and associated with wide differences in the dentition. Having many such instances in mind the writer felt that the fundamental agreement in skull structure between *Adapis* and *Notharctus* indicated a common origin of the two subfamilies, that from an evolutionary and taxonomic viewpoint the agreement in skull structure outweighed, for the moment, the divergence in the dentition, as it does in the families above cited. For the rest, when Dr. Stehlin states that: "Welches auch der Grund jener Structurdivergenzen sein mag, sie sind nun einmal Thatsache, haben eine bestimmte Zeit gebraucht, um sich herauszubilden und sind bei der Reconstruction des Stammbaumes zu berücksichtigen," he formulates an unassailable verity; and when he proclaims that "Die Divergenz der Stammlinien muss unter allen Umständen bis an den Zeitpunkt zurückgeschoben werden, wo die Divergenz der Gebissstructuren deutlich wird," he will encounter opposition from no one.

Dr. Stehlin's Concept of "Family"

The many striking differences in the dentition and skull of the Adapinæ and Notharctinæ which have been noted in the preceding pages will no doubt be judged by many authorities to justify Dr. Stehlin's arguments (1912, pp. 1287, 1290; 1916, pp. 1518–1520, 1538–1540) for keeping the Adapidæ and Notharctidæ as distinct families. But, before discussing this subject, it will be necessary to consider the different viewpoints of Dr. Stehlin and the present writer with regard to the content of the term "family" and with regard to the general aims and best methods of zoological classification.

To Dr. Stehlin a "family" of Eocene mammals apparently means a small group of extinct genera, founded chiefly on dental characters, but having in common such a strongly marked pattern of the whole dentition that there can be no doubt that they are more closely related to each other than to any other genera; the genera and species of such families are recorded during successive formations of the Eocene of Europe and North America, but their palæontological connections with modern families are not known. Dr. Stehlin refuses to assign to these families any genera as to the affinities of which his minute analysis has raised in his own mind the slightest doubt. He evidently aims to have his "families" represent an irreducible residuum, remaining after the elimination of the deceptive resemblances brought about by analogous evolution, and purged so far as possible of all hypothetic speculation and mental restoration of defective evidence. He develops at great length the vast complexity and difficulty of the problem of the Eocene Primates, sets apart a few small groups as ultimate categories, leaving the rest "incertæ sedis," and virtually declares the futility of further efforts, except as to minor problems, until the Paleocene records of Asia shall become available.

Dr. Stehlin appears to regard any more comprehensive groups, such as Dr. Wortman's "Neopithecini" and the writer's "Tarsiiformes" as mere "Rubriken" (1916, p. 1541), hypothetical and ephemeral guesses of no enduring value; although at the end of his memoir he himself speaks provisionally of vague superfamily assemblages, which he calls "Entwicklungsherden," designating them not by systematic names but by numbers and by the name of the continent wherein they are supposed to have originated.

Value of the "Linnæan System" of Classification

Dr. Stehlin's general attitude toward the so-called Linnæan system of classification and toward the synthetic or interpretative categories which he calls "Rubriken" is stated in the following passage:

> Die Linné'sche Begriffshierarchie ist und bleibt ein unvollkommenes Mittel, um das natürliche System der Tiere, d. h. den Stammbaum, zur Darstellung zu bringen. Da wir sie, aus practischen Gründen, gleichwohl nicht entbehren können oder nicht entbehren wollen, sollten wir wenigstens darauf bedacht sein, sie so zu gestalten, dass sie die phylogenetischen Zusammenhänge nicht verschleiert und dass sie da, wo diesselben noch nicht klar gelegt sind, der weiteren Forschung möglichst wenig vorgreift. Das heisst mit andern Worten, wir sollten es vermeiden, Rubriken aufzustellen, die sich nicht genügend motivieren lassen, oder aber Formen umfassen, von denen sich noch gar nicht nachweisen lässt, dass sie der Rubrikdefinition entsprechen. Rubriken dieser Art sind aber sowohl Gregorys Tarsiiformes als Wortmans Anaptomorphinæ, Omomynæ, Palæopithecini und Neopithecini, Osborns Mesodonta sowohl als Winges Tarsiidæ (Stehlin, 1916, p. 1541).

The present writer, on the contrary, regards the Linnæan system of classification, with all its imperfections, as a priceles heritage, an invaluable organ of learning and research. If the entire history of an "Entwicklungsherd" were known it would be possible to record in detail the anatomical characters of the ancestral genera, to trace step by step the divergent modifications among many phyla and to describe fully the final stages of each; but, without the aid of symbols or representative classifications, life would be too short either to complete such a history or to read it; and the prerequisite identifications of the material would be greatly hampered. Palæontologists, as well as all other investigators, labor under economic and psychological conditions which compel them to use systems of symbols in which a part represents the whole. The Linnæan system is a diagram, an outline, an invaluable mnemonic device, for the purpose of suggesting the more complete concept which the investigator has won for himself and is endeavoring to convey to other minds. More specifically, the functions of the Linnæan system as understood by the present writer are as follows.

(1) It serves as a preliminary index to the cumulative record of anatomical observations in the literature of the subject.

(2) It aims to express successive degrees of homological resemblances and divergences between the organisms classified. In general, the nearer they stand in the system, the greater is the number of homological resemblances between them; this, of course, implies that the observer has endeavored to discover and to discount such resemblances as have been produced by convergent evolution. In so far as it succeeds in expressing degrees of homological resemblances and differences, the Linnæan system at the same time symbolizes the degrees of consanguinity or kinship of the creatures thus classified.

(3) The Linnæan system in its entirety stands in general for the progressive loss of primitive characters (expressed in the definitions and diagnostic characters given for each group), as we pass from the more general and inclusive groups to the groups of lower rank, as in this series.

Vertebrata
    Amniota
        Mammalia
            Placentalia
                Primates
                    Lemuriformes
                        Lemuridæ
                            Lemurinæ
                                Lemur
                                    L. mongoz

This aspect of the Linnæan system is sometimes neglected by those specialists who prefer to raise the groups which they have intensively investigated to higher rank, rather than to keep them in due relation with the more inclusive groups of other investigators.

(4) Another function of the Linnæan system which has been greatly emphasized by some modern authors is that of indicating direct ancestral relationship of earlier to later forms which are placed by these authors in the same family, even though they may represent widely different stages of evolution. The result is that several very ancient genera which may be closely allied through the possession of many important common characters will be widely separated in such systems, being placed in the different modern families to which they are supposed to have given rise.

Naturally, the application of the Linnæan system in practice is beset by many difficulties arising either from the poverty of the available material or from its relative abundance. In both cases the chief obstacle to the recognition of natural groups and of true evolutionary phyla is the facility with which nature produces similar adaptations in related, and only to a somewhat less degree in widely removed, phyla.

The general, though tardy, recognition of the deceptive effects of analogous evolution has inspired such a degree of caution in many palæontologists that some refuse to admit the relationship or consanguinity of later to earlier forms unless a practically complete series of intermediate forms be known. In the lack of such complete series those who have an almost unlimited faith in the deceptive powers of analogous evolution confess their own inability to distinguish analogous from homologous characters; they will, therefore, probably read with considerable scepticism the opinion of the present writer that the ability to distinguish analogous from homologous characters grows with practice and is conditioned, first, by the extent of the investigator's experience in recognizing such differences among other orders of vertebrates, and, secondly, by the thoroughness of the investigator's knowledge of the divergent trends of evolution in the particular group under examination.[1]

After the descendants of a common stock diverge from it they frequently evolve many parallel, independently acquired, but in a sense homologous characters, and such resemblances in independently acquired homologous characters are usually more numerous between nearly allied stocks than between those which diverged at a very remote epoch. So that "analogous evolution" does not always tend to obliterate ancestral relationships and bring about false associations.

Reasons for Assigning Adapinæ and Notharctinæ to the Same Family

Fully recognizing the value and interest of Dr. Stehlin's conclusions, the weight of his authority, and the likelihood that his finely divided "families" will be approved and adopted by other investigators who favor analytical rather than synthetic classifications, the present writer will cheerfully abandon his own classification of the Lemuroidea[2] whenever, and as soon as, it shall be shown to be erroneous. After prolonged and repeated consideration, however, it has seemed that the groups therein recognized are to a greater or less extent "natural" groups and that they are reasonably free from intrusive or convergent admixtures. The classification is also in historic continuity with the main line of anatomical and systematic research on the Lemuroidea and the characters selected as diagnostic have been, so far as possible,

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[1] If the writer fails in the problem in hand to distinguish between analogous and homologous characters it will be in indication of his own incompetence rather than of lack of opportunity for acquiring the necessary experience. In the Department of Vertebrate Palæontology in this Museum the phenomena of convergence and divergence have been studied by a number of investigators for many years past, with the generally growing conviction that in most cases the deceptive effects of analogous evolution may be recognized by sufficiently thorough and comprehensive search for the divergent trends of evolution, and by a constant endeavor to discover the adaptive "purpose," as it were, of the observed changes in structure.

[2] Bull. Geol. Soc. Amer., XXVI, pp. 432–438.

verified by the writer. It is therefore retained, with some modifications, in the present paper, as a convenient mnemonic device, as a record of conclusions, and as a working hypothesis for further investigation.

In estimating the degree of homological agreement or affinity between two given forms, it seems important to remember that the "whole is greater than any of its parts" and that, as Linnæus is reported to have said, "the genus makes the character, not the character the genus." To the writer a sufficient reason for regarding two animals as divergent representatives of a single family is *not* that they resemble each other in any one character or in several characters taken independently, but that in all views of the skull and skeleton a common general stamp or underlying "family resemblance" is revealed, beneath many conspicuous differences in detail.

In any such case, the "underlying family resemblance," the effect of the whole, is apt to be lost as soon as we begin to record at great length the details that differentiate the skulls from each other. But each of these important details should be viewed in its correct and due relation to the organism as a whole and especially should such differences be considered as an expression of specific functions and habits, which differentiate the genera in question both from each other and from their common ancestor. In the case of *Adapis* and *Notharctus* the "family resemblance" is indicated in the accompanying illustrations of three aspects of the skull. The skull of *Notharctus*, as a whole, in general appearance and in fundamental construction, is closer to that of *Adapis* (*Leptadapis*) *magnus* var. *leenhardti* (Stehlin, 1912, pp. 1278, 1279, figs.) than to that of any other known primate outside of its own subfamily. There is, in fact, a striking agreement in general proportions of the face and brain-case, in the gentle inclination of the face to the basicranial axis, in the relatively slight expansion of the brain-case, in the sharp constriction of the skull behind the orbits, in the powerful build of the zygomata, and in the prominence of the sagittal and lambdoidal crests.

When the "underlying family resemblance" mentioned above is analyzed into its component parts, it yields a considerable list, comprising some thirty-odd characters of the skull and dentition (see page 184 above). Of these, eight of the more fundamental ones are preserved in several other families (Lemuridæ, Indrisidæ, etc.) which the writer believes to be derived from the ancestral Adapine-Notharctine stock, and which may therefore be considered as superfamily characters (listed under Lemuriformes); the remainder, comprising about twenty-five characters exclusive of those of the limbs, are diagnostic for the Adapidæ as here defined.

Important evidence for the relatively close relationship of *Adapis* and *Notharctus* to each other and to the modern Lemuridæ and Indrisidæ rather than to the Tarsiidæ and the higher primates is afforded by the construction (see pages 161–178 above) of the whole basis cranii, and especially of the auditory region, for *Adapis* and *Notharctus* preserve with slight modifications what is regarded by the writer as the primitive condition of the auditory region for the whole lemuriform series. The enclosure of the tympanic annulus by the expanded periotic bulla, the topographic relations of the osseous carotid canal and its stapedial branch to the cochlea, the contact between the bulla, the pterygoid plate of the alisphenoid and the entoglenoid region of the squamosal, the substantial identity in the positions and relations of nearly all the foramina of that region are all judged by the writer to outweigh in phylogenetic and systematic significance the moderate divergence in the dentition in the two subfamilies.

The assignment of a high systematic value to the characters of the auditory region is a natural result of the fruitful investigations of Winge, Forsyth Major, van Kampen, Stehlin, and others upon the morphology of this region in primates and in many other orders of mammals. For some years past the writer has applied and verified their results especially in the study of the marsupials, creodonts, Fissipedia, Pinnipedia, perissodactyls and primates, and in the course of these observations the high diagnostic value of the whole basicranial region has constantly been noted. Of course there are certain exceptions, certain apparently sudden departures from type, as in the cases of *Megaladapis*, *Palæopropithecus* and the Lorisiformes, which will be considered in detail in later sections of this work but, on the whole, the basicranial region and especially the auditory region often affords a sure clue to relationship, even when the dentition of divergent phyla is so diverse in character that it retains little evidence of their relatively close kinship.

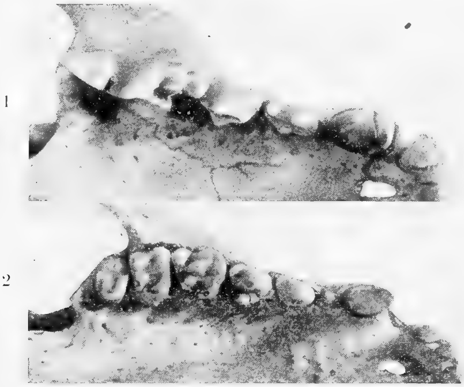

Fig. 72. Extremes of molar construction in the Viverridæ.

1. *Bdeogale jacksoni.* Amer. Mus. No. 36024. × [illegible].
2. *Cryptoprocta ferox.* Amer. Mus. No. 34861. × [illegible].

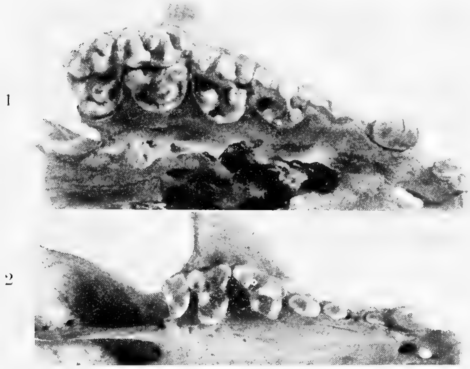

Fig. 73. Extremes of molar construction in the Procyonidæ.

1. *Bassariscus astutus flarus.* Amer. Mus. No. 10650. × [illegible].
2. *Aelurus fulgens.* Amer. Mus. No. 32650. × [illegible].

Several striking instances of this kind are afforded by the families of the Carnivora Fissipedia, especially the Viverridæ and the Mustelidæ. A selection of skulls representing fifteen genera of recent and extinct Viverridæ has been closely studied and it has proved possible to follow the divergent evolution of the dentition in many phyla. Between the extreme forms, *Cryptoprocta* and *Bdeogale*, the differences in the dentition are of so pronounced a character that at first sight the association of these genera in the same family seems unnatural; for in *Cryptoprocta* the dentition is cat-like with blade-like carnassial teeth and much reduced single upper molars, while in *Bdeogale* the carnassials are submolariform and the molars are of the low-cusped omnivorous type. (Figs. 72, *1*, *2*.) A markedly different style of dentition is exhibited by the Ichneumon (*Herpestes*) in which the narrow transversely widened molars seem to be adapted perhaps for snake-eating. But amid all this diversity in the dentition the whole basicranial region remains singularly constant in essentials throughout the family.

Among the Mustelidæ it has also proved possible to work out the divergent phyla from a study of the dentition and skulls of recent and extinct types; and, here again, the extreme forms, *Latax* and *Putorius*, differ so widely in the dentition that if they were not connected by many intermediate genera it is unlikely that modern systematists would allow them to remain in the same family. But the basicranial region throughout the family is essentially identical, although differing in minor characters such as the size and degree of inflation of the bulla, the development of accessory sinuses in the surrounding parts, the partial deflation and flattening of the bulla.

Perhaps even more striking is the difference in the dentition between *Ælurus* and *Bassariscus*, which are referred to the same family and reveal their relatively close relationship in the construction of the basicranial region. *Æluropus*, which according to Lankester[1] and Lydekker is also a member of the same family, as shown by many important characters, differs from the procyonid type in the region of the bulla only in the flattening of the bulla, a difference which can be matched between two genera of the Mustelidæ (*Latax*, *Zorilla*) or of the Lemuridæ (*Megaladapis*, *Microcebus*).

Among the primates themselves it will be recalled that the whole platyrrhine series have one characteristic basicranial pattern, while the Catarrhini, including the Old World monkeys, baboons, apes and man, have another which is divided into two well-marked sub-types: first, that which is characteristic of the Cercopithecidæ and the Hylobatidæ and, secondly, that which is characteristic of the Great-ape-Man group. Among the primates the evidence offered by these characteristic basicranial patterns, as seen from the ventral surface, is fully substantiated by the evidence of the encephalic surface of the whole under side of the skull as will be shown later.

A third reason for associating *Adapis* and *Notharctus* in the same family is as follows: the detailed studies of the two groups which have already been made, besides revealing the divergent tendencies in them and the numerous fundamental characters which they still retain in common, have also made it possible, by projecting backward the divergent trends to an assumed common origin, to reconstruct with reasonable probability the food habits and general structure of the common ancestral stock,[2] as described below (p. 229). That such a common ancestral stock existed is plainly indicated by the evidence at hand. When and if discovered in the Paleocene of Europe, Asia, or North America, it will surely establish the already patent fact that there is at least no greater degree of structural divergence between the extremes representing *Adapis parisiensis* and *Notharctus crassus* than there is between *Megaladapis insignis* and *Microcebus* which are commonly placed along with many genera of intermediate character in a single family, Lemuridæ.

After all this has been said in favor of uniting *Adapis* and *Notharctus* in the same family Adapidæ,

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[1] 1901, Trans. Linn. Soc. Zool., (2) VIII, p. 171.

[2] Such reasoning will of course not appeal to the advocates of "l'école des faits," who disapprove of reconstructions and prefer to await the discovery of complete material. The discerning student ought to be able to distinguish plaster from bone and inference from observation, but to make perfectly sure the present writer has always tried to label consistently the two kinds of material.

as has been done by Cope, Wortman, Schlosser, and the writer, it must readily be admitted that the important question is not whether the marked divergences of the European and American genera are to be symbolized by the subfamily termination "-inæ" or by the family ending "-idæ"; the real question is, rather, whether *Adapis* and *Notharctus* are structurally more nearly related to each other than either are to *Tarsius*, to *Tetonius*, and to *Necrolemur*. As to this, if we admit the force of the foregoing arguments, the skull characters of the last three genera show that they are rather widely removed from the *Adapis-Notharctus* group (see p. 230).

RELATIONS OF NOTHARCTINÆ AND ADAPINÆ WITH LEMURIDÆ, AND A DISCUSSION OF THE PROBABLE ORIGIN OF THE LEMURIDÆ

DENTITION

Preliminary Outline of the Divergence in the Dentition

It has already been noted that even the earliest members of the Notharctinæ are at once excluded from direct ancestry to the Adapinæ by the possession of certain specializations in the dentition described by Stehlin. The most general comparison of the dentition in the Notharctinæ, Adapinæ and Lemurinæ may be tabulated as follows.

	NOTHARCTINÆ	ADAPINÆ	LEMURIDÆ
Upper canines	Progressively caniniform	Stout dagger-like	Compressed
Lower canines	" "	Short, sub-premolariform	Procumbent, incisiform styliform
Lower incisors	Erect, spatulate	Erect, shovel-like	Procumbent, styliform
Posteroexternal cusp on p^4	Very late and feebly developed	Always well developed (except *A. sciureus?*)	Present only in 1 genus (*Myoxicebus*)
Hypoconid and talonid on p^4	Not yet developed	Well-developed	Usually degenerate (present in *Myoxicebus*)
True hypocone (from cingulum) on m_1 m_2	Absent	Well-developed	Absent (or degenerate)
Mesostyles on m^1 m^2	Progressive	Never developed	Never developed [1]
Pseudohypocones	Progressive	Never developed	Never developed
Entoconids on m_1 m_2	Progressive	Retarded	Degenerate
Metacristid on m_1 m_2	Barely indicated	Progressive	Often widely displaced posteriorly
Protoconules and metaconules	Originally distinct	Less distinct	Degenerate or absent
P_1	Present	Present, often small and crowded	Lost
P_2	Normal	Normal	Enlarged and subcaniniform

These facts are provisionally interpreted by the writer as follows.

(1) The dentition of the Notharctinæ, apart from a few well-marked specializations (pseudohypocones, mesostyles, etc.), represents a more ancient and primitive early Eocene type.

(2) The dentition of the Adapinæ, on the other hand, is on the whole a progressive derivative from the hypothetical common ancestors of the Adapinæ and Notharctinæ.

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[1] Except in *Megaladapis insignis* Major.

(3) The dentition of the Lemuridæ is for the most part a degenerate derivative of that of the most primitive Adapinæ such as *Adapis sciureus.*

(4) The "lemurine specialization" of the lower incisors and canines is correlated with the special development of the tongue.

Origin of the Peculiar Front Teeth ("Vordergebiss") of Lemurs. Evolutionary Processes Illustrated

Plates LII–LVIII

The upper INCISORS of *Notharctus* and its allies are not reduced as they are in most Lemuridæ; the central upper incisors have a compressed oval crown with a more or less elongate edge, the crown being supported by a long cylindrical procumbent root. The lateral upper incisors are much smaller, the crown convex externally, obtusely pointed, flattened or concave on the lingual faces. The upper incisors of *Adapis magnus* (Stehlin, 1916, pp. 1254, 1255) were fundamentally similar but the central incisors were wider. In *Chirogaleus furcifer* somewhat similar upper incisors persist although the medial pair are separated by a considerable diastema. The separation of the opposite incisors, the straightening of the opposite tooth rows and the truncate form of the premaxillæ are probably all connected with the great size and protrusile character of the tongue in lemurs. The upper incisors in Notharctinæ and Adapinæ surrounded the end of the tongue, which was doubtless not yet so thick and protrusile as it is in the Lemuridæ. The lingual surfaces of the upper incisors, with their pits and ridges, were doubtless more nearly related functionally with the tongue than with the lower teeth. The lower incisors have short-crowned, more or less truncate or spatulate crowns, whereas in existing lemurs the incisors are extremely long, compressed, styliform, and very sharply procumbent.

The upper CANINES in *Notharctus* males are round in section and subcaniniform, whereas in lemurs they are compressed with a very sharp posterior edge. The lower canines of *Notharctus* and *Pelycodus* males are caniniform; in females they have shorter crowns and an internal cingulum, so that they are somewhat premolariform; in *Adapis rütimeyeri* (?female, Stehlin, 1912, p. 1268, fig.) the small canine has a short crown and a strong internal cingulum; this apparently approaches the type of canine, intermediate in form between the lateral incisors and the first premolars, from which Dr. Stehlin believes (1916, p. 1531) that the canines, not only of *Lemur* but also those of *Adapis* and *Notharctus*, have been derived. In lemurs the lower canines have been taken over into the incisor series and are long, compressed and styliform, differing from the incisors chiefly in their greater size and width. Thus the lower canines of lemurs do not wear against the upper canines as in the normal mammalian dentition, but, reaching forward to the anterior end of the jaw, they lie below the two upper incisors from which they are more or less separated by the massive tongue; whereas in the Notharctinæ the lower canines, being erect and caniniform, do not reach the upper incisors but articulate in front of the upper canines, as in primitive mammals.

The FIRST LOWER PREMOLAR of both Notharctinæ and Adapinæ is small, simple and nearly erect; it articulates between the first and second upper premolars; in the lemurs this tooth has disappeared entirely, as well as the first upper premolar.

The SECOND LOWER PREMOLAR of Notharctinæ is likewise very simple and premolariform; it articulates between the second and third upper premolars. In the lemurs, on the other hand, the anterior lower premolar, which is homologous with the second lower premolar of *Notharctus,* is a large, compressed, triangular, sharp-edged, cutting, piercing tooth, which at first sight looks like the lower canine; but it articulates behind the upper canine like a premolar and not in front of the upper canine like a true lower canine.

Thus the subfamily Notharctinæ is distinguished from the family Lemuridæ by the following primitive characters: LOWER INCISORS SPATULATE OR TRUNCATE, NOT PROCUMBENT AND STYLIFORM; LOWER CANINES CANINIFORM, NOT INCISIFORM OR STYLIFORM; p_1^1 PRESENT; P_2 SMALL AND PREMOLARIFORM, NOT ENLARGED, COMPRESSED, TRENCHANT OR CANINIFORM.

Fig. 74. Lower jaws of *Notharctus* and *Lepilemur*. Lateral aspect. Natural size.

1. *Notharctus venticolus*. Amer. Mus. No. 14655. Lower Eocene, Lost Cabin beds, Wind River basin, Wyoming. Natural size.
2. *Lepilemur mustelinus*. Amer. Mus. No. 31251. Natural size.

Dissection of a lemur shows that all the lower and side teeth are pressed forward and outward by the greatly enlarged tongue, which settles into the interstices between the teeth and fills the concavities of their lingual surfaces. Especially the enlarged lower p_2 is pressed forward against the rear of the upper canine while the incisors and canines are pressed forward and extended beneath the tongue. The small p_1 of the ancestral lemuroids, which is nearly always a feeble tooth, has been crowded out of existence. The sublingua seems to have little to do with this peculiar modification of the front teeth, since it lies behind them above the dorsal slope of the symphysis.

Lemurs are said to feed on fruits, buds, insects, eggs and small birds; the procumbent lower front teeth may be used as scrapers as in *Myoxicebus*[1]; doubtless the large upper canines and lower p_2 are used in puncturing fruits, eggs, and the skulls of young birds; the motion of the jaw is chiefly orthal, with some ental movement. In correlation with the dwindling of the lower canines the mandible in typical Lemuridæ becomes shallow and relatively weak, with a flat lower border and reduced muscle areas, the zygomatic arch and temporal crests also become weak, although the anterior part of the masseter below the orbit remains strong.

In discussing the "Vordergebiss" (incisors and canines) of the Adapidæ and other primates Dr. Stehlin (1916, p. 1529) says:

> Eine sehr verbreitete, man kann sagen die herrschende, Ansicht geht dahin, die caniniforme Ausbildung des Mandibularcaninen, welche innerhalb der Primatenordnung das Hauptcharacteristicum des 'Affentypus' ist, sei bei den Säugetieren im allgemeinen ein schlechthin primitiver Zustand. So urtheilt, in der uns hier im speciellen beschäftigenden Frage, zum Beispiel Gregory, wenn er das Vordergebiss von Adapis im Vergleich zu dem von Lemur kurzweg als primitiv hinstellt.

The writer is unable, however, to find any passage in his own writings containing anything at all like the view which Dr. Stehlin erroneously attributes to him. The writer certainly never represented

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[1] Elliot, D. G., 1912, I, p. 129.

the "Vordergebiss" of *Adapis* "kurzweg als primitiv." He said only that the small insectivorous forms of the genus *Pelycodus* have the primitive dental formula of $I\frac{2}{2}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$ (1915, p. 439) and that *Notharctus* had not assumed the lemurid specialization of the incisors, canines and anterior premolars (p. 425).

Three possible views may be held as to the exact character of the canines in the common ancestors of the Notharctinæ and Adapinæ:

(1) they may have been subcaniniform as they are in the males of *Pelycodus frugivorus;*

(2) they may have conformed to the description of the primitive primate canines given by Dr. Stehlin (1916, p. 1530): "ursprünglich nicht verstärkt und caniniform, sondern brachyodont und structurell ein Mittelding zwischen vordern Praemolaren und hinteren Incisiven;"

(3) they may have been somewhat between (1) and (2), but nearer to (1), as in the canines of the female of *N. osborni.*

In *Adapis parisiensis* the upper canines and the first three premolars are more or less similar in form and they are crowded together into a continuous series, with sharp cutting edges and marked internal cingula; the incisors are very compressed and trenchant. In the lower jaw the canines have a short low crown of sub-premolariform shape, the premolars are crowded and the incisors have wide-edged crowns. This condition of the front teeth is associated with a fairly advanced stage in the evolution of the posterior premolars and molars and with the inferred habit of eating fruit covered with resistant fibrous rinds. The writer believes that this condition is decidedly more specialized than that of the Notharctinæ, especially the early forms (see pages 124–127), in which the incisors were of small size, with not widely expanded tips, the canines neither fully caniniform or premolariform, but much larger than the incisors and anterior premolars, the first premolars very small and separated by a diastema from the canines. These conditions were approached in *Adapis sciureus* (cf. Stehlin, 1916, p. 1515, fig.) which is older than the typical species of *Adapis* and in the opinion of the writer is much more primitive. In this very small and primitive species, the lower incisors as shown by their alveoli were small, the canines were relatively large, single-fanged, straight-crowned, upstanding teeth, with an obtusely conical tip, a strong internal cingulum and well-marked crista anterior; the crown is widened at the base much more

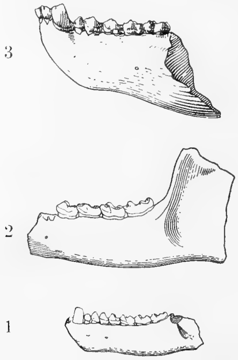

Fig. 75. Lower jaws of *Adapis*. Natural size. After Stehlin.

1. *Adapis sciureus.* Lower Eocene (Lutétien), Egerkingen, Switzerland.
2. *Adapis priscus.* Lower Eocene (Lutétien), Egerkingen, Switzerland.
3. *Adapis parisiensis.* Phosphorites (? Middle Eocene), France.

than that of p_1; it is separated from the small p_1 by a slight diastema. P_1, p_2, p_3 increase rapidly in size; there is a sudden increase in size and complexity as we pass from p_3 to p_4, and an equally wide structural gap between p_4 and m_1; m_2 is markedly wider than m_3. All these characters joined to the stoutness of the jaw impart a primitive facies, suggestive of the conditions in *Pelycodus frugivorus* and many other Eocene and Paleocene mammals, which according to Dr. Stehlin's hypothesis must all be specialized in these characters. In *Adapis rütimeyeri* also (cf. Stehlin, 1916, Taf. XXI, fig. 24), which has a very primitive type of molars, the lower canines (as shown by the alveolus, cf. Taf. XXI, fig. 24) were very much larger than p_1. In *Pronycticebus*, which has an extremely primitive type of premolars and molars, the upper canines were decidedly larger than p^1. (Fig. 81.) In this primitive genus with comparatively well developed canines the zygomatic arches are stout, while in its more specialized *Tarsius*-like relatives with very small canines the zygomata and jaw are weak.

Dr. Stehlin is so sure of his conclusion, cited above, that he says (p. 1531):

> Es ist mir keine Thatsache bekannt, welche mit dieser meiner Auffassung im Widerstreit stünde; wohl aber lassen sich solche namhaft machen, welche sie noch besser zu stützen vermögen.
>
> Vorerst ist von Belang, dass die von mir als ursprünglich betrachtete Einrichtung des Vordergebisses nicht blos ein theoretisches Postulat, sondern schon thatsächlich nachgewiesen ist.

He then cites the condition of the front teeth in *Parapithecus* Schlosser from the Upper Eocene or Lower Oligocene, a catarrhine primate with primitive molars and canines intermediate between the incisors and the anterior premolars. But it must be objected that *Parapithecus* probably belongs to a very different section of the primates from that of any of the known lemuriform Eocene primates; it may very well be true, as the writer has elsewhere maintained,[1] that in the catarrhine series the typical caniniform and tusk-like canines have been derived from short canines; but the marked reduction of the ante-molar formula in *Parapithecus* indicates that even although this genus may be primitive as compared with the Simiidæ it is very far from primitive as compared with the Lower Eocene lemuroids of the subfamily Notharctinæ which retain the primitive formula of $I\frac{2}{2}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$ and in which the dentition as a whole approaches that of the most primitive Paleocene representatives of the Insectivora, Carnivora, Creodonta, Condylarthra, Taligrada and other primitive orders.

A differentiation of the canines both from the incisors and the premolars had occurred even in the Permian Therocephalia and Cynodontia and in the Mesozoic mammalian orders Protodonta, Triconodonta, Trituberculata and Polyprotodontia. In these very early mammals[2] the lower canines seem to be associated functionally with the incisor series and yet they are fully caniniform and much larger than either the incisors or the first premolars. The upper canine being the first tooth behind the premaxillary suture and nearer the fulcrum would probably be subjected to different mechanical conditions from those affecting the incisors. In referring to the incisors and caniniform canines of early Eocene mammals Dr. Stehlin assumes (1916, p. 1529) that it is much more probable that all these ancient forms were not primitive but early specialized. From the evidence supplied by extensive collections of Paleocene and Eocene mammals in this Museum, however, one might equally well infer that in the remote ancestors of many placental orders the lower canines were subcaniniform and much larger than either the incisors or p_1; such teeth are borne in a fairly stout mandible, not elongate distally, with a curved lower border, a stout backwardly prolonged angular process; the zygomata are stout, the braincase small, with well-marked muscle areas.

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[1] See the discussion of this genus in Part II of the present series, 1916, Bull. Amer. Mus. Nat. Hist., XXXV, pp. 280–284.

[2] See the figures given in Osborn, H. F., 1907, Evolution of Mammalian Molar Teeth, pp. 19–30. New York.

The evidence offered by the milk teeth of *Adapis* (*op. cit.* p. 1532) for the view that the primitive canine was brachyodont and much more premolariform than in *Pelycodus frugivorus* has in the writer's judgment but little bearing on the question, because in spite of traditional reliance on the Biogenetic Law, it remains to be proved in each case whether the milk dentition is more primitive than the permanent dentition or whether it is specialized for its own purposes as larval structures frequently are. Moreover the total inability of the young to defend themselves is in harmony with the inoffensive character of the deciduous canine.

Dr. Stehlin (*op. cit.*, pp. 1531, 1532) cites the mode of evolution of the front teeth in the Eocene perissodactyls and artiodactyls for the purpose of showing that abnormal types of "Vordergebiss" are always derived from forms with low, small and subpremolariform canines, as in the Oreodontidæ, etc. To this it may be replied: first, that as shown by their astragalus the oldest bunodont Artiodactyla of the Lower Eocene [1] were already fairly well specialized in the Artiodactyl direction and that until their Paleocene and Upper Cretaceous ancestors be known it will not be safe to affirm that the small canines of Eocene Artiodactyls are a primitive and not a retrogressive character; indeed, the compressed form of the premolars, the elongate slender ramus, and the cropping character of the incisors all appear to the writer rather to be herbivorous specializations from a primitive type with stouter, shorter rami, less compressed premolars and less reduced canines. Secondly, it does not seem necessary to go outside of the Adapidæ themselves for information concerning the early form of the canines in that family. As already noted in the Lower Eocene species *Pelycodus ralstoni* and *P. frugivorus* of the Notharctinæ and in the Lutetian species of the Adapinæ, namely *Adapis sciureus* and *A. rütimeyeri*, the lower canines, although sharing some characters with the premolars, are on the whole more caniniform than premolariform and were much larger than the first premolar.

The peculiar specialization of the tongue and lower front teeth in the Lemuridæ, which is remotely paralleled among the ruminants and oreodonts, illustrates several important facts and principles, which have a direct bearing on the problem of the degree of relationship between different groups of Eocene lemuroids and the modern Lemuridæ. The principle of CONVERGENT EVOLUTION BETWEEN ADJACENT TEETH is well illustrated by the fact that the lower incisors and canines are doubtless now much more alike than they were in the remote ancestors. The well-known principle of CHANGE OF FUNCTION involving a no less radical change of form is also illustrated by the incisiform habitus and function assumed by the canines. A corollary of this is the PRINCIPLE OF SUBSTITUTION AND USURPATION; the canine taking the place of a long lost incisor, the second lower premolar performing the functions of a lower canine and usurping the position of the first lower premolar. A corollary of the preceding principle is that the DIRECTION OF EVOLUTION IS SUBJECT TO RADICAL CHANGES, involving the loss of old and the development of new and quite different tendencies. Whatever may have been the precise character of the lower canines, as long as they retained their normal articulating relations with the upper canines they must have been considerably different in form and function from the incisors which they now resemble.

This discussion may be concluded by an impartial summary of the opposing conclusions of Dr. Stehlin and the writer concerning the form of the front teeth in the ancestral Primates and especially in the ancestors of the Lemuridæ.

Dr. Stehlin (1916, p. 1530) rejects the suggestion of the present writer (1915, pp. 424, 425) that the lemurid specialization of the front teeth has been derived from the conditions illustrated in *Notharctus;* he believes that the canines in this genus were too specialized and after long search he can find no well-

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[1] Cf. Sinclair, W. J., 1914, Bull. Amer. Mus. Nat. Hist., XXXIII, p. 271, figs. 3, 4.

proved precedents for such a marked change in the direction of evolution in the dentition; he therefore believes, until further evidence is produced, that the Law of Irreversibility of Evolution here sets a limit to the possibilities of evolution. He will not admit that the canines of any group of Primates were originally caniniform, but holds that they were brachyodont and structurally intermediate between the anterior premolars and the lateral incisors. From such a ground-plan the canine of *Lemur* may be as easily derived as those of *Adapis* and *Notharctus* (p. 1531).

The writer, on the other hand, feels that the Law of Irreversibility is not incompatible with marked changes of function, of form and of the direction of evolution. He concludes that in the Lemuridæ a profound change of form and function in the lower incisors, canines and p_2 has been conditioned in part by the enlargement of the tongue in adaptation to frugivorous habits; that the ancestral Lemuridæ had the lower front teeth not dissimilar to those of *Adapis sciureus*, that is with subcaniniform canines much larger than the first premolar; that all groups of Primates may eventually have been derived from small insectivorous-frugivorous arboreal mammals with subcaniniform canines.

Premolars

Plates LIV, LV

Except for the marked enlargement of p_2 the premolar patterns in the modern Lemuridæ represent for the most part degenerative derivatives of a primitive Adapine type. The upper premolars of the Notharctinæ differ from those of the Lemuridæ as follows:

(1) The Notharctinæ as stated above retain $p\frac{1}{1}$ which have been crowded out in the Lemuridæ. The loss of p^1 provides a space for the reception of the tip of the enlarged p_2; the loss of p_1 permits p_2 to gain wide contact with the upper canine; when therefore diastemata are developed separating p^2 from p^3, as in *Microcebus*, it is a sign that the elongation of the face which has produced the diastema is secondary.

(2) The second upper premolar varies considerably in form in the Notharctinæ. In *N. venticolus* it has two distinct roots and a compressed conical crown; in *N. osborni* ♀ the roots are almost connate and the crown is smaller and less compressed; in the Adapinæ the roots of p^2 also seem to be either united or connate and the tooth is either compressed (*A. parisiensis*) or widened (*A. magnus*). So too in the Lemuridæ p^2 is either a small single-fanged tooth as in the Chirogaleinæ, or it has two roots and a large compressed crown as in *Lepilemur*, *Mixocebus* and *Myoxicebus*.

The second lower premolar, relatively small in the Notharctinæ, is compressed in the typical *Adapis parisiensis*, wider in *A. magnus*. In the very primitive *A. sciureus* it has an obliquely oval crown with an internal cingulum; it could readily be enlarged into the form characteristic of the Lemuridæ which is obliquely asymmetrical and directed forward and upward so as to engage with the posterior face of the upper canine.

The third upper premolar is distinctly premolariform and somewhat like p^4 in all the Notharctinæ and in *Adapis magnus* and *A. rütimeyeri*. In *A. parisiensis* it is compressed and simple. So too, in the Lemuridæ, p^3 is either much like p^4, as in *Mixocebus*, *Myoxicebus*, or it is peg-like and simple, as in *Atililemur*, *Chirogale*, *Myoxicebus;* or compressed conical with two widely separated external roots and with only a slight internal extension, as in *Lemur* and *Lepilemur*. The internal extension of p^3 also exhibits a wide range in form; in *Myoxicebus* it is very large and massive; in *Microcebus* it is practically absent.

A similar range of variation is seen in the structure of p_3 in the Notharctinæ, Adapinæ and Lemuridæ, the whole crown being more or less compressed or widened, and the talonid either very slight or better developed. Thus in the Chirogaleinæ p_3 is very simple, almost peg-like; in *Lemur* and *Lepilemur* it is compressed and pointed.

P^4 in the Notharctinæ is distinguished by the very delayed development of the posteroexternal cusp or metacone, which in the history of the typical Adapinæ appears very early. In *Adapis sciureus*, however, the very retarded condition of the hypoconid of p_4 makes it extremely probable that in p^4 the second external cusp (metacone) if at all differentiated was connate with the paracone. In the Lemuridæ this tooth has usually only one external cusp (exclusive of the parastyle). In *Myoxicebus* (*Hapalemur*), however, there is a large distinct metacone. The presence of a second external cusp in p^4 of *Myoxicebus* thus raises the question whether the single external cusp in the other Lemuridæ is a primitive or a secondary character. The extremely simple form in *Microcebus* is accompanied with other specialized characters and is no doubt secondary. In view of the evidence tending to show that p_4 also is partly degenerate in many Lemuridæ it seems probable that *Myoxicebus* (*Hapalemur*) alone among the Lemuridæ has retained the primitive posteroexternal cusp of p^4.

The internal or "protocone" extension of p^4 is also highly variable, being very wide and massive in *Myoxicebus*, almost absent in *Microcebus*, well developed in *Lemur*, *Lepilemur* and *Mixocebus*. Here again the conditions in *Myoxicebus* suggest those of *Adapis magnus*.

P_4 of the typical Lemuridæ as compared with those of the Notharctinæ and Adapinæ gives the impression of being variously degenerate; the talonid is widely unlike that of the molars, whereas in all primitive Eocene mammals, including the Notharctinæ and Adapinæ, the talonid of p_4 shows more or less distinct beginnings of a posterior V bearing an incipient hypoconid. In *Myoxicebus*, which as above noted has a less degenerate p^4 than Lemurs, p_4 has also, as might be expected, a well-developed talonid with a distinct hypoconid. In *Lepilemur* and still more in *Lemur*, on the contrary, the talonid is much reduced; *Lepilemur*, however, has the trigonid of p_4 in an unreduced condition, with a very distinct metaconid, the whole tooth being fundamentally identical with that of *Adapis* save for the reduction of the talonid. In other words, the simplification of the first three premolars, which is very marked in *Adapis parisiensis*, may have begun to affect the fourth premolars in the typical Lemuridæ more than in *Myoxicebus*.

Molars

Plates LIV, LV

In the primitive Notharctinæ $m\frac{2}{2}$ are notably wider than $m\frac{1}{1}$; $m\frac{3}{3}$ are notably narrower than $m\frac{2}{2}$; in the later forms there is a tendency for $m\frac{2}{2}$ and $m\frac{1}{1}$ to be of nearly equal width. In the Adapinæ there is considerable variation in proportions: there is a frequent tendency for the molars to become approximately equal in size, or m^3 may still be quite small (*Adapis magnus* var. *leenhardti*, Stehlin, 1912, p. 1279, fig. 287). In the Lemuridæ *Myoxicebus* suggests *Adapis parisiensis* var. *schlosseri* in the fact that m^3 is nearly as large as m^2. In *Lemur* on the other hand m^3 is quite small.

With regard to the detailed characters of the upper molars it has already been stated that in the primitive Notharctinæ these are tritubercular with only a faint beginning of the pseudohypocones and mesostyles which become progressively developed in the later forms; these two features exclude all the Notharctinæ from direct ancestry either to the Adapinæ or to the Lemuridæ. In the Adapinæ the molars are primitively tritubercular (*A. sciureus*) but always have a cingulum-hypocone; the protoloph is always sharp; typically the metaconule is less distinct than in the primitive *A. sciureus*. In the Lemuridæ the molars are more or less degenerate in the finer details; thus the proto- and metaconules are never distinct, the external cingulum is often obsolete, the internal cingulum is either much reduced or very strongly developed, the hypocone is absent. So also in general contours of the molars a wide adaptive radiation is shown: in *Myoxicebus,* which feeds on the leaves of the bamboo,[1] the molars have greatly expanded protocones and low conical para- and metacones, the protoloph is blunt and the surface of the crown is slightly wrinkled; in *Lemur,* which is practically omnivorous, the molars are more dog-like, with sharp protoloph and prominent internal cingulum. In *Myoxicebus* there is also an evident tendency, already manifested in *Adapis magnus,* for all the cheek teeth from p^3 to m^3 to assume a similar form with massive conical cusps. In *Chirogale* and *Atililemur* the molars are roundly tricuspidate, this giving a "tritubercular" pattern of omnivorous type which is primitive in name only, but is in reality degenerate and secondarily simple. In *Microcebus* the molars are small and delicate with pointed cusps, indicative of a partly insectivorous diet. The molars of *Lepilemur* are less degenerate in form than those of any other genus except perhaps *Mixocebus.* They are in general similar in outline to those of *Adapis parisiensis* as observed by Stehlin, save that they lack the hypocone; he, however, is unwilling to accept this as a sign of close relationship.

In general, the upper molars of the Lemuridæ may be grouped under two main types:

(1) the primitive sharp-cusped type with sharp cusps and cutting ridges recalling *Adapis parisiensis; Mixocebus, Lepilemur;* the molars of *Lemur* and *Microcebus* are very specialized derivatives of this type;

(2) the round type, with very obtusely conical cusps,
  a) with distinct hypocone: *Myoxicebus,*
  b) hypocone reduced or wanting: *Chirogaleus, Atililemur.*

As in the Adapinæ there is never any tendency to form either a mesostyle or a pseudohypocone; a cingulum-hypocone and the protoloph crest are primitively well developed.

The lower molars of the earlier species of Notharctinæ are of an exceedingly primitive tuberculo-sectorial type, common in its general pattern to many Paleocene and Eocene mammals and structurally approaching the ancestral lower molar patterns of all other primates; they have a small trigonid, retaining the primitive paraconid, and the third molar has a well developed hypoconulid; m_3 is much narrower than m_2; perhaps the chief specialized feature is the precocious development of the entoconid which attains a large size in the later members of this subfamily. In *Adapis parisiensis,* typical of the Adapinæ, the molars are on the whole considerably more specialized in type. The paraconids are absent; the protolophid crest is prominent and oblique; a metacristid is often present; the hypoconulid of m_3 is smaller; m_3 is sometimes nearly as wide as m_2. In the Lemuridæ the lower molar patterns, though more or less degenerate, are much closer to the Adapine than to the Notharctine type — *Lepilemur* in fact retains much of the *Adapis parisiensis* pattern: the metacristid has become much enlarged and displaced backward, usurping the position of an entoconid, for which it might readily be mistaken; behind this enlarged metacristid is a notch representing the medial inlet to the talonid basin, and behind the notch is the vestigial or absent entoconid and the crista posterior; the hypoconulid of m_3 though small is present. In the highly specialized genus *Lemur* the cusps of the lower molars m_1 m_2 have lost much of their pristine and Eocene distinctness and are merged with the crests (protolophid, crista obliqua, crista posterior). The metacristid crest is now very long and simulates a high sharp internal cingulum, a structure which is never present in primitive Eocene molars; comparison with *Lepilemur* and *Adapis* readily clears up the homologies. The medial inlet to the hypoconulid is now posterointernal in position;

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[1] Elliot, D. G., 1912, A Review of the Primates, I, p. 127.

m_3 has an abortive hypoconulid; m_1 is the largest of the series. In *Myoxicebus* the stout lower molars rather suggest the *Adapis magnus* type.

In brief, with regard to the pattern of the lower molars, the Lemuridæ are evidently more nearly allied to the Adapinæ than to the Notharctinæ, the latter representing in most particulars an older type. Special evidence of structural affinity with the Adapinæ is revealed by the lower molars of *Lepilemur* which are less degenerate than those of *Lemur;* analogies with *Adapis magnus* are shown in the lower molars of *Myoxicebus simus.*

Lower Jaw

Plate LII; Text Fig. 76

The evolution of the lower jaw of the Notharctinæ has been traced in preceding pages. It will be recalled that in the early forms of *Pelycodus* the mandible was fairly stout, with a robust horizontal ramus which was gently curved below, bearing canines of moderate size and small semierect incisors; the angle was produced backward into a long fairly strong apophysis, the symphysis remained open. In the latest types, the symphysis coalesced in adults, the ramus was stout but rather shallow, the coronoid unusually large, high and very little recurved, the condyle strongly convex both anteroposteriorly and transversely, the medial articular surface of the condyle being extended into a prominent apophysis directed downward and backward. In the Adapinæ, it will be recalled, the horizontal ramus becomes very stout with greatly

Fig. 76. Lower jaws of *Notharctus* and *Lepilemur*. Medial aspect. Natural size.

1. *Notharctus venticolus.* Amer. Mus. No. 14655.
2. *Lepilemur mustelinus.* Amer. Mus. No. 31251.

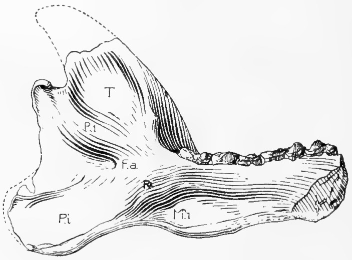

Fig. 77. Lower jaw of *Adapis parisiensis*. Medial aspect. After Stehlin. Natural size.

expanded angle and usually coalesced symphysis; the condyle is convex anteroposteriorly but more flattened transversely. In the Lemuridæ the mandible appears to represent a more or less degenerate derivative of the Adapine type, with an excessively sloping symphysis, a usually slender ramus with a straight lower border and a more or less delicate angle. The condyle is flattened transversely, but in *Lepilemur* it has also a deep posterior vertical extension which articulates with the large postglenoid process. In *Myoxicebus simus* the mandible in correlation with its heavy zygomata and wide crushing molars retains considerable resemblance to the Adapine type, as seen especially in the expanded angle, stout ramus and fairly convex chin.

Dr. Stehlin (1912, p. 1294) regards the early coalescence of the opposite rami of the mandible as one of five important specializations which tend to exclude the Adapinæ from further evolution in the direction of the recent and subfossil Lemuridæ, the latter term being apparently used in a very inclusive sense. The writer, on the contrary, would be inclined to associate the failure of the rami to coalesce in the typical Lemuridæ partly with the largely degenerate and feeble character of the canines and with the retrogressive character of all the muscle areas. According to this hypothesis a lemur with massive jaws and expanded muscle areas analogous with those of *Adapis* ought to exhibit an early coalescence of the rami and this is actually the case in a young jaw of *Megaladapis grandidieri* described by Standing.[1] As retrogressive changes often involve the permanent retention of originally transitory juvenile or infantile characters there is no apparently valid à priori reason why a race with normally coalesced rami should be incapable of giving rise to a race with a weak jaw and a persistent symphyseal suture. In this connection it is noteworthy that even in the Adapinæ there was considerable variation in the age of coalescence of the rami, as the following passage shows: "Die Symphysalnaht [of *Adapis magnus*] erlischt offenbar später als bei Adapis parisiensis, denn es liegen mir verschiedene Mandibelhälften adulter Individuen vor, an welchen die Verwaschsung eben erst begonnen hat" (Stehlin, 1912, p. 1259).

Mental Foramina

The position of the mental foramina of certain modern Lemuridæ in comparison with the Notharctinæ and Adapinæ is as follows.

Beneath

	c		p_1		p_2		p_3		p_4		m_1
Pelycodus frugivorus			×		×				×		
Notharctus venticolus			×	×				×			
" *pugnax*			×				×		×		(×)
Adapis parisiensis		×				×			×		
" *magnus*						×					×
" *sciureus*			×				×				
Lepilemur mustelinus	×						×		××		×
" "					×		×		×		
Lemur varius	×				××			×			
" "	×				×		×				
" *mongoz*	×						×				
" "					×		×				
Microcebus	×										×
Mixocebus							×		×		
Chirogale	×								×		×
Atililemur	×										×
Myoxicebus simus	×						×		×		

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[1] On recently discovered subfossil Primates from Madagascar. 1908, Trans. Zool. Soc. London, XVIII, part 2, p. 115.

This gives evidence that the arrangement of the mental foramina in the Lemuridæ is closely related to or derived from the primitive arrangement shown in the Adapidæ and that *Lepilemur*, as might be expected, is the most primitive of the modern types.

Skull

Plates LII — LV

The comparative morphology of the skull of the Lemuridæ, Notharctinæ and Adapinæ may now be discussed.

As compared with the Notharctinæ, the skulls of typical Lemuridæ exhibit the following important differences.

(1) They are much more advanced in evolution in respect of the following characters:

- (*a*) the brain-case is greatly expanded transversely and in consequence the sagittal and lambdoidal crests are typically lost, the interparietal is widely exposed on the top of the skull and the interorbital constriction is nearly obliterated; the frontals extend further backward over the parietals;
- (*b*) the orbits are relatively larger;
- (*c*) the lacrymal is extended on the face, carrying the lacrymal foramen in front of the orbit;
- (*d*) the bony muzzle is often more or less truncate and in correlation with this the premaxillæ are often widened and shortened anteroposteriorly;
- (*e*) the notch between the palatal border of the palatine and the alveolar region of the maxillary is converted into a tunnel;
- (*f*) the zygomatic process of the malar sometimes extends back nearly to the articular eminence, while in the Notharctinæ it apparently ended well in front of that point;
- (*g*) the pterygoid fossæ are typically more expanded than in *Notharctus;*
- (*h*) the bullæ are frequently more expanded and the mastoid is sometimes inflated (*Lepilemur, Microcebus*);
- (*i*) the fossa subarcuata on the encephalic surface of the petrosal is more expanded.

With the possible exception of *f*, every one of these, in the judgment of the writer, is a progressive character and not one excludes the notharctine type of skull from remote structural ancestry to the lemurid type.

(2) Retrogressive features in comparison with the Notharctinæ include the weakening of the zygomatic arches, the reduction of the temporal flange of the squamosal, the weakening of the premaxillæ and of the suborbital tubercle for the masseter, the loss or reduction of the prominent mastoid tuberosity. Here again these characters in the opinion of the writer are all relatively late acquisitions and by no means exclude the Notharctinæ from remote structural ancestry to the Lemuridæ.

Characters *a, b, c, d,* and *e* of the progressive series and all the retrogressive characters also distinguish the typical Lemuridæ from the Adapinæ, but do not exclude them from structural derivation from the latter; characters *g, h,* and *i* are already developed in the Adapinæ whence they may have been transmitted to the Lemuridæ.

In the course of his description of the skulls of *Adapis parisiensis* Dr. Stehlin records numerous resemblances with and differences from *Lemur* besides those already noted. In addition to the great increase in the facial exposure of the lacrymal in *Lemur*[1] and the consequent readjustments in the surrounding bones, the chief differences in the facial region are as follows.

(1) The premaxillary in *Lemur* is less extended upon the face in side view; this, however, is less apparent in *Microcebus, Chirogale* and *Atililemur,* which have well-developed incisors, a projecting muzzle and therefore relatively large premaxillæ.

(2) The general plane of the orbits in *Lemur* is more vertical, so that they are less directed upward. This is apparently conditioned by the fact that in *Lemur* and *Lepilemur* the forehead is higher. In *Chirogale* which has a low forehead the orbits are more widely seen in the top view of the skull.

(3) The suborbital portion of the malar in *Lemur* is less extended vertically than in *Adapis.* This is associated with the great expanses of the areas for the masseter in *Adapis* and with the partly retrogressive development of these areas in typical Lemuridæ.

The more striking differences in the brain-case are nearly all related to the great expansion of the brain in the modern forms which has conditioned such necessary readjustments as the more or less wide exposure of the fused interparietals and supraoccipital upon the top of the occiput. This exposure is comparatively slight in the primitive *Myoxicebus simus* and attains its maximum in *Lemur.*

The frontals in *Lemur* are produced backward above the cerebrum, so that the coronal suture is nearly transverse. In the primitive *Myoxicebus simus,* on the other hand, the coronal suture is almost V-shaped. In *Adapis,* on the other hand, the frontals are remarkably small (Stehlin, 1912, p. 1194) and take very little part in covering the cerebrum, but cover chiefly the olfactory chamber and the orbits. This is surely a primitive character which *Adapis* shares with many other Eocene mammals.

Another apparently primitive character of *Adapis* is that the floor of the brain-case is nearly parallel to the palate (Stehlin, 1912, p. 1198) while in *Lemur* it is considerably inclined toward it. In *Adapis* also by reason of the small size of the brain the plane of the foramen magnum forms a somewhat sharper angle with the base of the cranium than it does in *Lemur.*

The temporal flange of the squamosal is well developed in *Adapis,* and extends higher up on the side of the brain-case than in *Lemur,* in which both the temporal and the zygomatic portions are feebly developed. In *Adapis* the crest of the zygomatic process above the auditory meatus and the root of the process are inflated or pneumatic. In *Lepilemur* some of this condition remains, but in *Lemur* the air cells of this region as shown in several sections are of small size. The mastoid of *Adapis* is thoroughly pneumatic, like that of *Lepilemur,* but in *Lemur* the occipital surface of the mastoid while much expanded is thin and deflated. The lower side of the mastoid bears in *Adapis* an S-shaped groove, no trace of which remains in *Lemur* or in *Lepilemur.*

The under side of the skull of *Adapis parisiensis,* as Dr. Stehlin notes (1912, p. 1202), differs from that of modern Lemuridæ in the large size of the bullæ and in the size and strength of the pterygoid plate of the alisphenoid. This character is somewhat less pronounced in *Adapis* (*Leptadapis*) *magnus* var. *leenhardti.* Among the Lemuridæ *Mixocebus* and *Microcebus* have large bullæ, while *Atililemur, Chirogale* and *Myoxicebus* have the bullæ small and set well back near the occiput.

The palate in all types of *Adapis* is produced behind m^3, and ends in a median projection. In *Lemur, Lepilemur* and *Mixocebus* the palate ends in front of m^3. In *Microcebus, Chirogale, Atililemur,* however, the palate is produced behind m^3. In all the Lemuridæ the median projection of the palatal border is vestigial or wanting. The primitive notch between the vertical plate of the palatine and the alveolar

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[1] The phylogenetic interpretation of this character will be discussed by the writer in a later Bulletin of The American Museum of Natural History.

pouch of the maxillary is present in *Adapis* but has been converted into a tunnel in all the Lemuridæ.

Notwithstanding the sharp divergence of the internal and external pterygoid plates in *Adapis*, implying a strong development of the internal pterygoid muscle, the pterygoid bone itself is but weakly developed and lacks a hamular process, which is present in the Lemuridæ.

The occipital condyles of *Adapis* are wider than those of *Lemur* and directed more posteriorly. In *Chirogale*, however, the condyles are more like those of *Adapis*.

The interior of the brain-case of *Adapis* offers a few marked differences from *Lemur:* the roof-shaped projection of the presphenoid (?orbitosphenoid) above the optic foramina is wanting in *Lemur;* and so is the crest (crista petrosa) upon the dorsal ridge of the petrosal, to which is attached in *Lemur* the tentorium. The posterosuperior process of the alisphenoid, which in *Lemur* arches over the foramen ovale and overlaps the encephalic surface of the petrosal, is wanting in *Adapis*. The postglenoid foramen is not visible from the cerebral surface in *Adapis* as it is in *Lemur* and there is some difference in the course of one of the veins that drain through this foramen (Stehlin, 1912, p. 1218). In *Adapis* the roof of the sinus hypotympanicus takes a greater part in the cerebral cavity.

Mingled with these differences, there is perhaps an equal number of resemblances in skull structure between *Adapis* and *Lemur*, as observed by Stehlin. Many of these, however, are also preserved in the Indrisidæ and therefore for the most part belong to the heritage of the Lemuriformes. These agreements, which are in addition to those formerly discussed, may be summarized as follows.

(1) Preorbital region of the maxilla bearing a shallow fossa for the præorbicularis dorsalis muscle.

(2) Nasals narrow essentially as in *Lemur*.

(3) Infraorbital canal often double (it is frequently double in *L. mongoz*).

(4) Internal nares wide and low.

(5) Bullæ with two anterior processes:

- (*a*) processus anteromedialis, articulating with basioccipital and basisphenoid.
- (*b*) processus styliformis, connecting with external pterygoid plate.

(6) A horizontal ridge separating the temporal fossa from the external pterygoid fossa, running from the glenoid to the orbitosphenoid.

(7) External pterygoid plate pierced by foramen Civininii (pterygospinosum).

(8) With minor differences, osseous elements and pattern of brain-cavity substantially as in *Lemur:*

- (*a*) orbitosphenoid sharing but little in the brain-cavity;
- (*b*) squamosal also sharing but little in the brain-cavity;
- (*c*) petrous roof of sinus hypotympanicus taking a large share in brain-cavity;
- (*d*) topography of encephalic side of petrosal essentially the same as in *Lemur:* a capacious fossa subarcuata above the internal auditory meatus[1]; mastoid excluded by petrosal from brain cavity;
- (*e*) foramina in back of orbit essentially as in *Lemur* (optic, for. lac. ant., for. rot., for. cranio-orbitale);
- (*f*) venous sulcus occipitalis superior as in *Lemur;*
- (*g*) a considerable portion of the cerebral venous blood draining through the foramen magnum and venæ vertebrales (Stehlin);

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[1] Examination of this region in representatives of all the major groups of Primates shows that the orifice of the subarcuate fossa is always surrounded by the superior semicircular canal. This was also verified in a specimen of *Notharctus osborni* (Amer. Mus. No. 12569.) Presumably the rule will hold good also in the Adapinæ.

(*h*) two venous sulci opening into postglenoid foramen (Stehlin), but with certain differences in the course of one of them;

(*i*) Whole course of internal carotid and its branches as in *Lemur;*

Origin of the Lemuridæ

Dr. Stehlin (1912, p. 1294) concludes that the Adapidæ are definitely excluded from further evolution in the direction of the Lemuridæ by the following decisive characters:

(1) The early coalescence of the opposite rami of the mandible.
(2) The ossification of the "annulus membrane."
(3) The complication of the sinus hypotympanicus.
(4) The complication of p^4, which has two external cusps.
(5) The construction of the incisors and canines.

Of these, numbers 1, 4, 5 have already been discussed, the writer maintaining that numbers 1 and 5 are primitive characters of the Adapinæ and partly degenerate and specialized characters in the Lemuridæ; with regard to number 4 it has been argued (see p. 135) first that the primitive *Adapis sciureus* probably had a much more primitive p^4 than the typical *Adapis*, and that, in view of the obvious degeneration of the dentition in other characters, it would not be surprising if the ancestral Lemuridæ had a second external cusp on p^4.

With regard to characters numbers 2 and 3 it has already been noted that the "annulus membrane" is not a true tympanic membrane, but an infolded surface of the bulla where it has grown around the tympanic ring. It will be recalled[1] that the whole sinus hypotympanicus or cavity of the bulla is merely a diverticulum of the tubo-tympanal canal, which has either sunk into, and then become surrounded by, the periotic or has acquired in some mammals an independent ossification in its own wall (entotympanic).[2] Originally the hypotympanic sinus was entirely medial both to the true tympanic cavity, with which it communicated through the "pneumatic foramen," and to the tympanic annulus. Becoming greatly inflated the bulla grew ventrad to the tympanic ring and finally concealed it entirely from the ventral surface, at the same time the expanding bulla gained contact with the entoglenoid region of the squamosal and with the ectotympanic plate of the alisphenoid. In surrounding the tympanic annulus the membranous cavity of the bulla gave off diverticula, which, although differently developed in *Adapis parisiensis* (Stehlin, 1912, p. 1208) and *Adapis magnus* (idem., p. 1254), in both cases nearly cover the tympanic annulus with the infolded dorsal walls of the diverticula.

The writer infers that a progressive enlargement of the pneumatic foramen, and concomitant retrogressive withdrawal or resorption of the osseous folds surrounding this foramen would finally free the annulus almost entirely from the folds in question and at the same time so expand the diverticula that they would become lost in the primary hypotympanic sinus. According to this interpretation the conditions in the tympanic region of the modern *Lemur* represent a further advance, in the direction of simplification, upon the conditions observed in the Eocene Adapinæ, while according to Dr. Stehlin's interpretation (1912, p. 1215) the Eocene genera (*Adapis, Leptadapis*) are more specialized in this region than the modern Lemuridæ.

The writer's interpretation assumes only that the great size of the pneumatic foramen in lemurs

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[1] Kampen, P. N. van. 1905, Die Tympanalgegend des Säugetierschädels, pp. 337–340.

[2] *Op. cit.*, p. 363.

is secondary; it coincides completely with van Kampen's conclusion[1] that originally the hypotympanic sinus was sharply separated from the true tympanic sinus by a septum (formed by the osseous shell of the hypotympanic cavity) and that, by the enlargement of the pneumatic foramen, this septum was reduced, so that finally only vestiges of it remain (*Tupaia*, Lemuridæ, most Canidæ) or it vanishes entirely (Rodentia, many ungulates, etc.).

Fig. 78. Auditory region of *Adapis*, *Notharctus*, *Lemur*.

1. *Notharctus osborni*. Amer. Mus. No. 11466. Twice natural size.
2. *Adapis magnus*. After Stehlin. Twice natural size.
3. *Lemur varius*. Amer. Mus. No. 10424. Natural size.

This well-grounded conclusion from comparative anatomical data thus supplies a probable explanation of the fact that the tympanic ring lies freely within the cavity of the bulla instead of remaining morphologically outside of that cavity as it should in a primitive lemur and as it actually does, except to a very limited extent, in the Eocene Adapinæ.

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[1] *Op. cit.*, p. 339.

Perhaps no two investigators would give exactly the same evaluation to the totality of these resemblances and differences between the Adapinæ and the Lemuridæ. Dr. Stehlin, as above stated, believes that the Adapinæ are probably excluded from further evolution in the direction of the Lemuridæ by the five chief characters discussed above (pp. 211, 212). He therefore dissents from the conclusions of Leche, Forsyth Major, and Schlosser that the Adapinæ are more or less directly ancestral to the Lemuridæ both in dental and cranial characters.

The writer, on the other hand, would not only endorse the general conclusion of the above-named authors but would feel that nearly all the marked differences between Adapinæ and Lemuridæ are such as might be expected to distinguish Eocene from modern Lemurs. The same characters of the dentition which exclude the Adapinæ from close relationship with the Indrisidæ, Chiromyidæ, etc., tend to unite them with the Lemuridæ. The resemblances in the construction of the brain-case, of the whole auditory region, between Adapinæ and Lemuridæ are of the most intimate and fundamental character. The differences all illustrate the general principle that any modern forms have attained their present status through the following commingled and overlapping processes; (1) hypertrophy or progressive emphasis, (2) retrogression and secondary simplification, involving coalescence and convergence or dedifferentiation of adjacent parts, (3) change of trend in certain parts.

Certain features of the dentition suggest that the Lemurinæ have close relations with the *Adapis parisiensis* group while the Chirogaleinæ may be related to the *Adapis* (*Leptadapis*) *magnus* group. At any rate the remote ancestors of the Lemuridæ should be closely related to *Adapis sciureus*.

From all this it will be apparent that the writer gives no assent to the general principle that it is impossible to discover the relationships of modern to ancient families until all the missing stages from successive formations shall be discovered. The writer believes on the contrary that a sufficiently thorough and comprehensive morphological and systematic analysis of existing material will often yield evidence of great and permanent value. Morphological analysis alone, in addition to the valuable though imperfect palæontological evidence, is quite sufficient to establish beyond reasonable doubt that the Cetacea have been derived from terrestrial Placental mammals, that the Hominidæ represent a terrestrial offshoot of an arboreal catarrhine stock, that the various members of the Lemuridæ are more nearly related to each other than any of them are to the Indrisidæ, etc. The more precise questions may, indeed, have to await further discovery, but the limits to our knowledge of phyletic relations must be determined not by any such à priori negative principle as Dr. Depéret[1] and Dr. Stehlin have sought to establish, but by intensive, prolonged and comprehensive investigation of each case.

The broader stages in the origin and evolution of the Lemuridæ may be summarized as a working hypothesis as follows:

STAGE 1.— Paleocene protolemurines (hypothetical). Insectivorous-frugivorous. $I\frac{2}{2}$ $C\frac{1}{1}$ $P\frac{4}{4}$ $M\frac{3}{3}$. Lower incisors small, suberect; lower canine subcaniniform. Premolars simple; upper molars tritubercular, with cingulum-hypocone, proto- and metaconules; lower molars tuberculosectorial. Orbits relatively small. Lacrymal within orbit. Brain-case small. Moderate muscle crests. Hypotympanic sinus not covering tympanic ring. Brain macrosmatic, with small frontal lobes and smooth cerebra.

STAGE 2.— Eocene Adapinæ. Insectivorous-frugivorous-omnivorous. $I\frac{2}{2}$ $C\frac{1}{1}$ $P\frac{4}{4}$ $M\frac{3}{3}$. Lower incisors and canines as in *Adapis sciureus*. P^4 with incipient metacone; upper molars with low cingulum-hypocone and sharp protoloph. Lower molars losing paraconid, acquiring metacristid. Lacrymal within orbit. Brain-case widening. Jaw stout. Muscle crests very high, zygomata powerful. Hypo-

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[1] Les Transformations du Monde Animal.

tympanic sinus covering tympanic ring but separated from it by membrane. Brain macrosmatic, but with wider frontal lobes.

STAGE 3.— Pleistocene and Recent Lemuridæ. Diet various, more insectivorous in some, more frugivorous in others. Tongue enlarged. $I\frac{2-0}{2}\ C\frac{1}{1}\ P\frac{3}{3}\ M\frac{3}{3}$. Lower front teeth highly specialized. P_2 enlarged and subcaniniform. Dentition more or less degenerate and specialized: paraconids of lower molars, protoconules, metaconules and cingula of upper molars and metacone of p^4 usually lost or greatly reduced. Premolars simplified; metacristid and talonid often enlarged; hypoconulid of m_3 more or less reduced. Jaw typically slender. Muscle crests typically degenerate, zygomata usually weak. Orbits typically enlarged. Lacrymal expanded on face. Brain-case usually much expanded, exposing supraoccipital plus interparietals on top of skull. Membrane between hypotympanic sinus and tympanic ring reduced or absent, the latter lying freely within the bulla. Brain becoming microsmatic, with large, usually well-furrowed cerebra partly overlapping large cerebellum.

COMPARISON OF *NOTHARCTUS* WITH THE INDRISIDÆ

Plates LVI–LVIII

The general contrast in dentition and skull between *Notharctus*, representing a primitive Eocene lemuriform stock, and *Propithecus*, representing the highly modernized lemuriform family Indrisidæ, is as follows (*P.*, progressive; *Prim.*, primitive; *R.*, retrogressive):

	Notharctus	*Propithecus*
Dental Formula	$1\frac{1.2}{1.2}\ C\frac{1}{1}\ P\frac{1.2.3.4}{1.2.3.4}\ M\frac{1.2.3}{1.2.3}$	(*R*) $I\ \frac{1.2}{2}\ C\frac{1}{1}\ P\frac{2.4}{1^{*}.2.4}\ M\frac{1.2.3}{1.2.3}$
Probable Diet	Insectivorous-frugivorous	Leaves, fruits, flowers
Probable Deciduous Formula	$DI\frac{1.2}{1.2}\ DC\frac{1}{1}\ DM\frac{1.2.3}{1.2.3}$	(*Prim*) $DI\frac{1.2}{2}\ DC\frac{1}{1}\ DP\frac{2.3.4}{2.3.4}$
Lower Incisors	Two pairs gently procumbent, short, subspatulate	(*P.R*) One pair, sharply procumbent styliform
Lower Canines	Erect, subcaniniform	Procumbent, styliform
P_1, p_3	Present	(*R*) P_1 vestigial, lost with deciduous teeth, p_3 lost
P_2	Small, simple	(*P*) Enlarged, compressed, opposing p^3 and c
P_4	Primitive	(*P*) Compressed
Lower Molars	Tuberculosectorial	(*P*) With W-shaped crowns
" " Entoconids	Low	(*P*) High
M_3 Hypoconulid	Well developed	(*R*) Aborted
Upper Molars		
Proportions: anteroposterior elongation	Moderate	(*P*) Pronounced
Lingual Cusps	Subconic	(*P*) Sharply-V-shaped
P^1, p^3	Present	(*R*) Absent
P^2, p^4	Primitive	(*P*) Compressed with reduced internal cusps (*R*)
Muzzle	Moderately long	(*R*) Short and wide
Orbits	Moderate	(*P*) Larger, extended laterally
Frontal Sinus	Small	(*P*) Enlarged
Lacrymal Foramen	Marginal	(*P*) Preorbital
Malar	Moderate	(*P*) Robust
Glenoid Fossa	Shallow	(*P*) Deep

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* Vestigial, appearing with the milk dentition, but very early shed.

	Notharctus	*Propithecus*
Notch between Vertical Plate of Palatine and Maxilla	Open	(*P*) Converted into a tunnel
Expansion of Brain	Gentle	(*P*) Pronounced
Bullæ	Small	(*P*) Fairly large
Sagittal Crest	Present	(*R*) Absent
Mandible	Of moderate length	(*P*) Very short
Symphysis.	Moderate, ending beneath p_4	(*P*) Very long, ending beneath m_2
Ramus	Shallow	(*P*) Deep
Angle	Primitive	(*P*) Greatly expanded
Condyle	Moderately convex	(*P*) Strongly convex
Coronoid process	Large, high	(*R*) Short
Ental Excursion of Mandible	Moderate	(*P*) Pronounced
Brain	Macrosmatic	(*P*) Microsmatic

The available evidence indicates that the deciduous dental formula of *Notharctus* was the same as it was in *Adapis*. With regard to the dental formula of *Propithecus* the writer is inclined to agree with Flower and especially with Lydekker, who would interpret the adult formula as

$I\frac{2}{1}\ C\frac{1}{1}\ P\frac{2}{2}\ M\frac{3}{3}$; rather than $I\frac{2}{2}\ C\frac{1}{0}\ P\frac{2}{2}\ M\frac{3}{3}$ (Leche).

The detailed resemblance of the lateral lower procumbent front tooth to the true canine of *Lepidolemur* seems too close to be due to convergence; it means only that one pair of incisors persists in the Indrisidæ in accordance with their general tendency to reduce the ante-molar dentition. For similar reasons the first premolariform lower tooth, which articulates with the posterior edge of the upper canine, is p_2, not p_3. The deciduous dentition of *Propithecus, Indris, Avahis* is fully figured by Grandidier and Milne Edwards. The deciduous lower front teeth, as in the adult, comprise a *single pair of incisors* and a pair of procumbent incisiform canines. The vestigial low-crown tooth, the first of the cheek teeth,

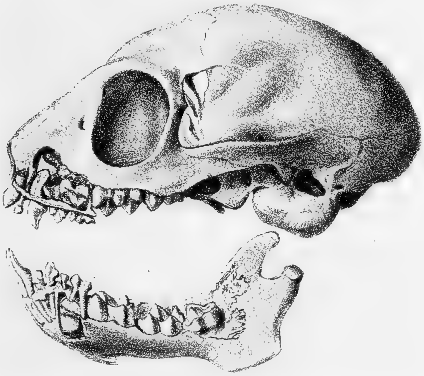

Fig. 79. Young skull and lower jaw of *Propithecus verreauxi*. After Milne Edwards. × $\frac{5}{4}$.

The external walls of the alveolar process and of the mandible have been removed to show the unerupted permanent teeth. In the upper jaw the following teeth are in use: di^1, di^2, dc, dp^3, dp^4. M^1 is coming into place; the permanent canine, the two premolars and m^2, m^3 are embedded in the jaw. In the lower jaw the following teeth are in use: di, dc, p_1, dp_2, dp_3, dp_4. M_1 is about to erupt, m_2, m_3 are buried in the jaw.

which is separated from the styliform deciduous canine by a considerable diastema, is possibly not a canine, as it was thought to be by Leche, but the vestigial P_1 which, as in other mammals, erupts with the deciduous teeth. Dp_2 ("D_1") suggests p_2 in form and is of relatively large size; Dp_3 ("D_2") again is vestigial and suggests the crowding out of p_3 from the adult series; Dp_4 ("D_3") is submolariform. In the upper milk series there are two incisors and a canine as usual; the deciduous cheek teeth are separated by diastemata and appear to represent Dp^2 (D^1) and Dp^4(D^3), Dp^3(D^2) being lost. In the Archæolemurinæ p^3 and p_3 are retained, but in all the other Indrisidæ the ante-molar cheek teeth are much crowded by the enlarged molars.

The most doubtful element in the foregoing interpretation appears to be the identification of the vestigial anterior tooth of the cheek series as p_1, which is a tooth not otherwise known in any modern *Lemur;* but in *Avahis* it lies immediately above the permanent canine, in the normal position of p_1 (cf. Grandidier and Milne Edwards, *op. cit.*, Pl. 44, fig. 5*b*); it is in place with the deciduous teeth, as is usual with p_1; and seems to lie behind the deciduous upper canine, as p_1 should.

A careful study of the whole family of the Indrisidæ in comparison with the Lemuridæ, Adapinæ and Notharctinæ, indicates that every one of the above noted characters of *Propithecus* represents an advance or specialization upon the corresponding characters of *Notharctus.*

The general architecture of the skull, including the base of the cranium, is the same as in *Notharctus, Adapis* and the Lemuridæ. The interior of the brain-case differs from that of *Adapis*, as figured by Stehlin (1912, p. 1216), in the relatively smaller size of the olfactory fossa and in the greater expansion of the frontal and orbitosphenoid walls of the cerebral cavity. This has conditioned the loss of the horizontal flange of the orbitosphenoid, above the optic foramina, and the confluence of the foramen rotundum with the foramen lacerum anterius. The posterior clinoid process and the crista petrosa are strongly developed and the subarcuate fossa is expanded — all modernized features.

Propithecus and the rest of the Indrisidæ are excluded from derivation from *Adapis* by the widely divergent character of the premolars and molars, which carry to an extreme the W-shaped pattern that is foreshadowed in *Notharctus.* In their present advanced stage of evolution it is difficult to decide whether the large posterointernal cusp of m^1, m^2 is a pseudohypocone or a true hypocone derived from the cingulum. Its intimate functional relations with the entoconid of the lower molars would suggest the former view.

It is not necessary, however, to infer that the modern Indrisidæ of Madagascar are the direct descendants of the American Eocene Notharctinæ, although in perhaps all their cranial and skeletal characters and in all or nearly all their dental characters they are *structural* derivatives of the Notharctine type. They may rather be derived from some Old World Eocene relatives of the Notharctinæ.[1]

With regard to the postcranial skeleton the writer has made a very large number of comparisons between the vertebræ, limb and foot bones of modern Indrisidæ with the homologous parts in the Eocene Notharctinæ, with the invariable result that the conditions in the Notharctinæ seemed to be evidently more primitive, potentially ancestral to the specialized conditions observed in the Indrisidæ.

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[1] In spite of its stout lower canines *Cænopithecus lemuroides* may prove to be an intermediate stage between the Protolemurine ancestors of the Notharctinæ and the modern Indrisidæ, for reasons which will be discussed later.

COMPARISON OF *NOTHARCTUS* WITH THE PLATYRRHINI

Plates XLVI, XLIX, L, LIX

All the existing South American monkeys are highly specialized and even the Santa Cruzian genus *Homunculus* is of modernized type, so that there is no direct palæontological evidence as to the characters of the stem form of this relatively compact, but fairly diversified, natural group. After prolonged, repeated comparisons of all views of the skull of the platyrrhine genera it is here adopted as a working hypothesis that the common ancestral form had the following characters in contrast with *Notharctus* (*P.*, progressive; *Prim.*, primitive, *R.*, retrogressive, reduction):

	Notharctus	Generalized Platyrrhine
Brain and Brain-case	Small, with sagittal and lambdoid crests	(*P*) Large, expanded vertically, transversely and anteroposteriorly. Much produced posteriorly, without sagittal and lambdoid crests
Face	Long, nearly in line with brain-case	(*P*) Short, depressed and deepened below brain-case
Orbits	Directed partly outward Not closed posteriorly	(*P*) Moved forward, lateral borders protruding (*P*) Closed posteriorly by a flange from the malar which grows inward between the temporal muscle and the orbits
Frontals	Expanded between orbits, posterior extension over brain small	(*P*) Restricted between orbits; posterior extension over brain large
Parietals	Normal	(*P*) Extended forward, often gaining contact with postorbital lamina of malar and separating the frontal from the alisphenoid
Postorbital Constriction	Marked	(*P*) Nearly obliterated by expansion of frontal region of brain
Interorbital Nasal Region	Wide (macrosmatic)	(*R*) Restricted (microsmatic)
Zygoma	Elongate, elevated	(*P*) Short, robust, widely arched outward, sharply decurved and depressed
Lacrymal Duct	Probably sloped gently toward nasal opening	(*P*) Steeply inclined. Duct enlarged
Lacrymal	At anterior corner of orbit behind crista anterior	(*P*) Same, but deepened vertically
Lacrymal Foramen	Immediately behind crista anterior	Same, or piercing middle of lacrymal (*P*)
Malar	Nearly or quite in contact with lacrymal	(*P*) Moved away from lacrymal (separated from it by wide exposure of maxilla)
Zygomatic Process of Malar	Probably ending in middle of zygomatic arch	(*Prim.*) Ending in middle of zygomatic arch
Jaw	Elongate, with narrow angle	(*P*) Very short and deep with much expanded angle (correlated with robust masseter)
Mandibular Symphysis	Suture distinct on surface	(*P*) Opposite rami completely coalesced
Motion of Jaw	Chiefly ental	(*Prim.*) Ental to Orthal
Occiput	Narrow and pointed above	(*P*) Very wide above, with broad exposure of supraoccipital and interparietal
Mastoid	Bearing a prominent tuberosity, which is more or less cancellous. Excluded from brain-cavity by periotic	(*P*) Greatly expanded, thin, without tuberosity, forming part of lateral wall of brain-cavity
Crista Petrosa	Not developed	(*P*) Forming a wide septum, in the tentorial plane
Petrosal behind int. aud. meatus	Short	(*P*) Much expanded

	Notharctus	Generalized Platyrrhine
Fenestra Cochleæ (f. rotunda)	Concealed by the post-tympanic process from a view from the outside through the tympanic ring	(*P*) Plainly visible, after the removal of the tympanic membrane; lying below and behind fenestra ovalis
Auditory bulla	Small, subcircular	(*P*) Elongate anteromedially
Hypotympanic Sinus	Enlarged, empty	(*R*) Reduced, cancellous
Tympanic	Slender, within bulla	(*P*) Expanded medially, lateral to bulla, which it overlaps
Carotid Foramen	At posterolateral angle of bulla	(*P*) Shifted medially, opening at posteromedial end of bulla
Carotid Canal ("arteria promontorii")	Running along lateral surface of cochlea (promontory), piercing basisphenoid, probably emerging lateral to sella turcica	(*P*) Deeply buried in the petrosal, not piercing basisphenoid, emerging at posterolateral angle of sella turcica
Stapedial Canal	Present	(*R*) Absent (Tandler)
Foramen Ovale	Small	(*P*) Large
Foramen Lacerum Posterius	Small	(*P*) Large
Foramen Civininii (pterygospinosum)	Piercing external pterygoid plate	(*R*) Absent
External Pterygoid Plate	Produced postero-externally to connect with anterolateral process of bulla and entoglenoid process of squamosal above Eustachian foramen	(*P.R.*) Separated from anterolateral process of bulla and entoglenoid process of squamosal by a wide vacuity
Temporal Flange of Squamosal	Elongate anteroposteriorly, with sharp supra-audital crest	(*R*) Abbreviate, with faint supraorbital crest
Postglenoid Foramen	Prominent	(*R*) Typically reduced or absent, occasionally prominent
Notch between Vertical Plate of Palatine and Alveolar Region of Maxilla	Open	(*P*) Converted into a tunnel
Pterygoid Fossa	Slight (pterygoid closely appressed to ext. pterygoid plate)	(*P*) Moderate
Palate	Moderately elongate	(*P*) Short and wide
Upper Dental Arch	Moderately elongate	(*P*) Abbreviate
Dental Formula	$I\frac{2}{2}\ C\frac{1}{1}\ P\frac{4}{4}\ M\frac{3}{3}$	(*R*) $I\frac{2}{2}\ C\frac{1}{1}\ P\frac{3}{3}\ M\frac{3}{3}$
Probable Deciduous Formula	$DI\frac{2}{2}\ DC\frac{1}{1}\ DP\frac{3}{3}$	(*Prim*) $DI\frac{2}{2}\ DC\frac{1}{1}\ DP\frac{3}{3}$
Arrangement of Upper Incisors	∧ shaped	(*P*) ∩ shaped
Central Upper Incisors	Compressed	(*P*) Enlarged, with transversely widened truncate crown
Upper Canine	Subcaniniform	(*R*) Small, not tusk-like; often becoming tusk-like
Lower Incisors	Small, gently procumbent, with truncate spatulate crowns	(*P*) Often with wider crowns, but essentially similar to those of *Notharctus*
Lower Canine	Subcaniniform	(*R*) Subcaniniform with short crown. Tusk-like canines secondary (*P*)
Upper Premolars	P^1 present, p^2, p^3, p^4 successively more complex	(*R*) P^1 absent, p^2, p^3, p^4 typically bicuspid (*P*) (more primitive in *Callithrix*)
Lower Premolars	P_1 present, p_2, p_3, p_4 successively more complex, p_4 with incipient trigonid and talonid	(*R*) P_1 absent, p_2 typically larger than p_3 (*P*), with vertically extended protoconid, opposing upper canine, and well marked internal cingulum; p_3, p_4 bicuspid (*P*) with much reduced talonid (*R*)
Upper Molars (m^1, m^2)	Quadritubercular with well developed external cingulum and mesostyle	(*R*) Quadritubercular wtih reduced external cingulum and mesostyle. Tribubercular groundplan preserved in *Callithrix, Nyctipithecus*; mesostyle present in *Mycetes*

	Notharctus	Generalized Platyrrhine
		(*Alouatta*) and occasionally in *Brachyteles*. Radiating into sub-bilophodont (*Cebus*) (*P*), flat-crowned (*Pithecia*) (*R*) and W-shaped crowns (*Alouatta*) (*P*)
Postero Internal Cusp	A pseudohypocone	(*Prim.*) Apparently a pseudohypocone. (In *Callithrix* it is connected by an isthmus with the protocone)
M^3	Tritubercular, erupting early	(*R*) More or less degenerate in pattern; erupting late
Lower Molars	Tuberculosectorial	(*P*) Quadritubercular, tending to become bilophodont, V-shaped pattern in *Alouatta* may be primitive
Hypoconulid of m_3	Well developed	(*R*) Absent
Metacristid	Absent	(*P*) Present in *Alouatta* (on m_3)

In view of the great number and importance of the above noted characters separating *Notharctus* from the Platyrrhini, which would be greatly extended if the characters of the vertebræ and limbs were added, it would seem highly inadvisable to adopt the classification proposed by Dr. Wortman (1903, pp. 410–414), in which *Notharctus* and *Adapis*, after being widely separated from the Lemuroidea, were bracketed with the Cebidæ, Cercopithecidæ, Simiidæ and Hominidæ in the "superfamily Neopithecini." To such extremes the "phylogenetic system" of classification inevitably leads; because it aims chiefly to express hypotheses as to lineal derivation, rather than to symbolize the degrees of homological resemblances and differences between related groups.

On the other hand, there may be considerable merit in Dr. Wortman's suggestion (*op. cit.*, p. 412) that the Adapidæ (including *Notharctus* and *Adapis*) "as far as can be now ascertained from the remains, occupies a position not far removed from the common primitive stem from which the great majority of the living simian population of the Old and New Worlds originated. In the case of the Old World families, the gap is as yet very wide, but in the case of the New World Cebidæ, the interval is much less, and is not greater than one would be reasonably led to anticipate between an ancestor of Upper Eocene time and a living descendant...."

Dr. Wortman was apparently led to this fortunate inference (which coincided with that of Leidy) by his observation that the *Tarsius*-like group (Paleopithecini) evince a precocious enlargement of the brain and reduction of the premolars combined with a "primitive" condition of the lacrymal; while "*Adapis* and *Notharctus* exhibit advance in the reduction of the lachrymals, but retain the more generalized features of the dentition and brain enlargement. These are the essential differences between the two lines and mark out very distinctly the trend as well as the possibilities of their future development. It is in just such a group as that which includes *Adapis*, *Notharctus* and *Limnotherium*, that we must seek for the beginnings of the higher monkeys and apes which follow; and while these species, at present the only well known types of the series, may not have been in the direct line of descent, they can not at the same time have been far removed from it. *Omomys* and *Washakius*, as far at least as we are permitted to judge from their scant remains, are closely related to *Adapis* and *Notharctus*, but had made greater progress in the reduction of the premolars. This gives an especially monkey-like appearance, pointing particularly in the direction of certain living Cebidæ...."

The writer cannot accept Dr. Wortman's view that the lacrymal of the *Tarsius* group is "primitive" as compared with that of *Notharctus*. For reasons which will be later given (Amer. Mus. Bull.) the preorbital extension of the lacrymal and the preorbital position of the lacrymal foramen in these animals are regarded by the writer as secondary, not primitive characters. Nor can the view that "*Adapis* and *Notharctus* exhibit advance in the reduction of the lacrymals" be accepted. The whole face of *Notharctus* appears to be in very primitive condition with characters ancestral to those of both the lemuroid and the platyrrhine groups.

Setting aside for the present the debatable question whether the Old World and the New World series have been derived from the same stock, and noting that *Omomys* and *Washakius* probably belong with the *Tarsius*-like Primates and have nothing to do with the Cebidæ, we find, after an extended comparison between *Notharctus* and the Platyrrhini, that the fuller evidence supports Dr. Wortman's conclusion that the "interval. . .is not greater than one would be reasonably led to anticipate between an ancestor of Upper Eocene time and a living descendant." There can be no doubt of this statement, with reference to the great majority of the characters separating the modern Platyrrhini from *Notharctus*, which are nearly all correlated directly with the progressive enlargement of the brain, with the shortening of the face and with the mingling of retrogressive and progressive changes. *Notharctus* also shows certain important special resemblances with the Platyrrhini in the form of the incisors, in the formulæ of the adult and deciduous dentitions and in the direction of evolution of the premolars; this last resemblance is especially striking if we compare the lower premolars of *Notharctus pugnax* with those of *Alouatta*. If the posterointernal cusps of the upper molars of the Platyrrhini be pseudohypocones, as the conditions in *Callithrix* apparently indicate, another and very important resemblance must be recorded.

There are other differences between *Notharctus* and the Platyrrhini, which certain investigators may be inclined to interpret as divergent specializations, tending to exclude the former from structural ancestry to the latter. Of first importance is the difference in the relations of the tympanic ring to the bulla. A working hypothesis as to the probable history of the tympanic region in the ancestors of the Platyrrhini is as follows.

The primitive mammalian condition (in which the tympanic ring was entirely outside of the bulla and which is still illustrated in the fœtal *Chiromys* [1]) had been replaced by the stage illustrated in *Adapis* and *Notharctus*, in which the expanding hypotympanic sinus had overgrown ventrally the tympanic ring. The rapid transverse expansion of the brain initiated a secondary uncovering of the ring in the following manner. The tympanic ring, retaining its connections with the entoglenoid and post-tympanic processes, shared in the general lateral displacement of this region, while the bulla itself remained fastened to the side of the basioccipital and to the posteroexternal corner of the basisphenoid. The ring was first exposed at the aperture of the bulla, then protruded from it and then began to overlap it. Meanwhile the cavity of the bulla itself diminishes, it retains the cancellous condition which usually precedes the resorption of its tissue, while the tympanic enlarges, spreads over the bulla and becomes cancellous. In favor of the view that the overlapping of the ring by the bulla in the Eocene and recent lemuriformes is primitive for all primates is the presumably primitive form of the tympanic ring in these animals, the association of this primitive ring with the relatively primitive position and course of the internal carotid artery (see above), the retention of the stapedial branch, the apparently primitive unexpanded condition of the brain, the prevailingly primitive dentition, etc. It might be objected that by the Law of Irreversibility of Evolution if the ring was originally exposed and was then covered up it would be impossible for Evolution to reverse itself and uncover the ring again. But such an interpretation of the Law of Irreversibility would require proof.

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[1] Forsyth Major, 1899, p. 987.

An alternative hypothesis is that the platyrrhine condition has been derived from a stage in which the bulla had not yet overlapped the ring, as may also be the case in the Lorisidæ and Tarsiidæ. Modern lemurs including *Chiromys* actually pass through this stage in their development (F. Major, 1899, pp. 987–988). The possible objection to this hypothesis is that even although all lemuroids pass through a stage in development in which the ring is outside the bulla, yet it is simply a primitive placental condition antedating the proto-lemurine stage.

Pari passu with the changes in the accessory auditory structures the position and course of the main carotid artery and its stapedial branch were materially changed. It sank beneath the surface of the periotic, lost the stapedial branch and passed through the body of the periotic, avoiding the basisphenoid and emerging in the brain-cavity behind the sella turcica. This arrangement of the carotid and its branches appears to represent an advance upon the conditions preserved in the Notharctinæ, Adapinæ, Lemuridæ, Indrisidæ and Chiromyidæ. If the arrangement of the carotid in the Platyrrhini is secondary it is not unlikely that the auditory region itself is equally modified and that here as elsewhere in the brain and brain-case the Lemuridæ and, still more, their Eocene relatives the Notharctinæ, have retained the ancestral conditions for all Primates.

SUMMARY OF THE STRUCTURAL AND GENETIC RELATIONS OF *NOTHARCTUS* WITH OTHER PRIMATES

The skeletal remains of the Middle Eocene lemuroid *Notharctus* described above are of great interest because they represent a primate which is at once the oldest and the most primitive that is known from adequate material. They afford a knowledge of the skull, vertebræ, girdles, and limbs, and thus they are of much greater morphological importance than many of the genera and species that were founded only upon fragments of the dentition. They also serve to establish the geological antiquity of a general skeletal type that is preserved, with some alterations, in the modern lemurs; finally, by comparison with other extinct and recent types, they supply an important chapter in the evolutionary history of the entire order. *Notharctus* and its predecessors thus stand relatively near to the base of the order and represent in many respects the earliest ancestors of the higher primates. They also tend to connect the primates with some group of arboreal insectivores, probably the Mesozoic ancestors of the Menotyphla.

The relatively primitive character of *Notharctus* becomes more evident when we compare it on the one hand with other Primates and on the other hand with the Paleocene and Eocene mammals of many orders, which are extensively represented in the collections of this Museum.

The more striking osteological characters of *Notharctus*, as well as its remarkably primitive nature, may be summarized by contrasting it broadly with *Homo*, *Lemur* and other Primates.

Limbs and Vertebræ

First, then, *Notharctus* was an arboreal, quadrumanous lemuroid of the Middle Eocene Epoch, whereas *Homo* is a terrestrial bipedal, bimanous anthropoid of the late Tertiary, Quaternary, and Recent epochs. This contrast in mode of locomotion, in environment, and in geological age is reflected in the entire anatomical difference between these respectively highest and lowest of the primates. The hands and feet of a mammal more readily reveal its mode of locomotion and probable environment than does any other part of the body, so that we look first to these elements in *Notharctus*, and we find that they differ only in minor details from those of existing lemurs; that is to say, the hands and feet were specially adapted for grasping and clinging to the branches of trees. In the hind feet the first digit, or hallux, is very large and normally set off at nearly a right angle from the other digits; its distal phalanx is flattened for the support of a broad nail and at the proximal end of the first metatarsal is a large, inwardly projecting process, for the attachment of the tendon of the peroneus longus muscle. The whole form of this digit implies that the flexors and adductors of the hallux were at least as powerful as they are in the modern lemurs. As a whole the hind foot, which is well adapted for both leaping and grasping, differs from that of *Lemur* chiefly in having the metatarsals shorter and stouter, the proximal phalanges elongate. In man, on the contrary, the foot has become adapted for terrestrial bipedal progression, the great toe having become parallel to the other digits, the instep arched, the phalanges much shortened, the toes extended and the foot planted firmly on the ground; so that the chief vestiges of ancestral arboreal habits are the great size of the first digit, the strong development of the flexors, adductor obliquus and transversus muscles of the hallux and the presence of flat nails on all the digits.

The hand of *Notharctus*, so far as preserved, appears to be in the main like that of modern lemurs and to be adapted rather for tightly clinging to the branches than for the manifold use of the hand that is attained in man. The scapula and clavicle are as in lemurs. The humerus, while nearest to that of *Lepilemur* among recent primates, is remarkable for its shortness and width, for the emphasis of the delto-pectoral crest, of the external epicondylar crest and of the entocondylar projection, all this implying powerful climbing muscles. The radius resembles that of *Lemur* except that it is shorter; its subcircular head shows that *Notharctus* had the power of supinating the forearm, which is a first requisite for a climbing animal and a heritage of all primates. In the man-anthropoid group this power has been developed to completion.

The vertebræ of *Notharctus* are closest to those of *Lemur;* their detailed conformation implies that the backbone as a whole was usually held in a more or less horizontal position rather than in the sitting posture so often assumed by the higher primates. The cervical vertebræ are relatively elongate, in conformity with the *Lemur*-like form and pose of the skull; the dorsal vertebræ are small, this implying a relatively small thorax. The lumbar vertebræ have elongate, vertically shallow centra with large parapophyses and forwardly directed neurapophyses, as in climbing and leaping mammals, especially the lemurs, whereas in the erect *Homo* and other primates which sit upright the lumbar centra are short and wide, the parapophyses are smaller and spring from higher up on the sides of the vertebræ and the wide neurapophyses are directed more or less backward. All these details of the lumbar vertebræ imply a development in *Notharctus* of the psoas, quadratus lumborum, erctor spinæ, and other muscles of the lumbar region similar to that of animals which leap on all fours. The detailed conformation of the sacral, coccygeal, and caudal vertebræ of *Notharctus* shows that the muscles for raising and lowering the tail and for moving it laterally were essentially the same as in *Lemur* only less robust, and that it was not a prehensile tail such as that of the typical South American monkeys.

The pelvis likewise offers a wide contrast to that of *Homo* and of all the Anthropoidea, a contrast which is expressive of the wide difference in mode of locomotion and habitual pose of the body. The ischial tuberosities are not expanded as they are in *Homo* and in all other primates which habitually sit upright. The narrow blade of the ilium differs from that of *Lemur* chiefly in its shortness and in the depth of the fossa for the deep gluteal muscles, whereas in the erect *Homo* the blade of the ilium is much widened for the support of the heavy viscera and robust abdominal muscles and for the insertion of the spreading muscles of the buttocks. Very characteristic of *Notharctus* and the lemurs is the presence of a strongly marked protuberance on the anteroventral border of the ilium in front of the acetabulum. This is homologous with the anteroinferior spine of the ilium in man and served partly for the origin of the powerful rectus femoris, a muscle of great importance in leaping.

From the more extended comparisons made in the preceding pages it is inferred that *Notharctus* and still more its primitive ancestors, the first primates, were somewhat less agile in their movements than are their more highly specialized descendants; that at first they climbed and leaped about the trees more cautiously, clinging tightly to the branches, and "brachiating" or leaping with the arms, less effectively.

Skull

When we compare the skull of *Notharctus* with those of *Homo* and of the higher primates the difference in general appearance is so great that were it not for the existence of a number of structural intermediates the cautious morphologist would hesitate to affirm that the remote ancestors of man had any special resemblances in the skull to this humble lemuroid.

In man, and to a less extent in the young of the great apes, the brain-case, especially the chamber that lodges the cerebrum and the cerebellum, is enormously expanded and dome-like; the facial part of the skull, which lodges the olfactory organs and supports the dentition, is excessively shortened and retracted beneath the anterior end of the brain-case. In *Notharctus* on the other hand, as in many other primitive mammals, the brain-case forms only about half the total length of the skull; the face is elongate and fox-like, with large olfactory chamber and long jaws, and is situated wholly in front of and not below the brain-case.

In man the premolars are reduced to two on each side above and below, in correlation with the shortening of the face; *Notharctus* on the other hand retains four premolars on each side above and below as do also the most primitive placental mammals.

In man the opposite premaxillary bones are much retracted and are fused with the true maxillæ; in *Notharctus* on the contrary the premaxillaries remain separate, occupy their primitive mammalian position and are extended far in front of the maxillaries.

In man the forward growth of the temporal lobes of the brain has, as it were, pushed forward the ascending wing of the alisphenoids so that they have gained contact with the orbital wall of the malars and with the postorbital flanges of the frontals, these three elements thus closing the orbital cavity posteriorly. Essentially identical conditions obtain in the great apes and in all the Old World and New World monkeys, but in *Notharctus*, as well as in the existing lemurs, this closing has barely begun: the temporal lobes of the brain and the temporal wings of the alisphenoids still lie far behind the orbits, which therefore open widely into the temporal fossæ. The chief feature which distinguishes *Notharctus* as a primate in this region is the narrow union of the ascending orbital process of the malar with the descending postorbital process of the frontal, so that the orbit is guarded posteroexternally by a bony ring as in lemurs. In man the orbits are directed forward; in the far more primitive *Notharctus* the orbits look outward and upward as well as forward.

In man as well as in the young of all the great apes the top of the brain-case is not surmounted by a median or sagittal crest for the attachment of the temporal muscles, and the dorsal limit of these muscles does not extend to the mid-line; but in *Notharctus* the occiput is narrow and not expanded and the lambdoidal crests which form its margins are sharp projecting ridges; so that in this region, as well as in the whole lateral and superior aspects of the skull, *Notharctus* is like an opossum, one of the most primitive of existing mammals, and its skull thus seems at first sight totally different from the large-brained, short-faced skull of man.

The palate of *Notharctus* is long and narrow whereas in many of the higher primates it becomes short and broad. The upper dental arch is pointed in front instead of arched or convex. The small pterygoid fossæ of *Notharctus* are most nearly represented in the modern lemurs but are variously widened in the Old World monkeys and in the man-anthropoid groups, perhaps in correlation with an increase in size in the internal pterygoid muscles. The descending or pterygoid plate of the alisphenoid of *Notharctus* is very large and extends backward and outward to the glenoid region and to the auditory bulla, as it did in primitive placentals of the Eocene and as it still does in somewhat reduced form in certain lemurs; whereas in the higher primates it is generally separated from the glenoid region and from the auditory bulla by a considerable interval. In this feature the closest resemblance is with *Adapis* of the Eocene of Europe.

The auditory bullæ of *Notharctus* also afford a ready means of distinguishing it from the Man-Great-ape group and from all other Primates except *Adapis* and the lemurs. The bullæ consist of hemispherical swellings, formed probably as a vesicular outgrowth of the petrosal, situated immediately behind the pterygoid plate of the alisphenoid and internal to the glenoid region; they cover the small auditory prominence of the petrous bone, and are continued anterointernally into processes which articulate with the basioccipital and basisphenoid. The ring-like tympanic bone was covered by the bulla. All the construction in this region conforms to the plan of *Adapis* and the lemurs and is far more primitive than the conditions seen in the auditory region of the New World monkeys, of the Old World monkeys and of the man-anthropoid group.

Notharctus differs from all apes and monkeys and even from all lemurs, except *Adapis*, in the shortness of the basioccipital segment. This is correlated with the much smaller brain-capacity and is in harmony with the low, short brain-case. The position of the condyles, which face chiefly on the back of the occiput instead of being more or less beneath the occiput, clearly shows that the head was not bent at so sharp an angle with the neck as it is in man and many other Primates, but that it was held more as it is in lemurs; the inclination of the basifacial to the basicranial axis was even less than it is in the modern lemur and offers a wide contrast to the sharply inclined basifacial axis of New World monkeys, Old World monkeys, great apes, and man.

Mandible

The lower jaw of *Notharctus* is distinguished from those of modern apes and of man by its greater length and slenderness and to a much less degree from that of *Lemur* by its greater depth and robustness. The symphysis is fused in old individuals, a character that foreshadows the early fusion of the symphysis in Man and all the Old World and New World Primates. The lower border of the jaw is curved and the angle is produced into a long, broad, posterior process which is incurved below. On the inner side of this process was inserted the internal pterygoid muscle, which had its origin on the elongate pterygoid plate of the alisphenoid and in the pterygoid fossa. This is very probably the primitive condition for all primates. The form of the condyles and of the teeth show that the jaw was moved obliquely from side to side in chewing. The mandibular condyles were rounder and less flattened than those of lemurs, less transversely expanded than those of New World monkeys, great apes, and man.

In this connection may be quoted Leidy's sagacious remarks in 1873 on the lower jaw and dentition of *Notharctus:*

> In many respects the lower jaw of *Notharctus* resembles that of some of the existing American monkeys quite as much as it does that of any of the living pachyderms. *Notharctus* agrees with most of the American monkeys in the union of the rami of the jaw at the symphysis, in the small size of the condyle, in the crowded condition of the teeth, and in the number

of incisors, canines and true molars, which are also nearly alike in constitution. *Notharctus* possesses one more premolar and the others have a pair of fangs. The resemblance is so close that but little change would be necessary to evolve from the jaw and teeth of *Notharctus* that of a modern monkey. The same condition which would lead to the suppression of a first premolar, in continuance would reduce the fangs of the other premolars to a single one. This change, with a concomitant shortening and increase of depth of the jaw, would give the characters of the living *Cebus*. A further reduction of a single premolar would give rise to the condition of the jaw in the Old World apes and man.

Dentition

The adult dental formula of *Notharctus* is

$$(I\tfrac{2}{2}\ C\tfrac{1}{1}\ P\tfrac{4}{4}\ M\tfrac{3}{3}) \times 2 = 40.$$

This is undoubtedly the primitive formula for Primates and it differs from that of the most primitive placental mammals only in the reduction of the incisor formula from $I\frac{3}{3}$ to $I\frac{2}{2}$. In later Primates this formula suffers various reductions: as by the loss of some of the incisors (Indrisidæ, Chiromyidæ), of the anterior premolars ($p\frac{1}{1}$) (most lemuroids, New World monkeys), of $p\frac{1}{1}$ and $p\frac{2}{2}$ (Indrisidæ, Old World monkeys, great apes, man).

The central upper incisors of *Notharctus* have short, anteroposteriorly elongate, compressed crowns and the lateral upper incisors are small and round-topped; the upper incisors are thus more primitive in form than the chisel-like incisors of man and of the Old World and New World monkeys; a somewhat similar style of incisors has survived in the modern *Chirogaleus*. The lower incisors of *Notharctus* are much less specialized than those of *Lemur* in their more or less spatulate form and wide cutting edge, much as in the New World and Old World monkeys, whereas in *Lemur*, the lower incisors are degenerate, procumbent, styliform, compressed. The upper and lower canines of *Notharctus* are caniniform, but of a more primitive type than the variously modified canines of later primates.

The first upper premolar of *Notharctus* is small and of little functional importance. The crown of the second upper premolar consists of a single compressed cusp supported by an incipiently two-rooted fang. In more recent lemurs the anterior upper premolar (p^2) often becomes much compressed; in the South American monkeys it becomes widened into a bicuspid tooth with a single external root; in the Old World monkeys, great apes, and man the second upper premolar (p^2) of the primitive mammalian dentition has been crowded out, and the first bicuspid tooth, immediately behind the canine, is p^3. Here again *Notharctus* is obviously more like other primitive placentals than are any of the later lemurs or monkeys.

The third upper premolar (p^3) of *Notharctus* has an outer wall with two roots, a well-defined external cingulum, a conspicuous external cusp, a small mesostyle or external intermediate cusp and a low narrow internal cusp which is continuous with the internal cingulum. This primitive style of premolar, which approaches that of Eocene Carnivores and other primitive placentals, is variously modified in the higher primates, often becoming bicuspid, as in man.

The fourth upper premolar (p^4) is considerably larger than p^3 and is also more complicated, as is generally the case in primitive Eocene mammals, the simpler pattern of the premolars in the higher primates being wholly unlike that of primitive Eocene mammals and obviously retrogressive. P^4 has a large internal cusp, which is rounder and more symmetrical than the corresponding cusp of p^3, its outer wall is higher, flatter, more symmetrical, and in the higher species of *Notharctus* it is divided into two cusps. This largely primitive type of p^4 is variously transformed in the higher primates: in many lemurs, its internal cusp is reduced and the outer wall is compressed, in the monkeys of the New and Old Worlds, as well as in the great apes and man, p^4 is widened transversely and is bicuspid.

The first and second lower premolars of *Notharctus* are small, slightly compressed, conical teeth, more like those of other primitive Eocene mammals than those of later primates. The third lower premolar, which is homologous with the anterior premolar of man and his allies is a compressed two-rooted tooth with a high anterior cusp and an extremely small rudiment of a posterointernal cusp. The fourth lower premolar, equivalent to the posterior premolar of later primates, has begun its transformation into the molar type, that is it possesses an imperfectly differentiated anterior trigonid and a low, small talonid, a primitive condition as compared with the variously modified posterior premolars of higher types. In the lemurs for example, it becomes much compressed, in the platyrrhines it is shortened and usually more bicuspid; but some primitive forms, e. g. *Nyctipithecus*, retain traces of the talonid; in the catarrhines it becomes bicuspid with a blunt wide talonid; in man it becomes entirely bicuspid.

The first and second upper molars of *Notharctus* retain clear traces of the tritubercular pattern, which is characteristic of primitive Eocene mammals; but this pattern is modified by two features of progressive specialization: first, the presence of a fourth, posterointernal cusp or pseudohypocone (which in this subfamily represents a posterior budding from the main anterointernal cusp or protocone); secondly, the presence of a mesostyle or external intermediate cusp, lying at the point of union of the two external V's or cutting wedges. This general type of upper molar has been several times evolved in various races of mammals which have changed from a partly insectivorous to a more frugivorous or vegetation diet. It is correlated with a slight lateral swing of the mandible in mastication. The third upper molar lacks the posterointernal cusp or "pseudohypocone." The molars have distinct internal cingula, a feature which is lost in many later primates. So far as the available evidence indicates the molar pattern of *Notharctus* may well be ancestral to those of the New World primates.

The ancestors of *Notharctus*, of the genus *Pelycodus*, which have been followed back far into the beginning of the Lower Eocene, show a closely graded series of stages in the evolution of the pseudohypocone, leading back to a nearly simple tritubercular type. The pure tritubercular pattern was very probably characteristic of the as yet undiscovered Paleocene ancestors of the whole primate series.

The general pattern of the crown of the first and second lower molars is similar to that of many Eocene mammals: each molar bore four main cusps arranged in two transversely placed pairs, and a vestigial anterior cusp or paraconid. The anterior pair, consisting of the anteroexternal cusp or protoconid and the main anterointernal cusp or metaconid, were joined by a low transverse crest, the protolophid; the talonid or posterior moiety of the tooth bore a broad V on the posteroexternal cusp or hypoconid and a low posterointernal cusp or entoconid. The third lower molar also bore an elongate third lobe or hypoconulid and its entoconid was reduced. The molars were all provided with external cingula. This quadritubercular type of lower molars is structurally ancestral, except perhaps in minor details, to the lower molars both of lemuroids and of higher primates, including man.[1] In the ancestral *Pelycodus* the anterior moiety of the molar crown consists of a small highly-set triad, or trigonid, of cusps followed by a low broad talonid. In association with tritubercular upper molars and small size these more or less "tuberculo-sectorial" lower molars of *Pelycodus* give evidence that the remote ancestors of *Notharctus* were probably more insectivorous and less frugivorous than the later genus, which may well have subsisted upon fruits, eggs, small birds, and insects, as in many recent primates.

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[1] Cf. Bull. Amer. Mus. Nat. Hist., XXXV, pp. 239–355.

TAXONOMIC CONCLUSIONS

I refer *Notharctus* to the suborder Lemuriformes rather than to the Neopithecini of Wortman, not primarily because it agrees with all the members of the former assemblage in a few arbitrarily selected structural details (which is a convenient method of analysis that has sometimes led to erroneous conceptions of genetic relations) but first because in the general stamp of its skeleton *Notharctus* is unmistakably nearer to *Adapis* and to the Malagasy lemurs than to any of the Anthropoidea.

Its lemuroid heritage is indicated in the following palæotelic lemuroid characters:

(1) The orbits are guarded posteriorly only by the conjoined processes of the postfrontal and malar, and the orbital fossa is not shut off from the temporal fossa by a frontal-alisphenoid partition, as it is in the anthropoidea.

(2) The auditory bulla, formed from the inflated entotympanic bone, covered over the delicate tympanic annulus, which thus did not form an exposed tympanic spout or ring as it does in the Anthropoidea.

(3) The course of the internal carotid artery (as indicated by the osseous tubes in which its branches coursed) was identical with that of a typical lemur.

(4) The inflated portions of the opposite bullæ were not extended inward toward the mid-line as they are in *Tarsius* and the Anthropoidea.

(5) The elongate pterygoid plates of the alisphenoids extended back to the auditory bullæ, whereas in the Anthropoidea they are well separated from them.

(6) In the lower jaw the horizontal ramus was of moderate depth with a well curved lower border, which contrasts with the slender elongate jaw, with a straight lower border, of *Lemur*. The angle formed a long stout backwardly projecting process, which is variously reduced in recent Lemuroidea and Anthropoidea.

(7) The anterior portion of the malar if not in actual contact with the lacrymal certainly came very close to it, whereas in tarsioids and anthropoids it becomes widely separated from the lacrymal and limited to the outer side of the orbit.

(8) The lacrymal was wholly within the orbit, instead of being widely extended on the face, as it is in modern lemurs; and the lacrymal foramen was marginal, instead of being anterior to the orbit.

(9) *Notharctus*, in common with *Adapis*, retained the high sagittal and lambdoidal crests which are characteristic of primitive placental mammals, but are reduced in modern lemuroids and anthropoids.[1]

(10) The brain-case was much less expanded than in modern lemuroids and the olfactory chamber was well developed, this indicating a low type of brain.

(11) The dental formula, $I\frac{2}{2}\ C\frac{1}{1}\ P\frac{4}{4}\ M\frac{3}{3}$, is undoubtedly the primitive lemuroid formula.

(12) The central or inner upper incisors have compressed low crowns, a type which is also represented in *Chirogaleus*, although somewhat modified in form. The lateral upper incisors had small rounded crowns.

(13) The lower incisors were spatulate or chisel-shaped, not procumbent and styliform as in modernized lemurs.

(14) The upper and lower premolars were more primitive (more like those of primitive Eocene placental mammals) than are those of any modern lemuroids.

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[1] The crests of the gorilla skull are regarded as secondary.

(15) The upper and lower molars retain clear traces of derivation from the more primitive almost pure tritubercular type exemplified in the earlier species of *Pelycodus*, but in *Notharctus* this lemuroid heritage had been masked by certain cænotelic characters mentioned below (p. 186).

(16) The vertebral formula was probably C7, D12, L8, S3, Cd?28. The vertebral column exhibits the following primitive lemuroid features: the neck was relatively long as in *Lemur*, the small dorsal vertebræ indicate a relatively small thorax; the lumbar vertebræ have vertically shallow elongate centra, with wide transverse processes and forwardly directed neurapophyses, as in leaping animals; the sacrum consists chiefly of a large widely expanded vertebra which bore nearly the whole of the articular surface for the ilium, followed by two much smaller vertebræ with widely extended transverse processes; the coccygeal and caudal vertebræ were in general similar to those of *Lemur*, but less robust.

(17) The whole forearm is stouter and shorter than that of *Lemur*, the humerus being especially robust, with marked development of the delto-pectoral and external epicondylar ridges, and a large entocondyle; the entepicondylar foramen is present. The radius, ulna, and metacarpals are also shorter and stouter than in *Lemur*. These are probably all primitive lemuroid characters.

(18) The pelvis is of a very distinctly lemuroid type: the blade of the ilium is short, narrow and projects far in front of the sacrum; its gluteal surface is not flattened and expanded transversely as it is in typical Anthropoidea; the process for the insertion of the rectus femoris muscle, in front of the acetabulum, is very prominent; the ischial tuberosities are little if at all expanded transversely (this indicating little if any special fitness for sitting upright).

(19) The femur is similar to that of *Lemur*, but the head is more sessile, the great trochanter smaller, and the patellar trochlea has a more prominent external condylar ridge. The tibia and fibula were shorter and more robust than in *Lemur*. Presumably these are all primitive lemuroid characters, which may indicate a leaping power somewhat inferior to that of *Lemur*.

(20) The pes is typically *Lemur*-like in the form of the astragalus, calcaneum, and other tarsals and especially in the form of the hallux, a very large powerful digit which was normally set off from the other digits nearly at right angle. The proximal end of the first metatarsal bears a large, long, inwardly directed process for the attachment of the tendon of the peroneous longus muscle. The large distal phalanx of digit I was widely flattened for the support of a broad nail. The metatarsals of digits II–V were much shorter and stouter than those of *Lemur*, that of digit II being especially short. The proximal phalanges were longer than those of *Lemur*. It is not certain whether digit IV or digit III was the longest.

So far as the available evidence indicates, all the above-mentioned characters appear to constitute a primitive lemuroid heritage which has been variously modified in the later lemurs. *Notharctus* itself, as well as all the other members of the subfamily Notharctinæ, are apparently excluded, however, from direct ancestry to modern lemurs by the presence in the upper molars of external intermediate cusps, or mesostyles, and of well-developed posterointernal cusps or pseudohypocones. In *Notharctus crassus* these specializations are further advanced. *Pelycodus*, the direct ancestor of *Notharctus*, has more primitive tritubercular molars, which approach but do not actually realize the structural ground plan for all higher primates.

The nearest known contemporary relatives of the Notharctinæ were the Adapinæ of the Eocene of Europe, which were probably closely related or directly ancestral to the modern Lemurinæ, Chirogaleinæ and Megaladapinæ, as held by Leche and Forsyth Major.

As stated above (p. 219) it is quite possible that the New World primates have been derived from

Notharctus or its allies, a suggestion first made by Leidy in 1873 and independently put forth by Wortman in 1903. Indeed there is no feature hitherto observed in the entire skeleton of the New World primates which may not very probably be regarded as a derivative of a more primitive condition in *Notharctus;* in other words, in spite of the wide structural and palæontological hiatus between the Middle Eocene *Notharctus* on the one hand and the Miocene and recent New World primates on the other, we can feel reasonably confident that although *Notharctus* may not be a direct ancestor of the latter group, it is in general a structural ancestor.

INFERRED CHARACTERS OF THE COMMON LEMURIFORM STOCK ANCESTRAL TO ADAPINÆ AND NOTHARCTINÆ

While the earliest known members of the Notharctinæ and of the Adapinæ have already entered upon the paths of specialization leading to their respective terminal stages, they are so much nearer to the common stem form than are the later types that with the aid of the "Law of Trituberculy" it is not difficult to reconstruct that form with some approach to accuracy. As to the general doctrine that the Eocene representatives of many modern orders were tending back toward generalized insectivorous dentitions, with the formula $I\frac{3}{3}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$, with tritubercular upper molars and tuberculosectorial lower molars, the evidence is so abundant and so familiar to palæontologists that it need not be itemized at this point. Even Dr. Stehlin, whom none could justly accuse of being hasty in such matters, admits that all the diverse patterns of the molars of Eocene Primates have been derived from a "tritubercular-sectorial" structural plan. He says (1916, p. 1533)

> Es bedarf keiner unständlichen Nachweise, dass der Molarstructur der Primaten der "tritubercular-sectoriale" Bauplan zu Grunde liegt. Bei den meisten Stämmen des Eocaens sind die Grundzüge desselben noch sehr deutlich erhalten, nur bei den neogenen Cercopitheciden finden wir sie völlig verwischt. Immerhin machen sich zahlreiche kleinere und grössere Modificationen des Urplanes schon im Eocaen geltend. Sie erfolgen wie bei den Artiodactylen nach stark divergierenden Richtungen und liefern uns für die Ergründung der Stammesgeschichte schätzenswerthe Anhaltspunkte, welche schon darum ein sorgfältiges Studium verdienen, weil ja nur gar zu viele Formen vorderhand ausschliesslich oder fast ausschliesslich durch ihre Backenbezahnung belegt sind.

The probable characters which may be assigned provisionally to the dentition of the ancestral subfamily of the Adapidæ appear to be as follows.

Paleocene of Asia (?). Size small, diet insectivorous or incipiently frugivorous. Upper molars tritubercular, with neither hypocone nor pseudohypocone; upper molar cingula well marked, para- and metacone conical, not V-shaped. No mesostyles; m^2 wide transversely. Lower incisors of small size, not chisel-shaped, not strongly procumbent; canines single-rooted, of moderate size; premolars simple, p^4 with a single external cusp and but little internal spur (protocone); p_4 with very small low talonid, no distinct hypoconid; lower molars with high primitive trigonid, retaining the paraconid, and low, not much expanded talonid, with very low entoconid; m_3 with basin-like hypoconulid; all molars in use along with the deciduous molars.

Some of the foregoing characters are retained in the more primitive members of the known subfamilies.

To this hypothetical primitive subfamily may also be assigned such primitive dental characters as are retained by both the known subfamilies, especially dentition $I\frac{2}{2}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$; $DI\frac{2}{2}$, $DC\frac{1}{1}$, $DP\frac{3}{3}$; protoconule of upper molars forming with the protocone a low oblique crest; metaconule tending to connect metacone and protocone.

It may be objected that most of these are generalized dental characters of Eocene primates and do not give a very detailed picture of the precise characters of the teeth in the ancestral Adapidæ; but if it be admitted that this reconstruction is supported by the available evidence, it would certainly be injudicious to attempt to carry the process into the finer details which invariably impart specificity to actual specimens.

Our conception of the ancestral characters of the dentition in the primitive Adapidæ should be clearly adjusted to our conception of the ancestral skull characters and vice versa. And here it becomes necessary to consider the probable relations of the ancestral Adapidæ to the *Tarsius*-like primates of the Lower Eocene. These, so far as known, are mostly very small animals, with large orbits, delicate muzzles, a wide expanded brain-case with slight or no sagittal crest, malars delicate and widely separated from lacrymal, a wide rounded occiput, much enlarged bullæ, wide and triangular upper molars, more or less crowded or reduced incisor and premolar series, often with one or another of the lower incisors enlarged and procumbent and with the lower canines either reduced or enlarged procumbent. Although this group of primates in the known palæontological record is nearly as old as the oldest of the Notharctinæ, the writer has little hesitation in regarding them as in all characters more specialized than the hypothetical ancestors of the Adapidæ described above. Probably more or less nocturnal, and with many relatively advanced specializations for the quick pursuit of hardshelled insects in the trees, they were among the earliest specialized side groups of the primates, with precociously enlarged brains and sense organs and correspondingly specialized skull characters and with aberrant specializations of the dentition.

The hypothetical ancestors of the Adapidæ or even the most primitive Lower Eocene members of the Notharctinæ on the contrary had more slowly and conservatively developed the general primate tendency to enlarge the brain-case; they had also begun to develop insectivorous-frugivorous specializations in the dentition. The little that is known of the skull of the oldest members of the Lower Eocene Notharctinæ indicates that in these small animals the brain-case and orbits were somewhat larger and all the muscular crests less extremely developed than in their descendants of the Middle Eocene. It is, in fact, a well recognized general rule, cited by Dr. Stehlin (1916, p. 1526), that small mammals have relatively larger brains, less elevated sagittal and lambdoidal crests than those of their large-bodied relatives, the species of *Marmosa* and *Didelphys* as well as the genera of the modern Lemuridæ furnishing beautiful examples of this principle. There are also Eocene genera of somewhat doubtful position (*Pronycticebus, Aphanolemur*), with the brain-case less expanded than in the known *Tarsius*-like primates, but more expanded than in any of the typical Adapinæ and Notharctinæ. Of these *Pronycticebus* has the malar region more like that of the Adapidæ; it has retained the primitive dental formula[1] and its dentition as a whole is of an extremely generalized character. It was formerly classed by the writer as a primitive member of the Adapidæ, using that term in its widest sense, and was regarded by its describer as ancestral to *Nycticebus*. Whatever its more precise systematic position may be it tends to confirm the view that the common ancestors of the *Tarsius*-like group and of the *Adapis-Notharctus* group were small animals with a moderately expanded brain-case and with all the dental characters assigned above to the ancestral primates.

The excessive development of the sagittal and lambdoidal crests in the later Adapinæ and Notharctinæ is not regarded by the writer as a part of their heritage from small-brained Mesozoic placentals. They are more probably progressive specializations correlated with progressive expansion of the muscles of

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[1] Although the incisors are lacking the very primitive number and character of the canines and premolars warrant the expectation that the incisors were equally primitive.

mastication and with the enlargement of the canines for fighting purposes and for the purpose of penetrating the tough rinds of fruits. More or less close analogies to the dentition and skull form of the later Notharctinæ are offered among the Procyonidæ (*Ælurus*) and even by the gorilla, of which the high sagittal and lambdoidal crests are clearly secondary and associated with a combination of frugivorous with pugnacious habits. The skulls of supposed females in the Notharctinæ have small canines, low muscular crests, a wider forehead and less constricted brain-case than in the far more specialized males. In the Adapinæ the excessive expansion of the jaw and muscle areas, joined with the presence of wide chisel-like incisors more or less analogous with those of the chimpanzee, the daggerlike canines and the sharp-crested molars, all indicate that in this subfamily the fruit eaten had a tough rind which enclosed resistant fibrous material out of which the juice was pressed and the nutritive tissue cut.

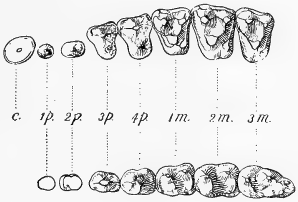

Fig. 80. Upper and lower teeth of *Pronycticebus gaudryi*. Middle Eocene (Bartonien). Twice natural size. After Grandidier.

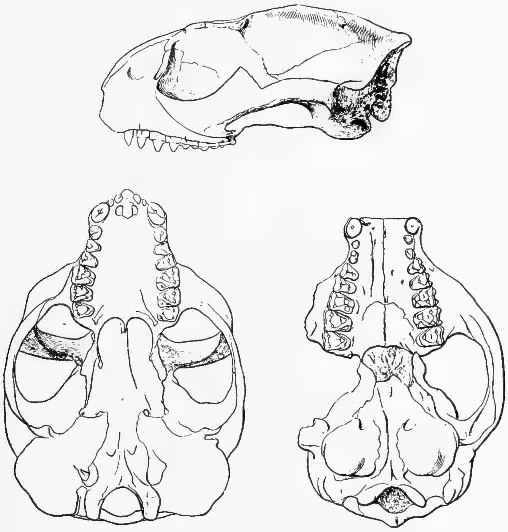

Fig. 81. Skulls of *Pronycticebus gaudryi* and of *Nycticebus tardigradus*. Natural size. After Grandidier.

From such considerations and from the detailed study of the divergent characters of the skull in the Adapinæ and Notharctinæ it seems probable that the ancestral protoadapine stock had the following skull characters:

Skull mesocephalic; orbits guarded posteriorly by a fronto-malar bar, orbits not very large; malar closely approaching or touching lacrymal; lacrymal wholly within orbit; lacrymal foramen marginal; malar probably not extending back to glenoid; low sagittal and lambdoidal crests, postorbital constriction moderate; brain-case not greatly expanded; supraorbital and interparietal not expanded to form a flat occipital roof; lower jaw slender with unexpanded angle; opposite rami not fused at symphysis. Middle part of cranium not shortened. Pterygoid plate of alisphenoid elongate, extending posteroexternally to contact with interoexternal process of bulla and with entoglenoid region of squamosal. Auditory region as in *Notharctus*: ring-like tympanic enclosed within bulla; anterior end of tympanic in contact with entoglenoid region, posterior end in contact with periotic, in front of carotid foramen and below post-tympanic process of squamosal; internal carotid canal running from posteroexternal angle of bulla forward on outer side of cochlea, piercing basisphenoid; stapedial branch present; bulla formed as an "osseous bubble" in the periotic, surrounding the membranous cavity of the latter (sinus hypotympanicus); communicating with the true tympanic cavity through the pneumatic foramen; osseous cochlea with about two coils; fenestra rotunda concealed from external view by post-tympanic process

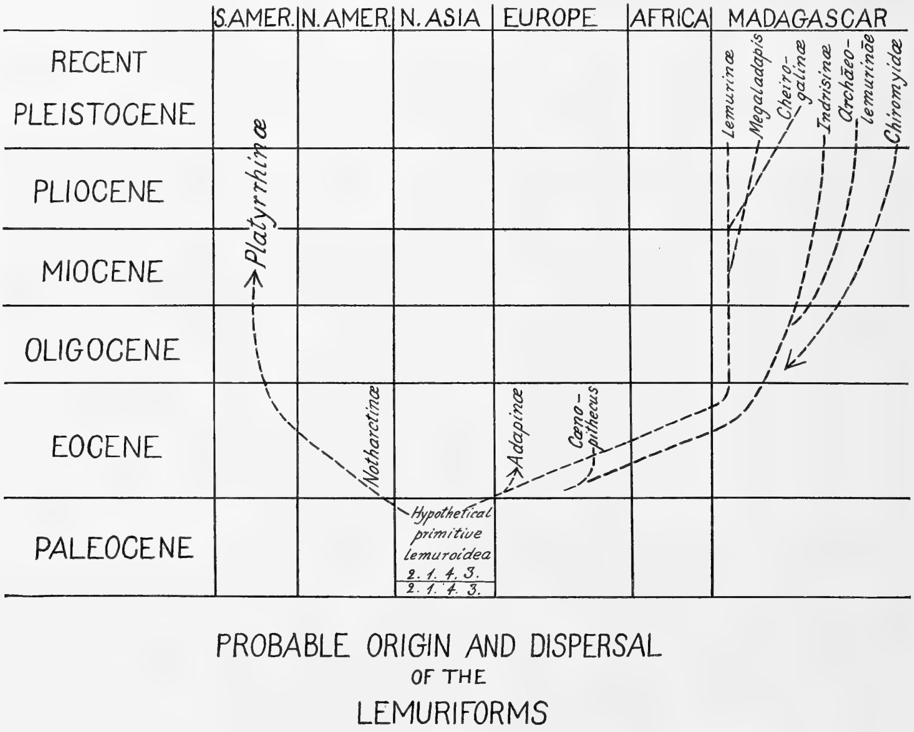

Fig. 82. Summary of the author's provisional conclusions regarding the origin, dispersal, and genetic relations of the lemuriform primates.

and mastoid; superior semicircular canal near the rim of the subarcuate fossa; mastoid not inflated, forming a prominent tuberosity. Vertical plate of palatine separated by a notch from alveolar region of maxilla. Basioccipital condyles extended vertically on occiput. Occiput triangular in general outline. All cranial foramina of primitive placental type. Foramen pterygospinosum present (piercing pterygoid plate of alisphenoid). Brain macrosmatic with large olfactory lobes, small frontal lobes and small cerebellum.

From present evidence it seems probable that these characters, or the great bulk of them, will also be found to describe the common Paleocene stem of all the divisions of the primates.

SUMMARY OF THE EVOLUTION OF THE LIMBS OF PRIMATES

At least as far back in geologic time as the Lower Eocene, certain primitive Primates (*Pelycodus*) which were the direct ancestors of *Notharctus* exhibited the same general type of limbs as that described above. Let us consider briefly the probable origin and evolution of this type. Many millions of years earlier, in Triassic times, the remote ancestors of the mammals probably arose from cynodont reptiles with very short hands and feet and stout limb bones. The existing monotremes may possibly be the remote descendants of these cynodonts, or, more probably, they may have been derived from some of the Therapsid group, such as the deinocephalians or the anomodonts which they resemble in many characters of the skull and skeleton. If the monotremes ever passed through an arboreal stage they have retained no clear trace of it at the present day, and more probably they branched off before the arboreal life was assumed. During the long ages of the Mesozoic era the ancestors of the existing marsupials gradually became adapted to arboreal life. They lost the subreptilian character of the pectoral and pelvic girdles that have been retained by the monotremes, and especially by sacrificing the bony connection between the coracoid and the sternum and by making a movable joint between the clavicle and the sternum, they gained great freedom of the forearms, which was a distinct gain in climbing.

Meanwhile the pads and friction ridges on the palms and soles and beneath the digits became segregated, differentiated and located at advantageous points, so as to increase the grasping power of the manus and pes. The pollex in the forefoot and still more the hallux on the hind foot became divaricated from the rest of the digits; the hallux especially increased in size and power of flexion and adduction. At the same time the muscles, joints, and ligaments of the hands and feet were improved so that the palms and soles could at one moment be spread out very flat and at the next moment drawn together, so as to press the epidermal pads and friction ridges against the branches.

The movements of the earliest arboreal mammals in climbing were probably cautious and rather slow. A striking and probably very primitive characteristic of the existing opossums (which are survivors of the Cretaceous ancestors of the marsupials) is their deliberate and cautious method of climbing, so that a close observer, Mr. S. H. Chubb, describes them as "flowing" over a surface. They do not fling themselves carelessly and lightly about among the branches, but grasp each branch very firmly, bringing the strong hand-like hind foot well forward and obtaining a firm grip before letting go with the hands. In climbing downward the tail trails along close to the branches in the rear, ready to seize hold if the feet slip. But the main grasping organs are the hind feet.

Certain arboreal marsupials on the contrary, especially the flying phalangers of several families, have entirely overcome this cautious timidity in climbing and take long leaps and gliding flights. So also we may infer that after the primitive marsupio-placental stock had learned to climb cautiously, some of them, especially the line leading to the primates, became more agile and began to leap from branch to branch.

But little is known concerning the evolution of the claws, which are usually of assistance in primitive climbing types. The claws on the oldest and most primitive known therapsid limbs (*Galepus*, *Galechirus* Broom) were of primitive reptilian type, somewhat compressed, gently curved and downwardly pointed. In the cynodont genus *Microgomphodon* Seeley (1895, plate I) the ungual phalanges were blunt and partly flattened, much like those of *Echidna*. In *Ælurosuchus browni* Broom (1906, Pl. X) the single claw phalanx preserved is moderately narrow, but less so than those of *Ornithorhynchus*. The change from compressed claws to flat claws is not a profound one, and in many groups (e. g., Chelonia, Dinosauria, Monotremata) we find both types represented.

In the arboreal ancestors of the marsupials the claws became compressed, curved and pointed, as they are in the opossums. The diversified descendants of the primitive Cretaceous opossums have the feet variously adapted for running (e. g., *Thylacinus*), swimming (*Chironectes*) hopping (*Peramelidæ*, *Macropodidæ*), digging (*Phascolomys*, *Notoryctes*), and so forth; meanwhile the primitive compressed claws and the characters of the palms and soles have undergone appropriate modifications, which have been described by Dollo, Bensley and others. Thus very probably the compressed claws of the opossum are near the primitive marsupial type. Accordingly the marsupials furnish some instructive hints as to the way in which the most primitive arboreal adaptations were first evolved, and the history of the group shows that this arboreal stage is capable of giving rise to a great diversity of terrestrial types.

The precise relations of the various placental orders to the marsupials are still unsettled, but it is evident that after setting aside a few aberrant specializations, the marsupials as a whole represent an earlier and lower grade of evolution. And since the earliest known placentals have a great many characters in common with the primitive arboreal marsupials, it seems that all the evidence so far examined tends to support Dr. Matthew's view (1904) that the placentals also were originally arboreal in habit.[1] The construction of the hands and feet in many Eocene mammals (e. g., *Hyopsodus*, *Meniscotherium*, *Thryptacodon*, *Vulpavus*, *Limnocyon*, *Dissacus*, *Periptychus*, etc.) seems especially to favor this view, since their hands and feet were spreading and the pollex more or less divergent — an apparent remnant of better developed grasping power. The pads on the palms and soles of primitive placental mammals are homologous with those of arboreal types (Whipple) and may owe their peculiar placing to a primary arboreal adaptation. As shown by Matthew arboreal life makes possible the preservation of primitive characters in the limbs, but terrestrial habits, if long continued, result in evident specializations: such as enlarged claws and powerful flexor muscles for digging, compressed elongate feet for running, etc.

Long before the opening of the Paleocene record, the placentals had differentiated into distinct orders, many of which had already become terrestrial. Assuming provisionally the ultimate derivation of the placentals as a whole from an arboreal stock, the main outstanding questions with regard to the origin of the primates is: were the primates eventually derived from terrestrial unguiculate placentals, and were they thus secondarily arboreal mammals? Or were they derived from a primitive marsupio-placental group which had not yet come down out of the trees?

Categorical replies to these questions may not be safely given, but the evidence available at present seems to point to the following hypothesis: at a very early period the opossum-like arboreal placentals

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[1] Some time after this memoir was set up in type I received a paper from Mr. J. W. Gidley, "Significance of divergence of the first digit in the primitive mammalian foot" (Journ. Washington Acad. Sci., IX, May 19, 1919, pp. 273–280), in which he opposes the hypothesis of the arboreal ancestry of the placental mammals. After a candid study of Mr. Gidley's paper I see no reason for modifying either the present discussion or the conclusions stated above on pages 70, 71. W. K. G.

gave rise to more active arboreal types, which began to leap from branch to branch. In the course of this line of evolution the tarsus was slightly lengthened and the head of the astragalus became separated from the trochlea by a distinct neck which is wanting in the primitive marsupials. At the same time a closer fitting joint was developed between the astragalus and the tibia, through the upraising of the fibular facet and the strengthening of the internal malleolus of the tibia; the digits became quite long and slender, but claws were still retained, the expanded finger tips not being developed below the Lemuroidea.

This stage is illustrated in the Lower Eocene Plesiadapidæ which, as suggested by Matthew, seem to be near the borderland between Primates and Menotyphla. These animals also had long delicate fingers and grasping hands and feet. Even at the present day the pen-tailed tree shrew *Ptilocercus* retains extremely primitive hands and feet of arboreal type.

In short, present indications suggest that the Menotyphla-primate stock may have been derived directly from primitive arboreal or semiarboreal placental mammals of the Mesozoic era and that all the other orders of placentals sooner or later became terrestrial, so that in many Lower Eocene mammals the grasping power of the hallux especially was reduced.

This provisional conclusion as to the origin of the primates, based on a comparative study of the limbs, is in harmony with the evidence drawn from a comparative study of the skull and dentition, which suggests that even in the Eocene the Primates and the Menotyphla, although at that time closely related with each other, were already widely separated from any other order of the placentals.

The primitive Lemuroidea are distinguished from arboreal unguiculate mammals of other orders by their very long, slender phalanges and more or less flattened nails. The flexor muscles of their hands and feet are relatively slender and the heads or lower ends of the metacarpals are ball-like. In arboreal unguiculate mammals, on the other hand, such as *Cercoleptes*, the phalanges are very short and wide, the claws are very large, compressed and pointed, the flexor muscles, which are short and powerful, ride above the large paired sesamoids and between the sesamoids there are strongly marked keels on the metacarpals.

The modern Indrisidæ have certain highly specialized characteristics and functions of the limbs and of the hands and feet, which were already evolved in less degree among the Eocene lemuroids. Observers tell us, and their anatomical construction indicates, that the indrisine lemurs make long leaps from branch to branch and at the end of every leap clutch the branches and limbs of the trees with their great hands and feet. They also spend much time in perching quietly among the branches. Hence it is that their limbs, including the wrist and ankle, are self moving compound levers for leaping, while their extremities, especially the hind feet, are so modified for grasping that they look like long narrow mittens, the great toe being set off over against all the others. In *Notharctus* the long phalanges and partly expanded finger tips, the very large hallux, which is sharply divaricated from the other digits, and many other characteristics throughout the skeleton, constitute certain proof of a protracted course of adaptation to arboreal life. Such specializations for climbing and leaping among the branches could hardly be derived from any other of the specialized modes of terrestrial life which are exhibited by Eocene mammals of other orders, and we are again forced to conclude that the immediate ancestors of the Menotyphla-primate stock were not terrestrial mammals but arboreal mammals of a more primitive evolutionary stage, represented rather by the existing opossum than by the terrestrial insectivores.

The relatively high specialization of Eocene lemuroids has in its turn become the point of departure for a new adaptive radiation or embranchment during the millions of years of post-Eocene time. Just as in countless other groups, many of the cænotelic characters of earlier generations have persisted as palæotelic characters in their remote descendants, and the habitus of the ancestral stock has become the underlying and more or less concealed heritage of the diversified branches.

Therefore it is not surprising that, as regards the construction of the limbs, the Middle Eocene *Notharctus* is a kind of synthetic lemuroid, foreshadowing many recent types in different characters, but probably on the whole more primitive than any now living. But, some may say, the palæontological record is obviously very imperfect, and doubtless there were many genera in each larger group of which we have no direct knowledge; it is therefore very unlikely that the only Eocene lemuroid which is at present known from adequate skeletal material should chance to be a primitive representative of its own times. Against such an argument one may cite the fact that with respect to a long list of characters in the skull and dentition, *Notharctus* is demonstrably more like other Eocene placental mammals of different orders than are any of its modern relatives, the existing lemuroids and platyrrhine monkeys.

It may be held by some that the long phalanges and more or less flattened nails of *Notharctus* are less primitive than the shorter phalanges and compressed nails of the marmosets; in other words that the marmosets represent a primitive division of the primates, which have retained true claws, and that *Notharctus* and the Lemuroidea have specialized away from the more primitive type. Against this view may be advanced the following facts:

(1) In the entire construction of the dentition and skull the marmosets are very closely allied to the typical Cebidæ, especially *Callithrix*. The compression of the nails in the marmosets is only an accentuation of the tendency toward compression seen in *Cebus*, *Ateles*, *Callithrix* and *Nyctipithecus*.

(2) If the marmosets are primitive unguiculates, we should expect them to have very powerful flexor and pronator muscles and stout short phalanges. On the contrary their phalanges are delicate and narrow and are not dissimilar in type to those of the smaller Cebidæ, such as *Callithrix*.

(3) If the claws of the marmosets are primitive, how is it that the pollex and hallux still retain obvious traces of a nail-like condition?

Coming now to the structural relationships of *Notharctus* to the Lemuroidea, the writer has constantly been impressed with the fact that only moderate changes would be required to convert the limbs and the pectoral and pelvic girdles of *Notharctus* into any one of the modern lemuroid types. The indrisine type of skeleton would be derived immediately by lengthening all the limb bones, especially the metacarpals and metatarsals. Otherwise there is surprisingly little change, except in proportions.

In *Chiromys* the chief specialization is the elongation of the hand, and the extreme attenuation of the third digit.

Even less modification would be required to convert the limbs of *Notharctus* into those of *Adapis*, of *Lepilemur*, or of *Lemur*. *Megaladapis* is a specialized type with secondarily shortened, widened limb bones, but its affinity with both *Adapis* and *Notharctus* is apparent in every bone of the limbs. The limbs of *Galago* could be derived directly from the *Notharctus* type simply by lengthening the neck of the astragalus and the cuboid, characters which are already foreshadowed in ordinary lemurs and which are carried to an extreme in *Tarsius*. In the opposite direction, the limbs of *Perodicticus* have shortened tarsals and a vestigial second digit in the manus, but everywhere the derivation from a less specialized *Notharctus*-like type is patent.

In general the modern lemuroids have merely accentuated different characters which were already foreshadowed in *Notharctus*.

On the other hand, the Cebidæ show many radical differences from the *Notharctus* type, pointing to a marked change in the direction of evolution. We find that in the Cebidæ the simple technic of leaping and grasping is complicated by more restless and varied movements: running on the branches, brachiating, sitting upright, using the hands to manipulate the food, etc. In some of the Cebidæ the hands become hook-like, the pollex being lost. In the nearly allied Hapalidæ the nails become compressed into claws, which resemble those of tree shrews. In correlation with these differences the metapodials are longer, the phalanges shorter, the ungual phalanges compressed, the fourth digit is no longer than the third. The great process on the proximal end of the hallux for the tendon of the peroneus longus muscle is less developed. That these conditions are all secondary, and not as primitive as the conditions seen in *Notharctus*, is suggested by the fact that the Cebidæ have obviously evolved in the direction of the higher primates, as fully shown by the advanced stage of construction in the auditory region, brain-case and dentition.

In conclusion, the chief stages in the evolution of the limbs of Primates appear to be as follows:

(1) Permian. Primitive therapsid or gorgonopsian stage, of which the hands and feet are well represented by *Scymnognathus* (Broom, 1913) and *Theriodesmus* (Seeley, 1888). The phalangeal formula is transitional from the primitive reptilian (2, 3, 4, 5, 3) to the mammalian formula (2, 3, 3, 3, 3). Of the primitive elements of the reptilian shoulder girdle only the cleithrum is lacking; coracoid and metacoracoid both present. The elbows and knees everted less than in primitive crawling reptiles. Humerus very primitive, with flattened head and widely spread bicipital fossa. Femur with flattened sessile head and no neck. Great trochanter a low ridge on side of shaft. Ilium directed forward. Pubi-ischium plate-like.

(2) Triassic. Cynodont reptilian stage with very short spreading pentadactylate feet. This stage is known in *Microgomphodon* and *Ælurosuchus*. The carpals and tarsals are plainly homologous with those of mammals. A second centrale carpi, which has been lost in the mammals, is retained. The phalangeal formula is 2, 3, 3, 3, 3, as in mammals. Phalanges and metapodials very short. Scapula with everted anterior border forming the spina scapulæ. Prespinous fossa at most incipient. Pectoral girdle as a whole approaching the monotreme stage. Humerus submammalian but with flattened head. Femur with large great trochanter and a small lesser trochanter. Head oval, sessile. Ilium directed forward with expanded gluteal surface. A small obturator fenestra. Epipubic bones probably present. Elbows more or less everted, knees straightened in running.

(3) Jurassic (?). (Predicated from indirect anatomical and palæontological evidence.) Primitive arboreal metatherian stage. Hallux and pollex divergent. Digits moderately short, with compressed claws. Pads and friction ridges specialized to secure firm grasp on branches. Tarsus very short, astragalus practically without neck. Coracosternal connection broken, coracoid short, only a single coracoid present. Scapula with prespinous blade. Humerus with convex head and long delto-pectoral crest. Femur with ball-like head and distinct great trochanter. Digital fossa pronounced. Ilium long and narrow. Thyroid fenestra enlarged. Epipubic bones present. Elbows and knees drawn in towards flanks. Moderate supination of forearms and inturning of hind feet. Such animals doubtless climbed slowly and clung to the branches.

This primitive metatherian stage is largely preserved in the Cretaceous and modern opossums. It gave rise at a later epoch to all the specialized marsupial types and possibly also to the stem placental (stage 4).

(4) Cretaceous (?). (Predicated from indirect anatomical and palæontological evidence.) Primitive arboreal placental stage. Differs from (3) chiefly in the improvement of the tibio-tarsal joint through the development of a distinct neck on the astragalus, and the wedging upward of the astragalus between the fibula and the tibia, so that the articular surface for the fibula comes to lie nearly at right angles with

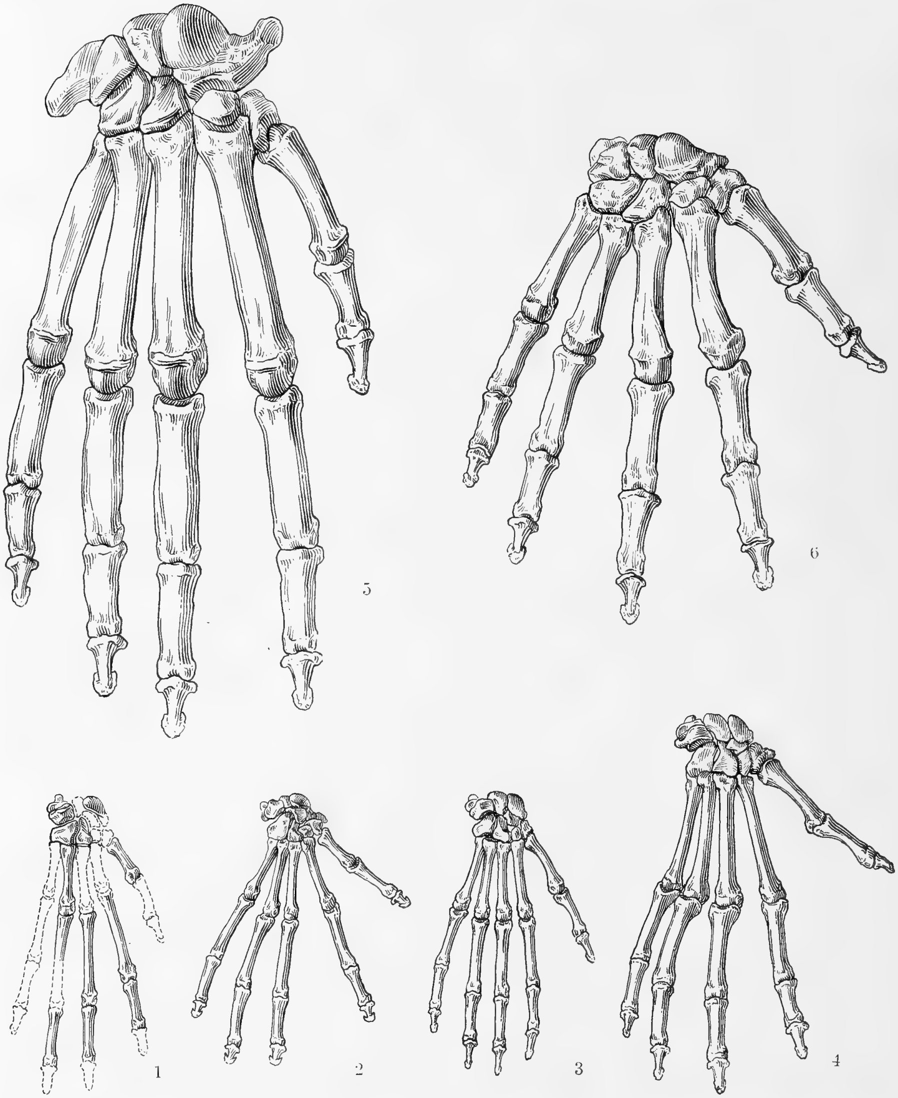


Fig. 83. Comparative series: manus of *Notharctus, Lemur* and higher primates. Lower four figures natural size.

1. *Notharctus osborni.* Amer. Mus. No. 11474. Middle Eocene (Lower Bridger). The oldest and most primitive known primate manus, with narrow carpus, short metacarpals and long digits. Adapted mainly for grasping the branches of trees and for leaping from branch to branch.

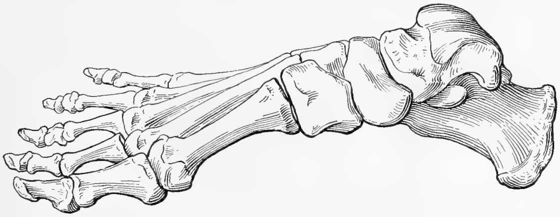
2. *Lemur mongoz.* Amer. Mus. No. 22886. Manus differing from that of *Notharctus* chiefly in the lengthening of the metacarpals and flattening of the digits. Hallux widely divergent, digit IV the longest.

3. *Cebus hypoleucus.* Amer. Mus. No. 14016. Manus adapted partly as a true hand, partly for running along the branches of trees. Digits 2, 3, 4 subequal in length.

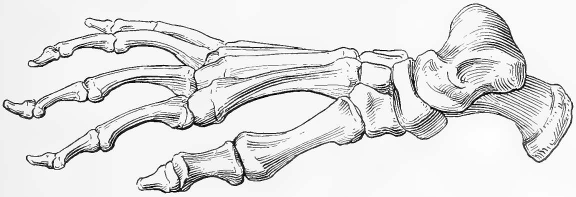
4. *Macacus nemestrinus.* Amer. Mus. No. 14012. Manus a true hand, with very mobile thumb. Adapted also for running on the ground. Carpus wide.

5. *Gorilla* sp. Amer. Mus. Nat. Hist. Manus of modified brachiating type, in which the hands are used partly as hooks in climbing. Thumb somewhat degenerate. Giantism reflected in the great size and robust character of the hand.

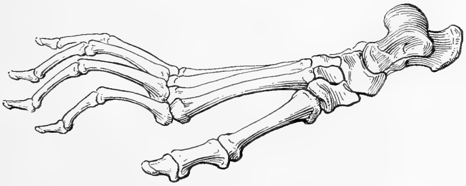
6. *Homo sapiens.* This particular hand is very short and wide, but evidently represents a modification of a primitive brachiating type.



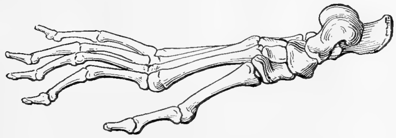
Homo sapiens. Human stage: advanced adaptations for erect posture. Hallux dominant, facing downward and permanently adducted; other digits much shortened. Tarsus very large, with down-turned heel and arched instep.



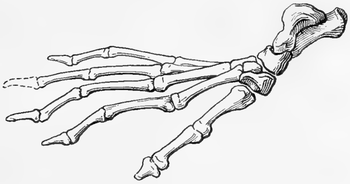
Gorilla sp. Amer. Mus. No. 35400. Young gorilla representing advanced anthropoid stage, adapted both for climbing and for semi-erect progression on the ground. Hallux powerful, digits relatively short. Tarsus large, with down-turned heel.



Macacus nemestrinus. (Amer. Mus. No. 14012). Catarrhine stage: pes adapted both for running and grasping. Digits long.



Cebus hypoleucus. (Amer. Mus. No. 14016). Platyrrhine stage: with mobile hallux.



Notharctus osborni. (Amer. Mus. No. 11474). Primitive primate stage: with long digits, weak flexors and very large, sharply divergent hallux.

Didelphis virginiana. Primitive arboreal unguiculate stage: with short digits, powerful flexor muscles and strong divergent hallux.

Fig. 84. Comparative series: pes of *Didelphis, Notharctus,* and higher primates.

the oblique facet for the tibia on the top of the astragalus. This denotes greater activity and freedom of movement than is displayed by the slow climbing opossums. This primitive arboreal placental stage by adaptive radiation probably gave rise to the various orders of terrestrial unguiculate and ungulate placentals most of which were already well differentiated at the opening of the Paleocene record.

(5) UPPER CRETACEOUS. (Predicated from indirect anatomical and palæontological evidence.) Primitive tupaioid or pre-Primate stage, represented by more or less specialized descendants (Plesiadapidæ, Mixodectidæ) in the Paleocene and Lower Eocene. Beginning of advanced arboreal specializations. Phalanges elongate and slender, but claws retained. Pads and friction ridges essentially as in lemuroids, but terminal digital pads not so much expanded. The animals leap actively among the branches.

(6) PALEOCENE (?) AND LOWER EOCENE. Primitive lemuroid stage, described in preceding pages. Distinguished from (5) by the still more advanced specializations for grasping, leaping, and perching. Hallux strongly divergent, with very large process for attachment of peroneus longus muscle. Finger tips, ungual phalanges and nails more or less expanded. Phalanges elongate, heads of metapodials ball-like. The animals leap actively among the branches but do not sit altogether upright. Notharctinæ, Adapinæ and their Paleocene ancestors. This central type probably gave rise to the following branches:

(7*A*) LOWER EOCENE TO RECENT. Hopping arboreal types with elongate astragalus and cuboid. Tarsioids, Galagininæ.

(7*B*) OLIGOCENE (?) TO RECENT. Far-leaping arboreal lemurs finally with very long hands and feet and extreme specializations for grasping and perching: Lemuridæ, Indrisidæ. *Chiromys* in limb structure is merely a specialized member of this group.

(7*C*) OLIGOCENE (?) TO RECENT. Lethargic clinging lemuroids with secondarily shortened tarsus: Lorisinæ.

(7*D*) PLEISTOCENE TO RECENT. Gigantic lemurs with very stout and secondarily shortened limb bones and large hands and feet: *Megaladapis*.

(7*E*). EOCENE OR OLIGOCENE TO RECENT. Very agile climbing and running monkeys using the hands as such rather than as mere clinging organs. Entepicondylar foramen often lost, humerus with long cylindrical shaft, low crests and spherical head. Third trochanter of femur reduced or absent: primitive Cebidæ and undiscovered Eocene ancestors of the catarrhine primates. In this stage the specializations for leaping and grasping become overlaid by specializations for running lightly on the branches and for sitting upright. This stage gives rise to:

(8*A*) MIOCENE (?) TO RECENT. Small squirrel-like forms, using the secondarily compressed nails as claws in climbing: Hapalidæ.

(8*B*) OLIGOCENE (?) AND MIOCENE TO RECENT. Subterrestrial, cursorial and more or less quadrupedal types: baboons.

(8*C*) MIOCENE (?) TO RECENT. Thumbless, narrow-handed types, using the hands both as hooks and as feet. Tail long, more or less prehensile: *Ateles, Colobus*.

(8*D*) UPPER (?) EOCENE. Brachiating acrobatic types, sitting upright; tail vestigial; perfected supination of fore limb; thumbs more or less opposable: Ancestral man-anthropoid stock. From this stage was derived:

(9*A*) MIOCENE TO RECENT. Extremely long-limbed brachiating anthropoid types: orang, gibbon.

(9*B*) OLIGOCENE (?). Subterrestrial semi-erect anthropoids with moderately long arms and shorter legs; astragalus and calcaneum of subhuman type; entocuneiform retaining saddle-shaped articulation for opposable hallux; ilium becoming expanded for enlarged glutei, iliacus and abdominal muscles: ancestors of chimpanzee, gorilla, and man. Giving rise to:

(10*A*) MIOCENE TO RECENT. Forest-living subterrestrial anthropoids, with reduced thumb and very short hind legs; finally becoming gigantic; chimpanzee, gorilla.

(10*B*) MIOCENE (?) TO RECENT. Primitively plains living, fully terrestrial erect types, with perfected thumb, widely expanded pelvis, long hind limbs; the pes readapted for terrestrial progression. Entocuneiform facets flattened, hallux made parallel to other digits, which become much shorter while the hallux grows longer, phalanges much abbreviated: Hominidæ.

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[Lacrymal region, pp. 255–260, palatal sinus, pp. 260–268. *Adapis*, p. 268.]

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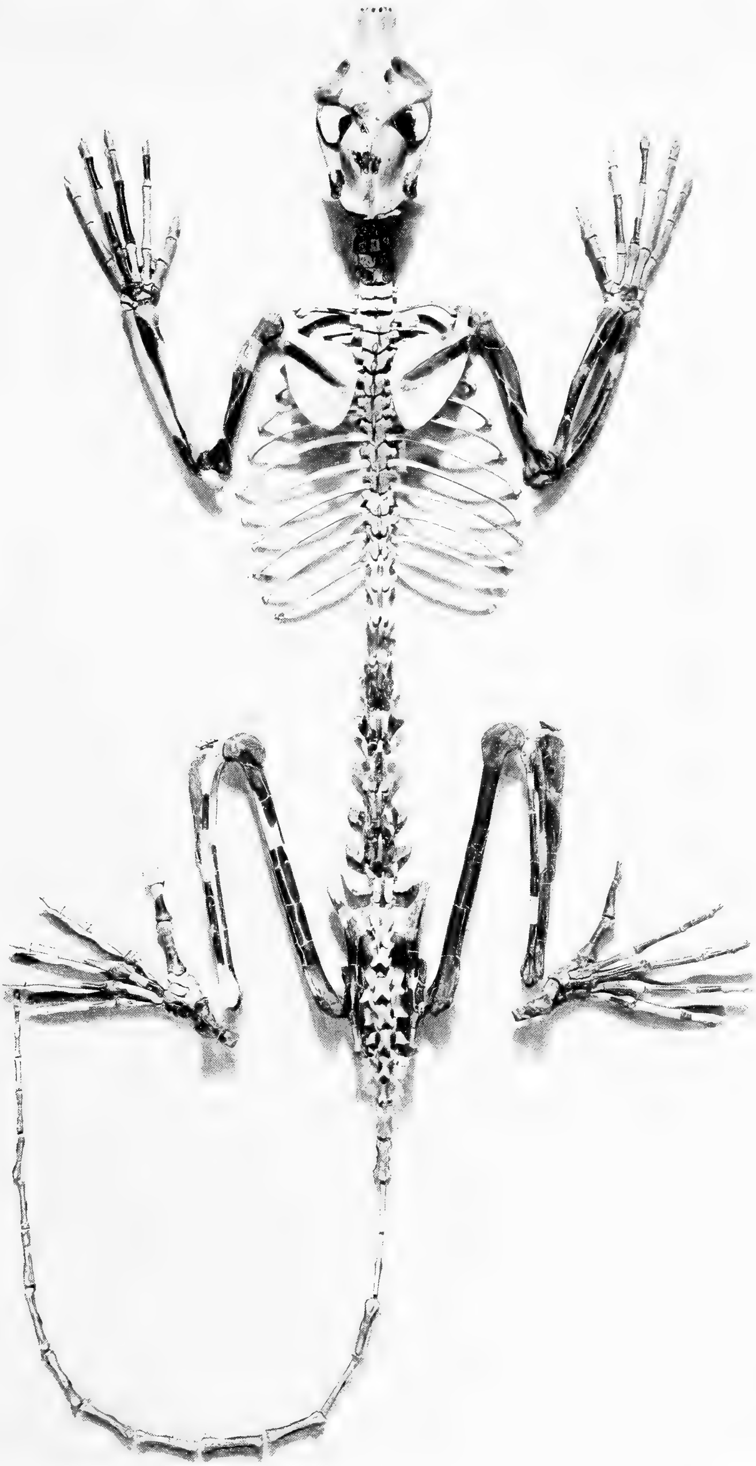
PLATE XXIII

Plate XXIII

Skeleton, Partly Restored, of *Notharctus osborni*

Paratype. Amer. Mus. No. 11474. Middle Eocene, Lower Bridger (Horizon B), Bridger Basin, Wyoming.
About one-half the natural size.
Missing or unknown portions, as restored by Mr. Albert Thomson, are indicated by light gray color.



Notharctus osborni

PLATE XXIV

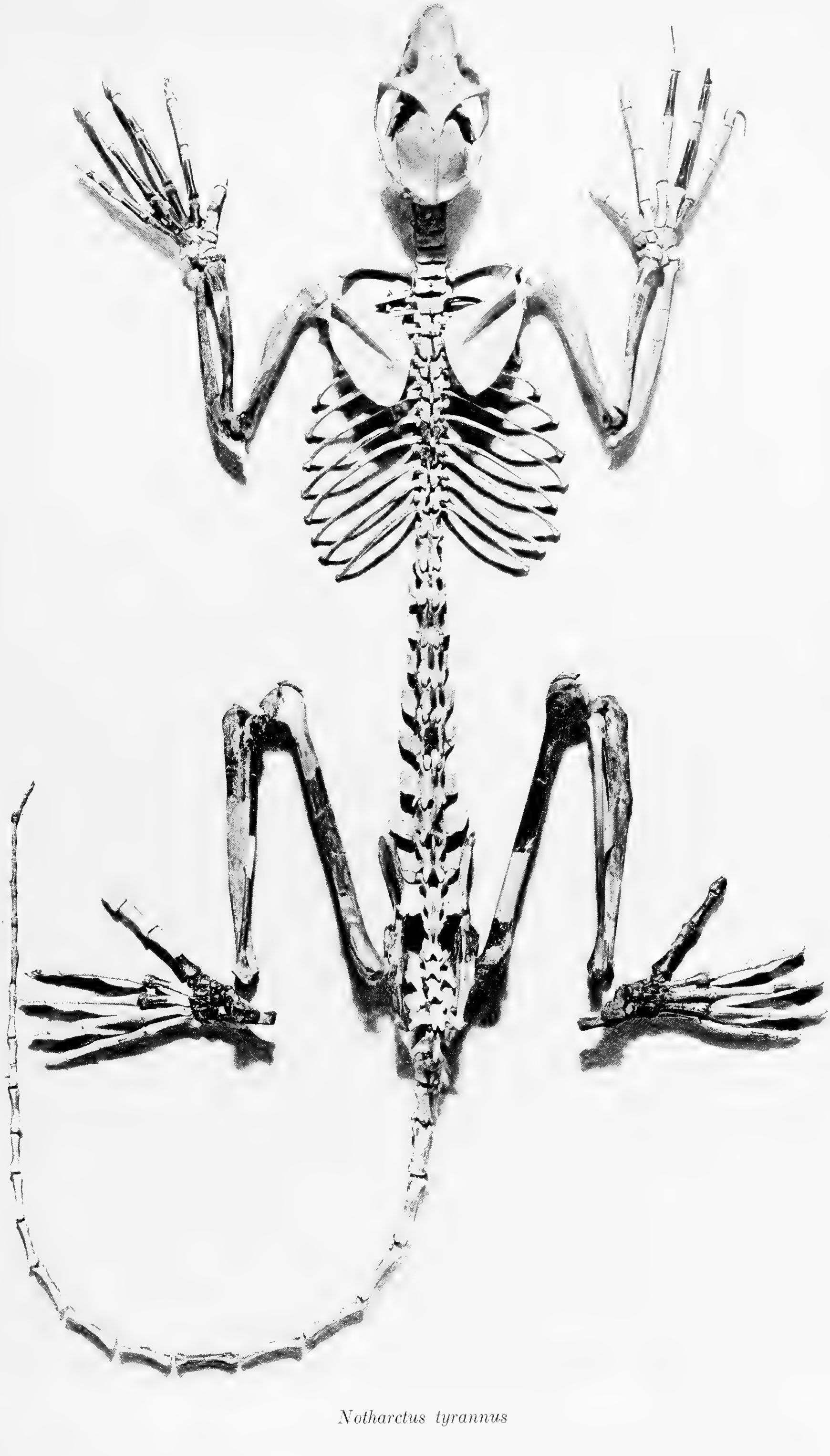
PLATE XXIV

Skeleton, Largely Restored, Referred to *Notharctus tyrannus* Marsh

Amer. Mus. No. 11478. Middle Eocene, Lower Bridger (Horizon B), Bridger Basin, Wyoming.

About one-half the natural size.

The principal portions preserved include parts of the skull and dentition; the endocranial cast; and parts of vertebræ, limb, and foot bones. Missing or unknown portions, as restored by Mr. Albert Thomson, are indicated by light gray color.



Notharctus tyrannus

PLATE XXV

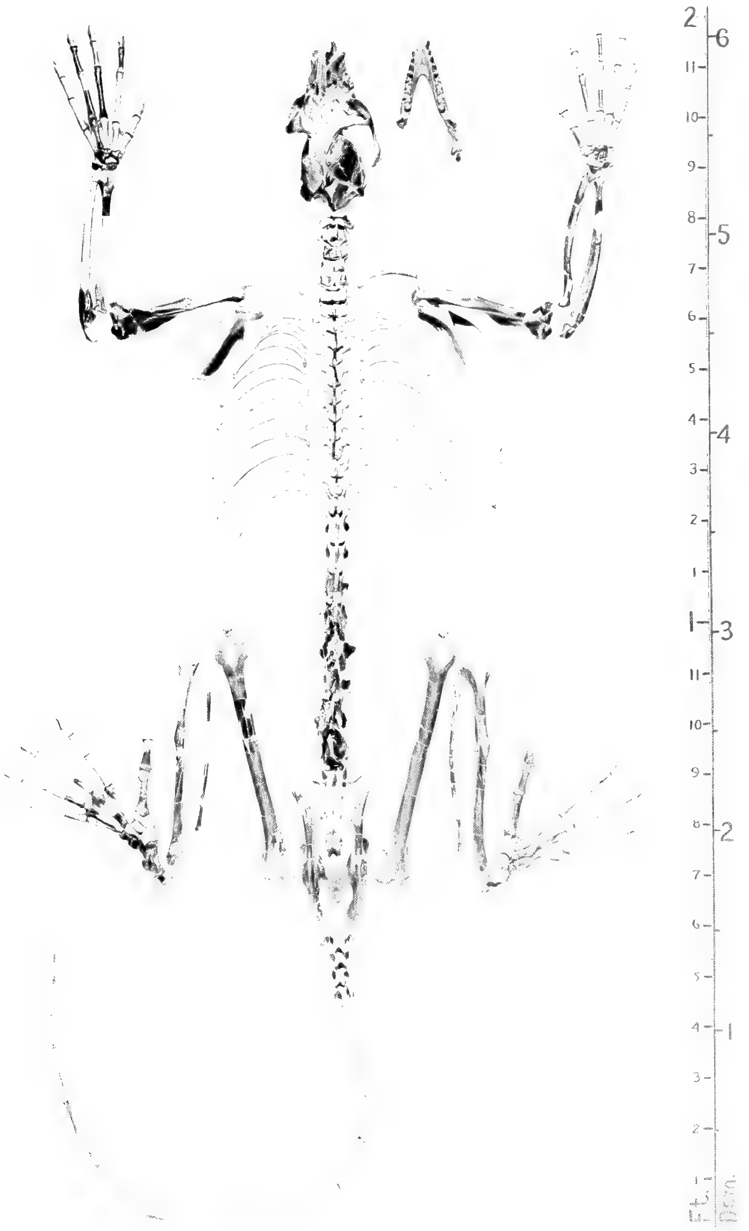
PLATE XXV

Skeleton, Partly Restored, of *Notharctus osborni*

Skull and mandible of the type (Amer. Mus. No. 11466); postcranial skeleton of the paratype (Amer. Mus. No. 11474). Middle Eocene, Lower Bridger (Horizon B), Bridger Basin, Wyoming.

Size indicated by ruled scale.

Missing or unknown parts, as restored by Mr. Albert Thomson, are indicated by light gray color.



Notharctus osborni

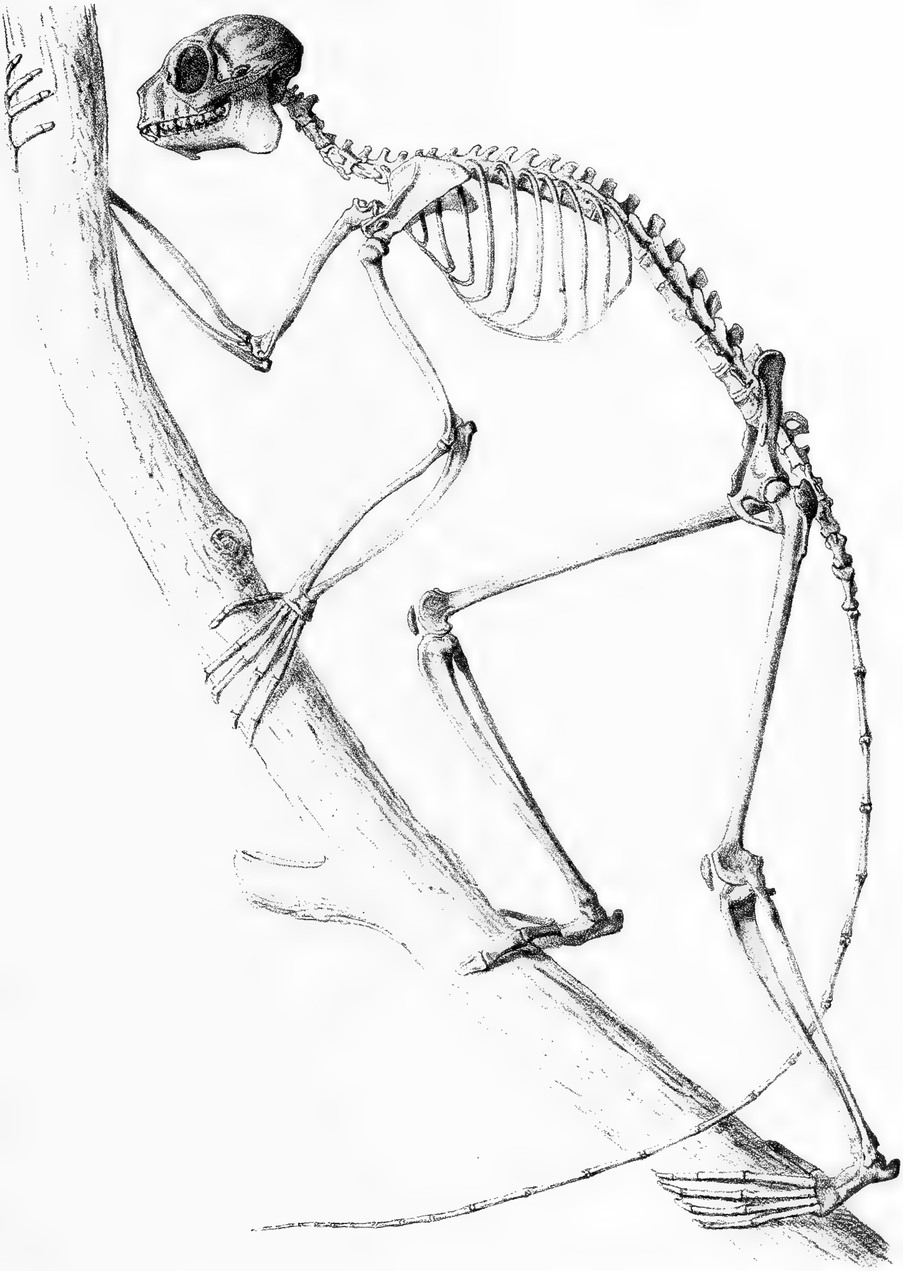
PLATE XXVI

PLATE XXVI

Skeleton of *Propithecus verreauxii*. After Milne Edwards

One-half natural size.

This modern indrisine lemur differs from *Notharctus* chiefly in the expanded brain-case and longer limbs and extremities, but the general pattern of the skeleton is remarkably similar to that of the Eocene type.



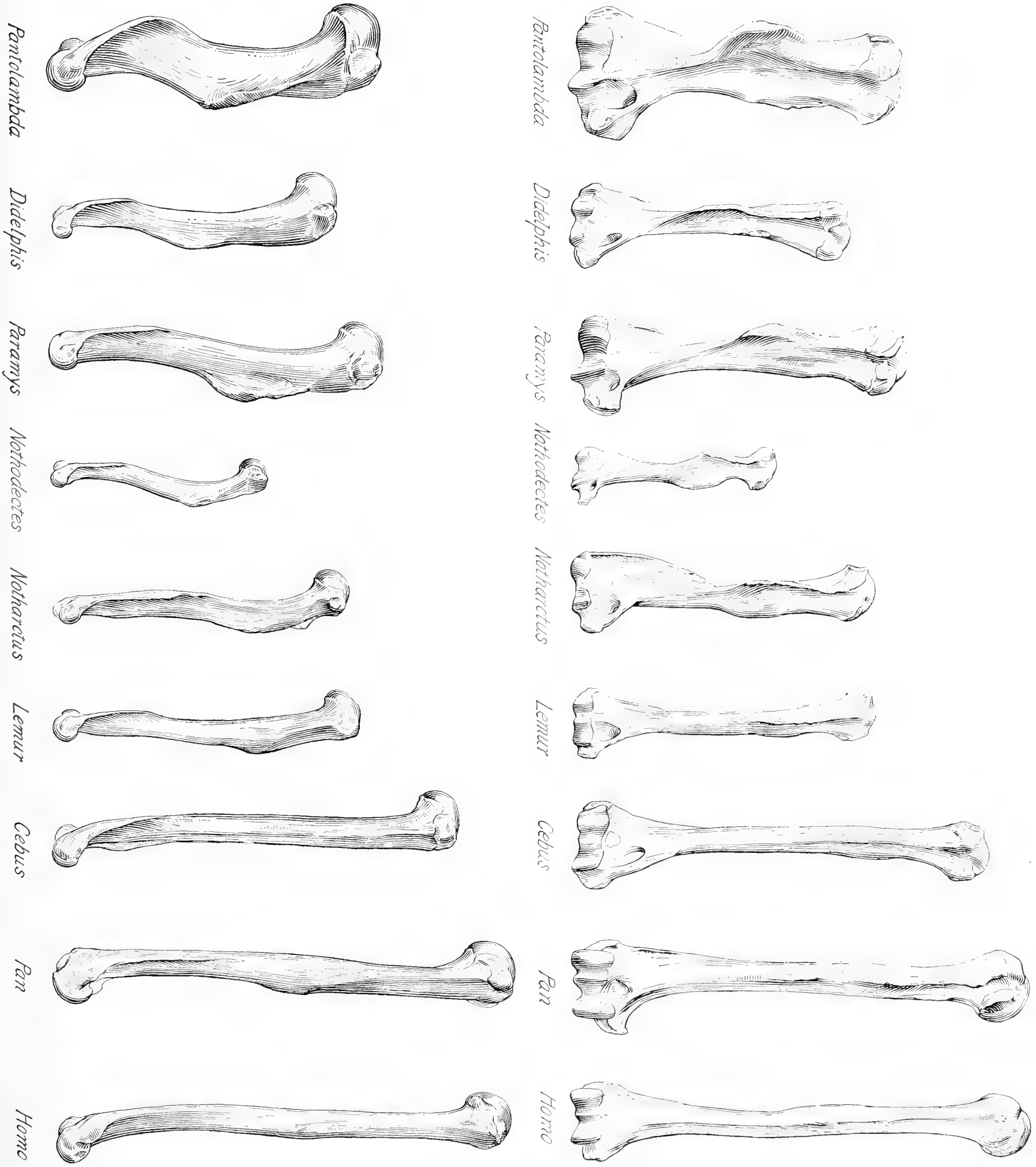
Propithecus verreauxii

PLATE XXVII

PLATE XXVII

Comparative Series: Humeri of primitive placentals, *Didelphis, Notharctus,* and higher primates

Scales various.



Comparative Series of Humeri

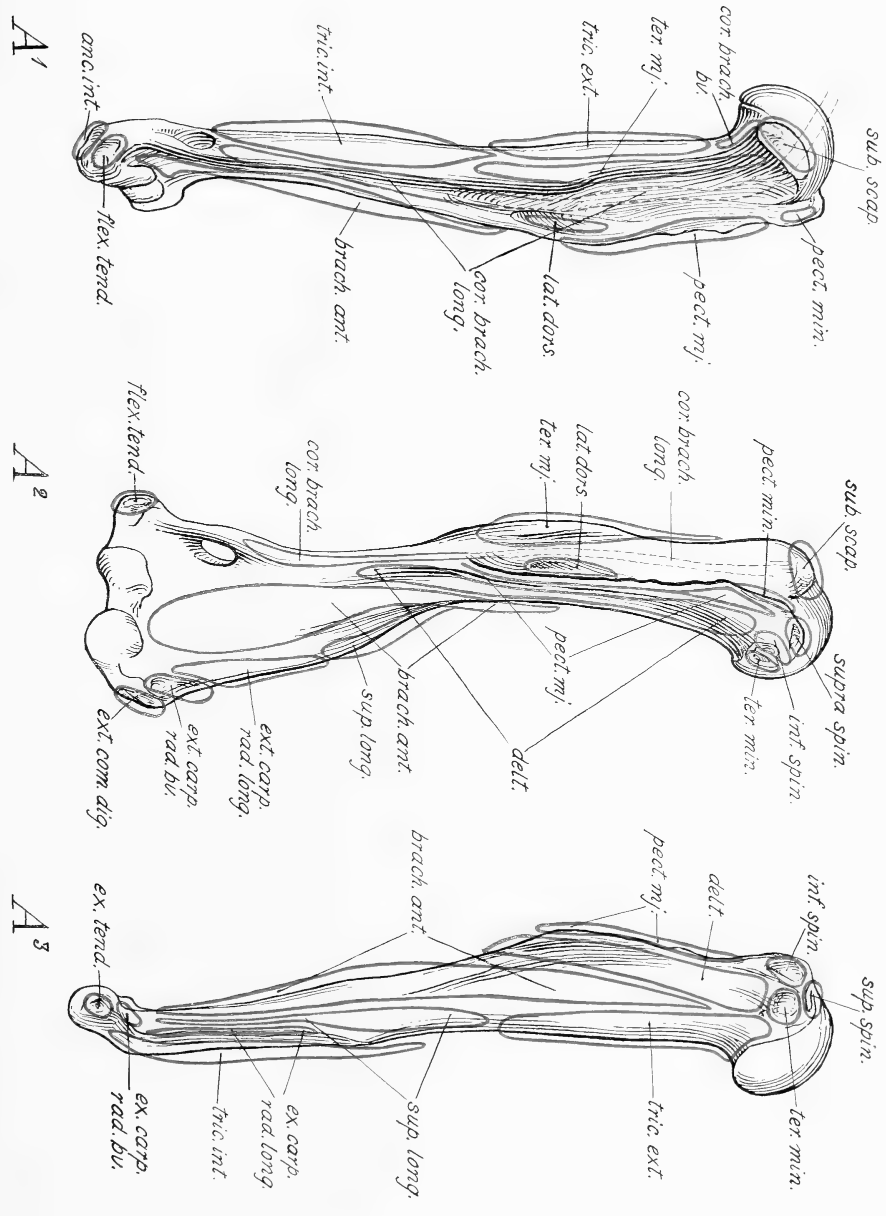
PLATE XXVIII

Plate XXVIII

Diagram Showing Approximate Location of Muscle Attachments on the Humerus of *Notharctus,* based on Comparison with Modern Lemurs

A^1, inner side; A^2, front; A^3, outer side.

The general course of the coraco-brachialis longus, after it leaves the surface of the humerus, is indicated by a broken red line.



Muscle areas, humerus of *Notharctus*

PLATE XXIX

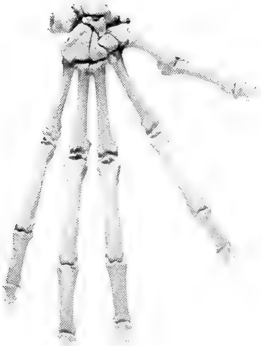
PLATE XXIX

Comparative Series: Manus of *Notharctus* and other Primates

All figures natural size.

1. *Notharctus osborni.* Amer. Mus. No. 11474. Right manus, largely restored by Mr. Albert Thomson. Showing the first metacarpal, the magnum, the unciform (in part), the cuneiform, and parts of the phalanges. Compare Text Figure 83.
2. *Notharctus osborni.* Amer. Mus. No. 11474. Left manus, reversed and largely restored. Showing the scaphoid, magnum, unciform, fourth metacarpal, and some of the phalanges. Compare Text Figure 83.
3. *Notharctus tyrannus.* Amer. Mus. No. 11478. Left manus, partly restored by Mr. Albert Thomson. Showing the second, third, fourth, and fifth metacarpals and some of the proximal phalanges.
4. *Lemur mongoz.* Amer. Mus. No. 22886. Left manus.
5. *Cebus apella.* Left manus. After De Blainville.
6. *Macacus nemestrinus.* Amer. Mus. No. 14012. Left manus.

4



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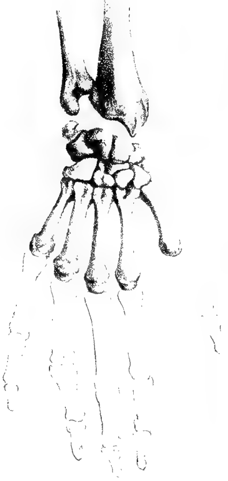

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Comparative series: manus

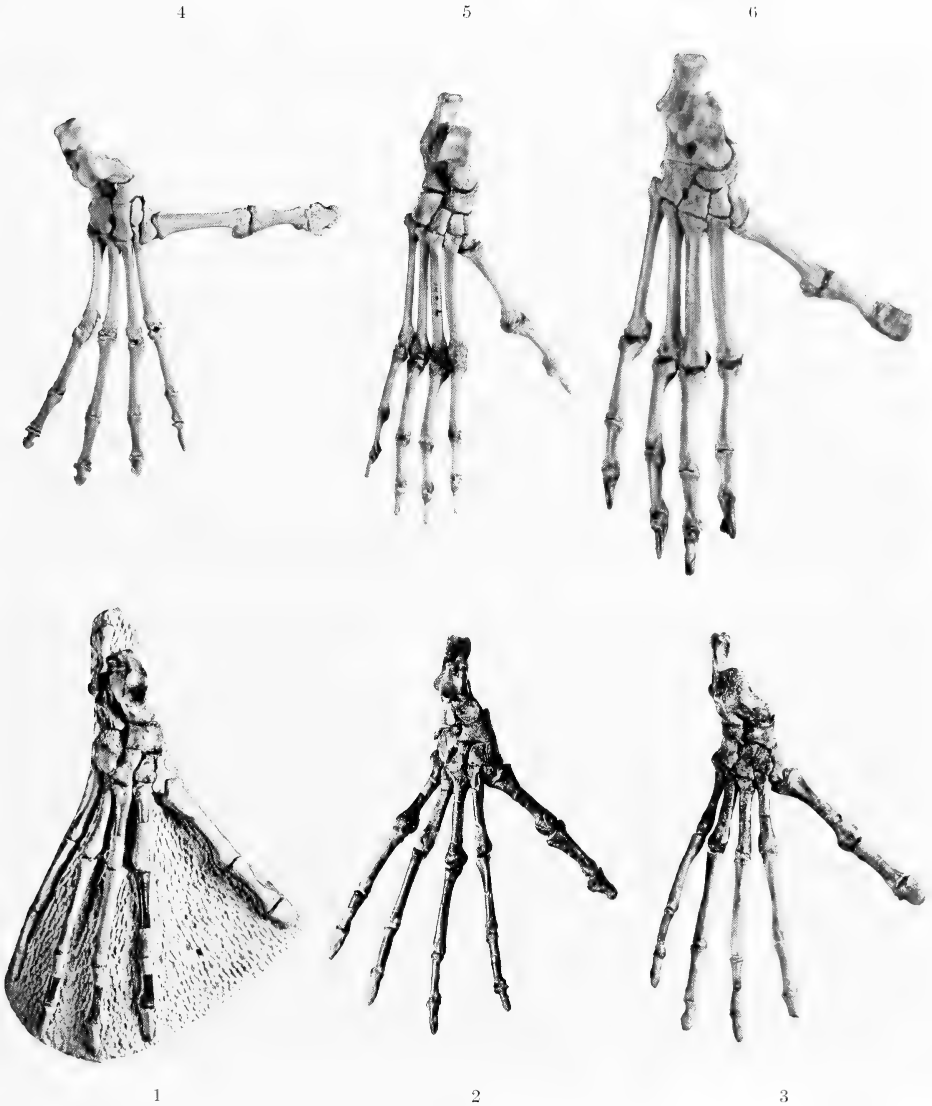
PLATE XXX

PLATE XXX

Comparative Series: Dorsum of Right Pes of *Notharctus* and other Primates

All figures natural size.

1. *Notharctus tenebrosus*. Amer. Mus. No. 13024. Lower Bridger. Incomplete pes, mounted and restored by Mr. Albert Thomson. The parts preserved include the astragalus, navicular, mesocuneiform, ectocuneiform, cuboid, and parts of the metatarsals and phalanges.
2. *Notharctus osborni*. Amer. Mus. No. 11474. Lower Bridger. Incomplete pes, mounted and restored by Mr. Albert Thomson.
3. *Notharctus tyrannus*. Amer. Mus. No. 11478. Lower Bridger. Incomplete pes, mounted and restored by Mr. Albert Thomson.
4. *Lemur mongoz*. Amer. Mus. No. 22886.
5. *Cebus hypoleucus*. Amer. Mus. No. 14016.
6. *Macacus nemestrinus*. Amer. Mus. No. 14012.



Comparative series: dorsum of pes

PLATE XXXI

PLATE XXXI

Comparative Series: Plantar Aspect of Right Pes of *Notharctus* and other Primates

All figures natural size.

1. *Notharctus osborni.* Amer. Mus. No. 11474. Right pes, as mounted and partly restored by Mr. Albert Thomson.

In this animal the hallux could not be adducted beyond the position here shown, because the process for the tendon of the peroneus longus, on the proximal end of the hallux, abuts against the mesocuneiform and the second metatarsal.

2. *Lemur mongoz.* Amer. Mus. No. 22886.

Hallux essentially as in *Notharctus.*

3. *Cebus hypoleucus.* Amer. Mus. No. 14016.

The hallux can be fully adducted.

4. *Macacus nemestrinus.* Amer. Mus. No. 14012.

The hallux, as in *Cebus*, can be fully adducted.

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Comparative series: pes, plantar aspect

PLATE XXXII

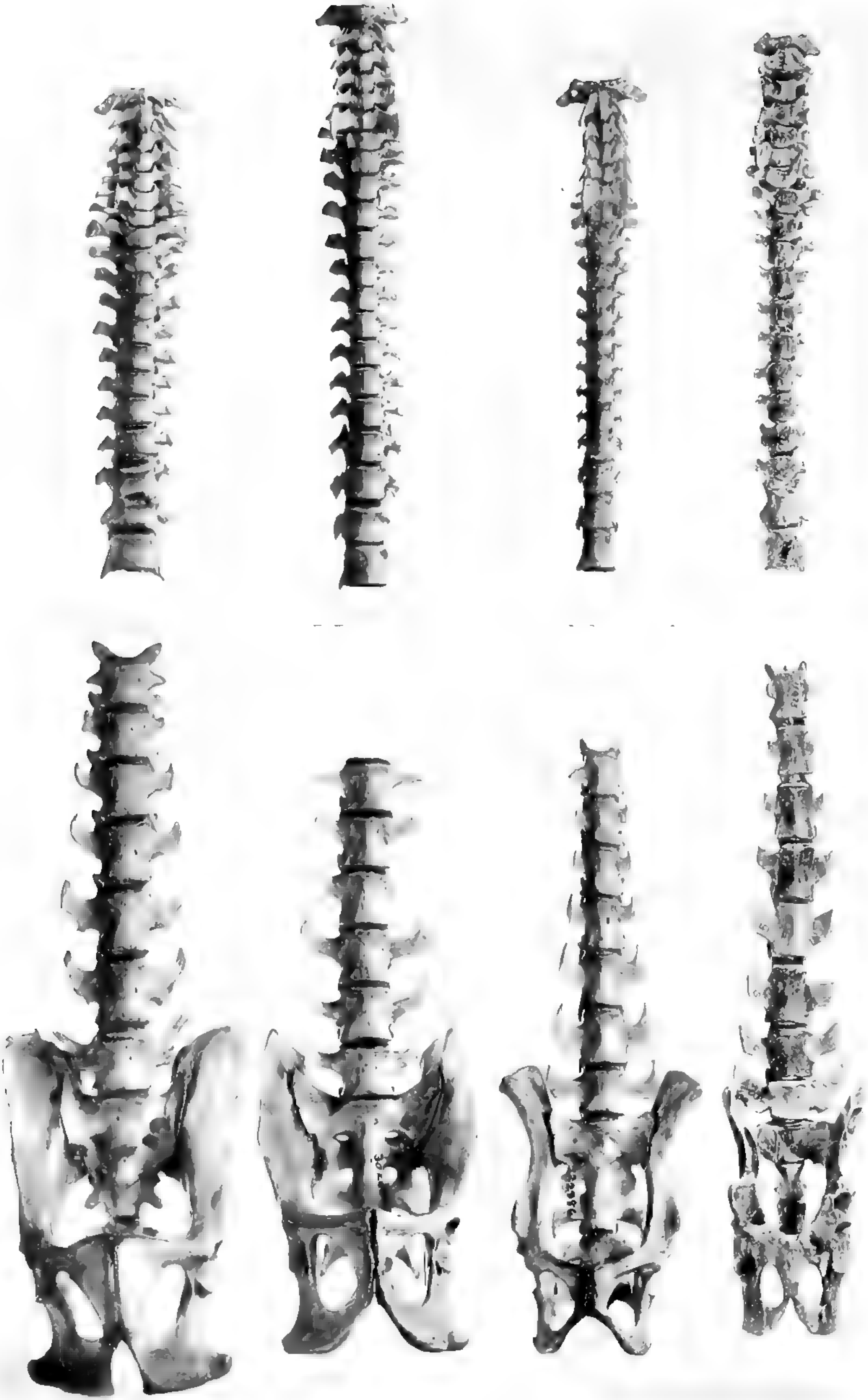
PLATE XXXII

Comparative Series: Vertebral column and pelvis of *Notharctus* and other Primates, ventral Aspect

All figures natural size.

1. *Notharctus osborni.* Amer. Mus. No. 11474, prepared and restored by Mr. Albert Thomson. The following parts are supplied from other individuals: axis (No. 11479), dorsals 9, 10, 12, and lumbar 1 (No. 11473). Sacral 2 is restored from No. 11478. Cervicals 6 and 7, lumbar 8, are restored entirely from a study of adjacent vertebræ and of the vertebræ of modern lemurs.
2. *Lemur mongoz.* Amer. Mus. No. 22886.
3. *Cebus apiculatus.* Amer. Mus. No. 30200.
4. *Macacus* sp. Amer. Mus. No. 41999.

Comparative series: vertebral column and pelvis, ventral aspect



1. *Macacus* *Canis* 2. *Lemur* 1. *Notharctus*

Comparative series: vertebral column and pelvis, ventral aspect

PLATE XXXIII

Plate XXXIII

Comparative Series: Lumbar, Sacral, and Coccygeal Vertebræ and Pelvis, Lateral Aspect

All figures natural size.

1. *Notharctus osborni.* Amer. Mus. No. 11474. Lumbar 1 is supplied from No. 11473.
2. *Lemur mongoz.* Amer. Mus. No. 22886.
3. *Cebus apiculatus.* Amer. Mus. No. 30200.
4. *Macacus* sp. Amer. Mus. No. 41999.

Comparative series: lumbar, sacral and coccygeal vertebræ and pelvis, lateral aspect

PLATE XXXIV

PLATE XXXIV

Comparative Series: Caudal Vertebræ

All figures natural size. Figs. 1–5, dorsal aspect; figs. 6–10, ventral aspect.

1 and 6. *Lemur mongoz.* Amer. Mus. No. 22886.

2 and 7. *Notharctus osborni.* Amer. Mus. No. 11474. Caudals 1 (?)–4(?), 7(?), 10(?), 12(?)–17(?). Prepared and restored by Mr. Albert Thomson.

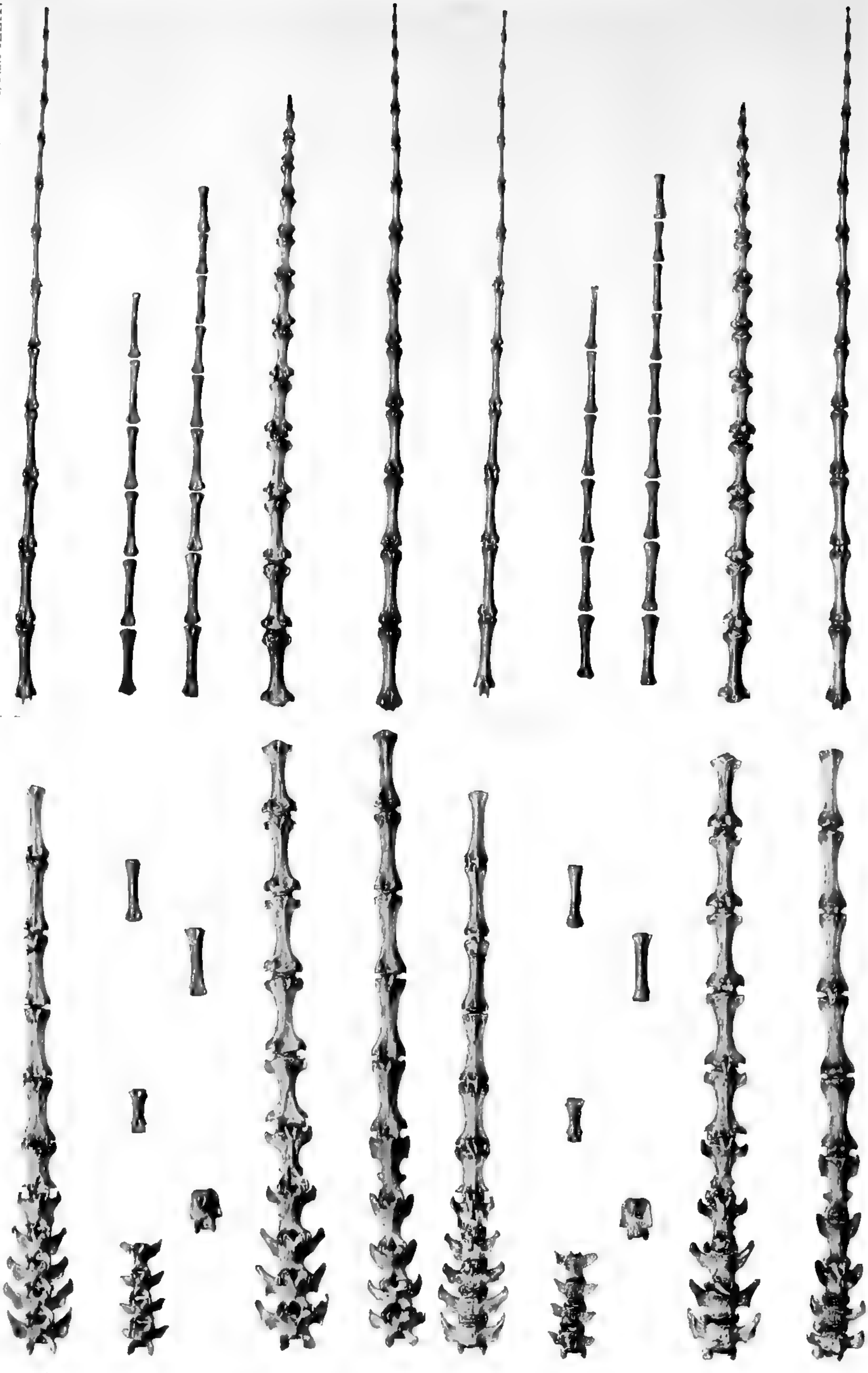
Vertebræ 12(?)–17(?), so far as preserved, are similar to those of *Lemur mongoz,* but apparently shorter.

3 and 8. *Notharctus tyrannus.* Amer. Mus. No. 11478. Caudals 5(?), 9(?), 12(?)–19(?). Prepared and partly restored by Mr. Albert Thomson.

Caudals 12(?), 15(?) are the only ones in which the length is known. If correctly numbered, they appear to indicate that the caudals in this species were somewhat shorter and stouter than those of *N. osborni.* Caudals 16(?)–19(?) as restored are probably too short.

4 and 9. *Cebus apiculatus.* Amer. Mus. No. 30200.

5 and 10. *Macacus* sp. Amer. Mus. No. 41999.



Comparative series: caudal vertebræ, dorsal and ventral aspects

PLATE XXXV

Plate XXXV

Evolution of the Upper Molars in the Notharctinæ

All figures three times natural size.

For the generic and specific characters see especially Matthew, 1915, Bull. Amer. Mus. Nat. Hist., XXXIV, pp. 434–444, and Granger and Gregory, 1917, idem, XXXVII, pp. 845–856. The morphological and phylogenetic aspects of this series are discussed in the present work, pages 133 to 143.

Middle Eocene

BRIDGER
Bridger Basin, Wyo.

UPPER

Notharctus crassus. A. M. 11982

LOWER

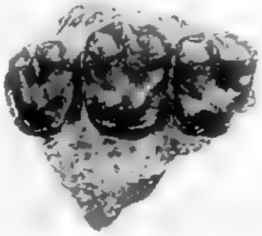
N. matthewi A. M. 11471

N. osborni. A. M. 11466

N. pugnax. A. M. 14567

LOST CABIN
Wind River Basin, Wyo.

N. nunienus. A. M. 4735



N. venticolus. ? A. M. 14637

LYSITE
Bighorn Basin, Wyo.
Wind River Basin

(*Pelycodus frugivorus*)

(*Pelycodus* [illegible])

Lower Eocene

GRAY BULL
Bighorn Basin, Wyo.

UPPER

P. frugivorus. A. M. 15022

P. jarrovii A. M. 15018

LOWER

P. trigonodus. A. M. 15054

P. ralstoni. A. M. 15681

P. trigonodus. A. M. 15017

SAND COULEÉ
Clark's Fork Basin, Wyo.

Pelycodus ralstoni. A. M. 16089

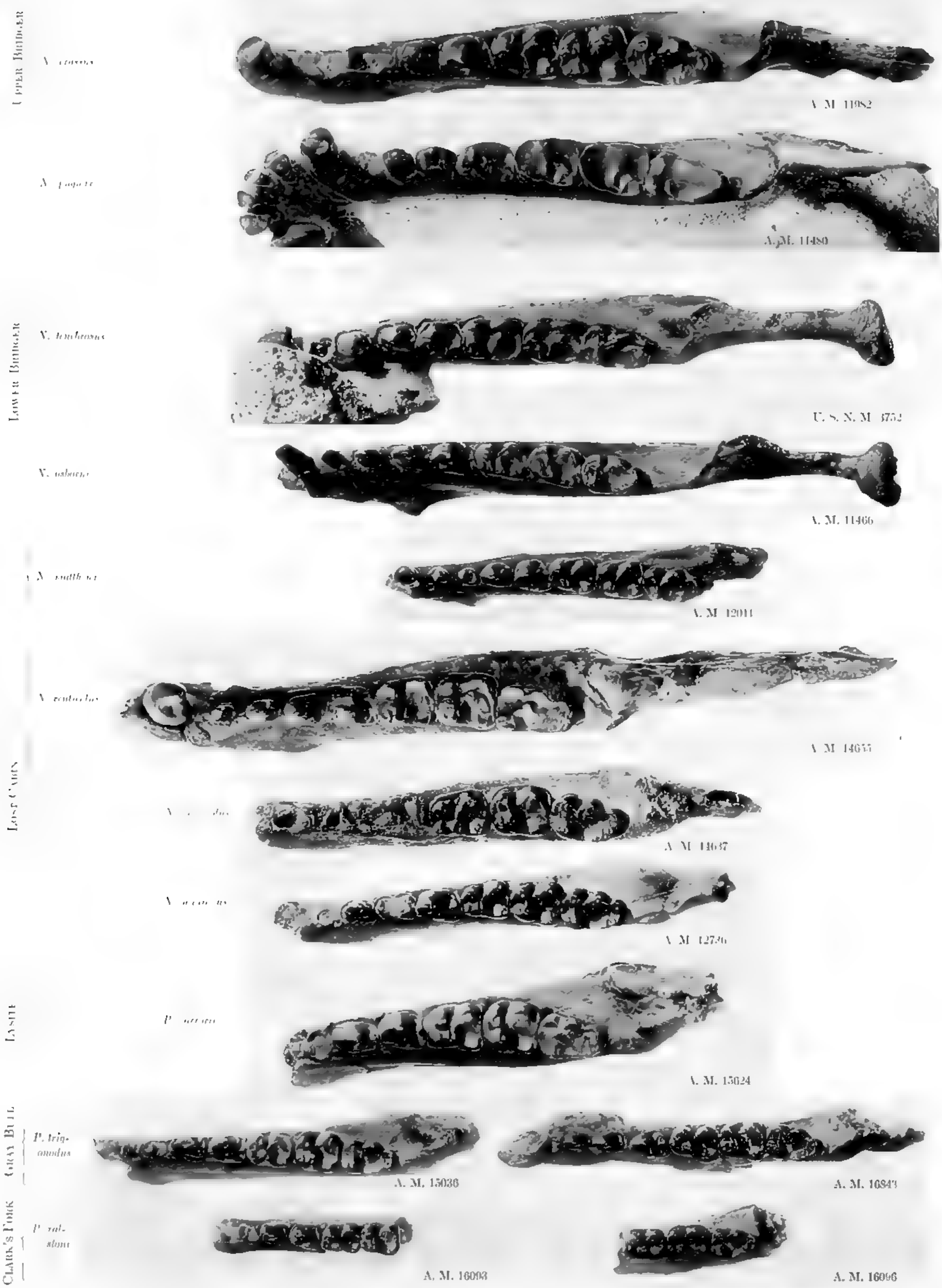
Evolution of the Upper Molars of the Notharctinæ

PLATE XXXVI

Plate XXXVI

Evolution of the Lower Molars in the Notharctinæ

All figures three times natural size.
Compare Plate XXXV and its legend.



Evolution of the Lower Molars in the Notharctinæ

PLATE XXXVII

Plate XXXVII

Evolution of the Lower Jaw and Teeth in the Notharctinæ. Lingual Aspect

All figures three times natural size.

Upper Bridger

N. crassus

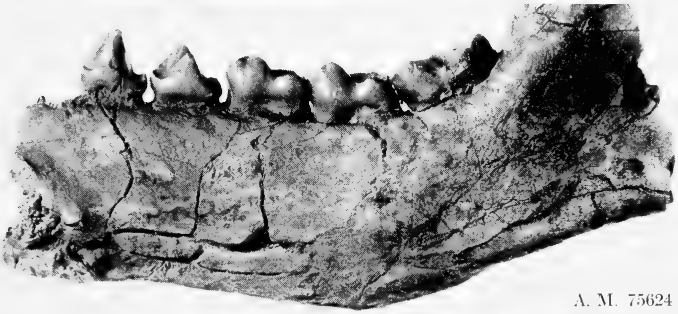
A. M. 11982

Lower Bridger

N. osborni

A. M. 11466

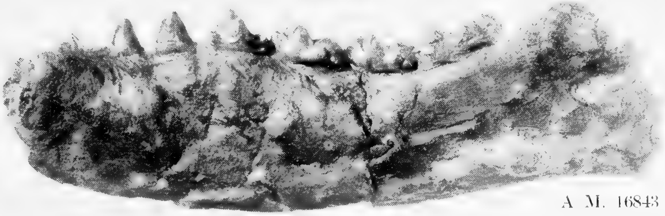
Lysite



P. jarrovii

A. M. 75624

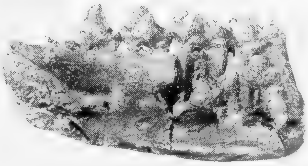
Gray Bull



P. trigonodus

A M. 16843

Clark's Fork



Pelycodus ralstoni

A. M. 16093

Evolution of the Lower Jaw and Teeth in the Notharctinæ, Lingual Aspect

PLATE XXXVIII

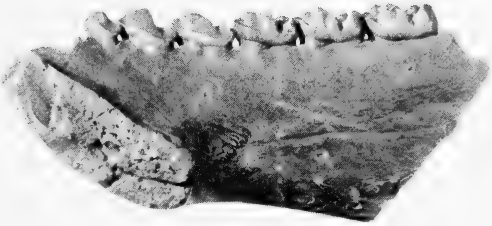
Plate XXXVIII

Comparison of *Adapis* and *Pelycodus*.— Right Lower Premolar-molar series and Ramus of Mandible, Lingual Aspect

All figures three times natural size.

1. *Pelycodus trigonodus.* Amer. Mus. No. 16843. Lower Eocene, Middle Gray Bull Beds, Bighorn, Wyoming.
2. *Adapis magnus.* Amer. Mus. No. 10511. Upper Eocene. Euzet les Bains, Gard, France.
3. *Adapis parisiensis.* Amer. Mus. No. 10007*a*.

3



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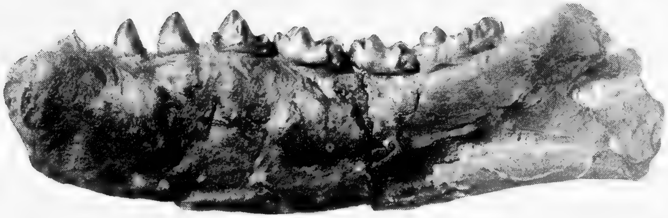

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PLATE XXXIX

Plate XXXIX

Comparison of *Adapis* and *Notharctus*.— Upper and Lower Cheek Teeth, Crown View

All figures three times natural size.

1. *Notharctus crassus.* Amer. Mus. No. 11982. Middle Eocene, Upper Bridger, Henry's Fork, Wyoming. Right maxilla with canine and p^3–m^3. P^1, p^2 not preserved. The molars have large mesostyles and pseudo-hypocones.

2. *Adapis magnus.* Amer. Mus. No. 10511. Upper Eocene, Euzet les Bains, Gard, France. Right maxilla with p^3–m^3. The molars have no mesostyles and the hypocones are continuous with the cingulum.

3. *Notharctus osborni.* Amer. Mus. No. 11466. Middle Eocene, Lower Bridger, Wyoming. Right ramus mandibuli with canines to m_3 inclusive.

4. *Adapis parisiensis.* Amer. Mus. No. 10007. Right ramus mandibuli with canine, alveolus of p_1 and p_2–m_3 inclusive.

5. *Adapis magnus.* Amer. Mus. No. 10011. Right ramus mandibuli with p_4–m_3 inclusive.

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PLATE XL

PLATE XL

Comparison of the Lower Teeth of Adapinæ and Notharctinæ

1. *Pelycodus trigonodus.* Amer. Mus. No. 15036. Lower Eocene, Gray Bull Beds, Big Horn, Wyoming. Right ramus of mandible and lower premolar-molar series. × $\frac{3}{1}$.

2. *Adapis priscus.* Lower Eocene, Egerkingen. Left ramus of mandible with p_1–m_3 inclusive and alveoli of p_3, p_2. × $\frac{3}{1}$. After Stehlin.

3. *Adapis sciureus.* Lower Eocene, Egerkingen. Left ramus of mandible with canine–m_3 inclusive and alveoli of the central and lateral incisors. × $\frac{4}{1}$. After Stehlin.

4. *Adapis magnus.* Phosphorites, Larnagol (Lot). Left ramus of mandible with canine — m_3 inclusive. × $\frac{2}{1}$. After Stehlin.

5. *Notharctus matthewi.* Amer. Mus. No. 12011. Middle Eocene, Lower Bridger, Wyoming. Left ramus of mandible (reversed), with canine — m_3 inclusive. Lingual aspect. × $\frac{3}{1}$.

6. Buccal aspect of the same.

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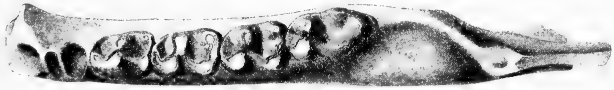

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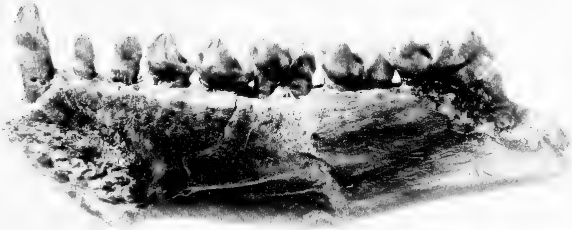


6

PLATE XLI

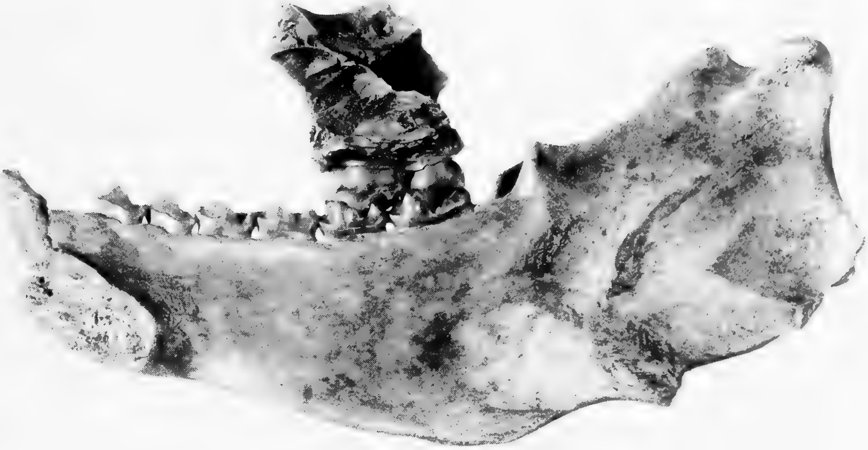
PLATE XLI

Comparative Series: Occlusal Relations of the Upper and Lower Cheek Teeth

Lingual aspect.
All figures three times natural size.

1. *Pelycodus trigonodus*. Amer. Mus. No. 15017. Lower Eocene, Gray Bull Beds, Bighorn Basin, Wyoming.
2. *Notharctus crassus*. Amer. Mus. No. 11982. Upper Bridger, Henry's Fork, Wyoming.
3. *Adapis parisiensis*. Amer. Mus. No. 10007 (mandible) and 10005 (second and third upper molar).

3



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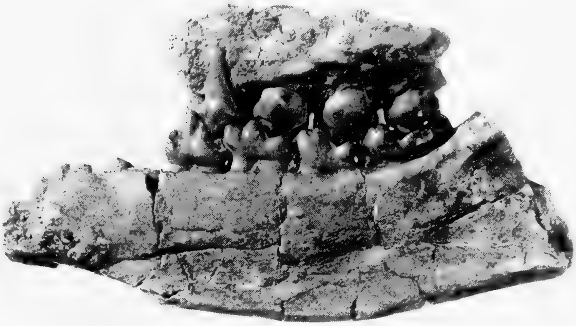


2

PLATE XLII

PLATE XLII

Comparative Series: Lower Jaws of *Notharctus;* Milk Teeth of *Notharctus* and *Adapis*

1–5. Right ramus of mandibles of *Notharctus* from the Bridger Basin, (Middle Eocene), Wyoming. Lateral aspect. Natural size.

1. *N. osborni,* Amer. Mus. No. 11466. Lower Bridger.
2. *N. tenebrosus,* Amer. Mus. No. 5009. Lower Bridger.
3. *N. tenebrosus,* U. S. Nat. Mus., No. 3752 (Leidy's type). Lower Bridger.
4. *N. pugnax,* Amer. Mus. No. 11480. Lower Bridger.
5. *N. crassus,* Amer. Mus. No. 12588. Upper Bridger.

6–10. Milk teeth of *Adapis* and *Notharctus.*

6. *Adapis magnus.* Phosphorites of Larnagol (Lot). Right alveolar process with permanent m^1, three deciduous premolars, alveolus of permanent p^1, and deciduous canine. $\times \frac{2}{1}$. After Stehlin.

7. *Notharctus tyrannus.* Amer. Mus. No. 13025. Middle Eocene, Lower Bridger. Right alveolar process with deciduous premolars and two permanent molars in place; p^4 and m^3 not erupted. Crown view. $\times \frac{2}{1}$.

8. The same, lingual aspect. $\times \frac{2}{1}$.

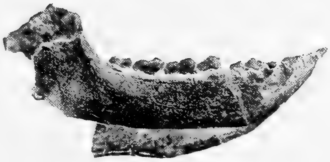
9. *Notharctus tyrannus.* Amer. Mus. No. 13029. Lower Bridger. Right ramus of mandible with broken remnants of the deciduous premolars, and the three true molars, of which m_3 is not yet fully in place. The crowns of p_4, p_3 and p_2 lie embedded in the jaw. $\times \frac{2}{1}$.

10. *Notharctus tyrannus.* Amer. Mus. No. 12578. Lower Bridger. Right ramus of mandible with m_1, m_2 and alveoli of m_3 and of the deciduous premolars (molars). The permanent canine is beginning to erupt, and p_4 lies embedded in the mandible. $\times \frac{2}{1}$.

5


4


3


2


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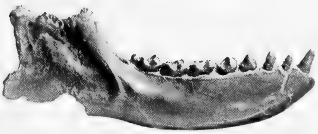


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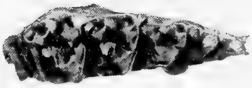
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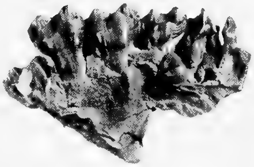
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9


10

PLATE XLIII

Plate XLIII

Comparative Series: Left Inner and Middle Ear of *Lemur varius*

Amer. Mus. No. 14024. Seen obliquely from a point below and in front of the left auditory bulla, the latter having been removed. Showing the stapes *in situ,* traversed by the osseous stapedial canal. Specimen and stereoscopic view prepared by Mr. A. E. Anderson. × $\frac{4}{1}$.

Abbreviations

aq. Fal.	broken wall of the canalis facialis (aqueductus Fallopii).
art. car. in.	bristle leading into canal for the "arteria promontorii."
art. st.	canal for stapedial branch of internal carotid artery.
coch.	auditory prominence of cochlea.
f. c.	foramen condylare (N. XII).
f. l. p.	foramen lacerum posterius, jugular foramen.
f. ov.	foramen ovale (N. V3).
f. pt. sp.	foramen pterygo-spinosum (for the internal pterygoid branch of the internal maxillary artery).
f. st. m.	foramen stylomastoideum (N. VII), leading into the canalis facialis.
pr. p. gl.	processus postglenoideus.
rec. epity.	recessus epitympanicus or attic, after the removal of the malleus and incus.
st.	stapes.
tu. au.	tuba auditiva, or Eustachian opening.
sinus hypotymp.	sinus hypotympanicus, or cavity of the bulla.

MEMOIRS AMER. MUS. NAT. HIST. N. S., Vol. III, Plate XLIII

Left Inner and Middle Ear of *Lemur varius*

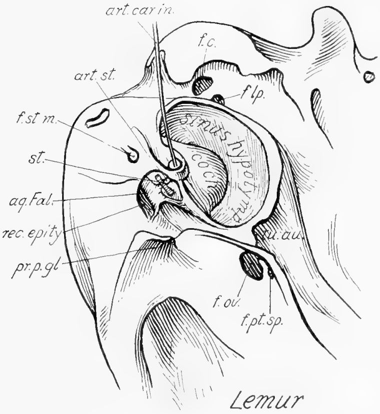


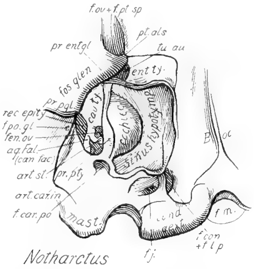
PLATE XLIV

PLATE XLIV

Comparative Series: Right Inner and Middle Ear of *Notharctus* and *Lemur*

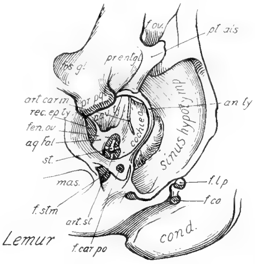
Specimens and stereoscopic views prepared by Mr. A. E. Anderson. × 4/1. For abbreviations see explanation of Plate XLIII.

1

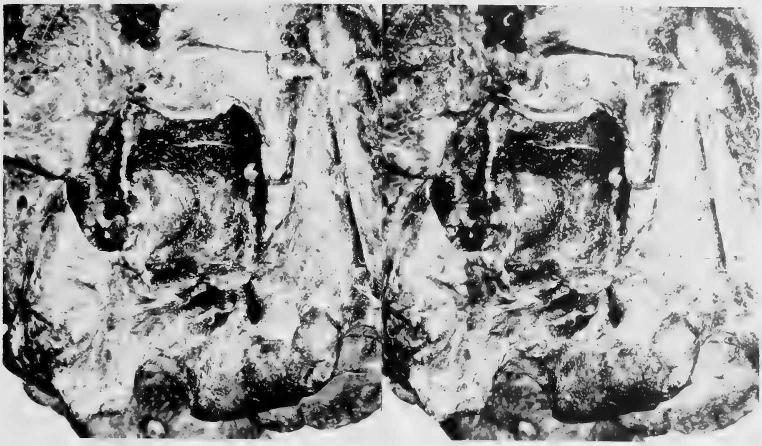


1. *Notharctus osborni.* Amer. Mus. No. 11466. Inner and middle ear of the right side, seen obliquely from below and from the outer side; after the removal of the lower part of the bulla, the tympanic annulus and the ossicles.

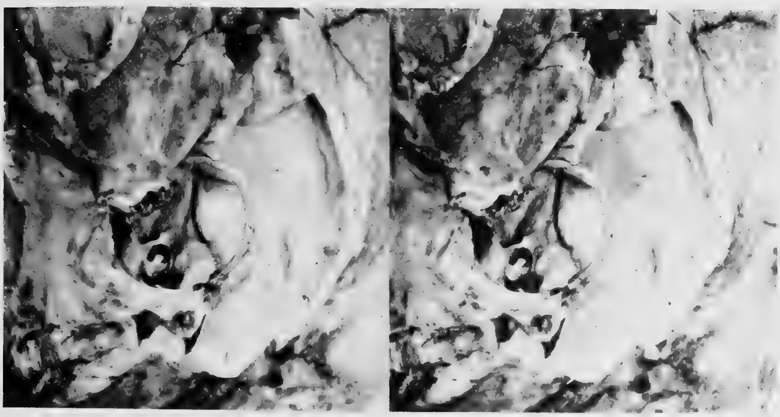
2



2. *Lemur varius.* Amer. Mus. No. 14024. Preparation of the right auditory region similar to that shown above in *Notharctus,* but with the tympanic annulus left *in situ.*



Right Inner and Middle Ear of *Notharctus osborni*



Right Inner and Middle Ear of *Lemur varius*

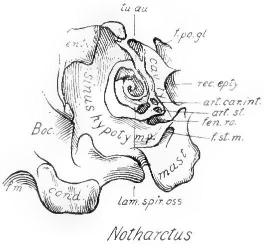
PLATE XLV

Plate XLV

Comparative Series: Left Inner and Middle Ear of *Notharctus* and *Lemur*

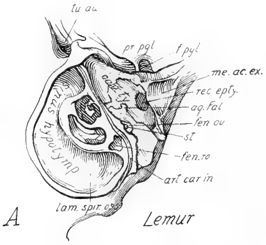
Specimens and stereoscopic views prepared by Mr. A. E. Anderson. × $\frac{4}{1}$. For abbreviations see Plate XLIII.

1



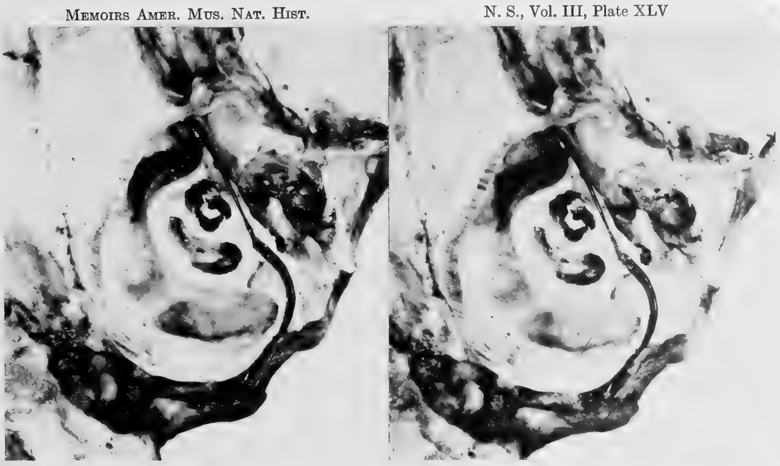
1. *Notharctus osborni.* Amer. Mus. No. 11466. Inner and middle ear of the left side seen from below, showing the broken wall of the bulla (*enty.*), the large hypotympanic sinus, the canals for the arteria promontorii and art. stapedia, and the interior of the bony cochlea.

2



2. *Lemur varius.* Amer. Mus. No. 14024. Inner and middle ear of the left side, for comparison with *Notharctus.*

Left Inner and Middle Ear of *Notharctus osborni*



Left Inner and Middle Ear of *Lemur varius*

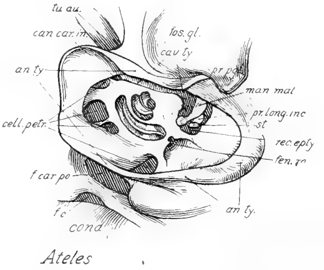
PLATE XLVI

Plate XLVI

Comparative Series: Left Inner and Middle Ear of *Ateles* and *Propithecus*

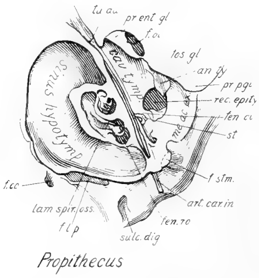
Specimens and stereoscopic views prepared by Mr. A. E. Anderson. × 4/1.

1

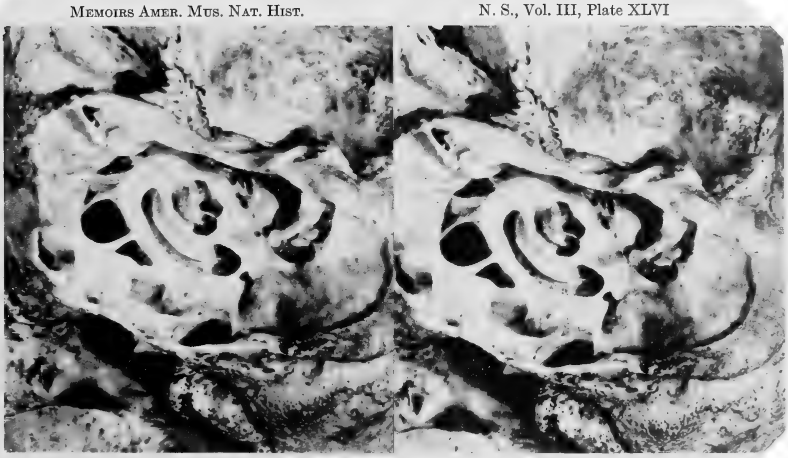


1. *Ateles* sp. Amer. Mus. No. 6336. Part of inner and middle ear of the left side, after the removal of the lower part of the bulla, showing the middle ear, with the ossicles *in situ*, the interior of the bony cochlea, and the cellulæ petrosæ of the hypotympanic sinus.

2



2. *Propithecus coquerelli.* Amer. Mus. No. 31255. Inner and middle ear of the left side. Exposure of the cochlea, hypotympanic sinus, cavum tympani, attic (*rec. epity.*), etc., after removal of the lower part of the bulla, tympanic annulus, membrana tympani, malleus, and incus; the stapes (*st*) being left *in situ*. The bristle shows the course of the internal carotid canal (arteria promontorii).



Left Inner and Middle Ear of *Ateles* species

Left Inner and Middle Ear of *Propithecus coquerelli*

PLATE XLVII

Plate XLVII

Comparative Series: Auditory Ossicles of *Northarctus* and other Primates

Specimens and stereoscopic views prepared by Mr. A. E. Anderson. $\times \frac{6}{1}$.

Upper figure: Auditory ossicles, right side, dorso-medial aspect. Also, the left malleus of *Notharctus*, seen from below.

3. *Macacus rhesus*
Amer. Mus. No. 26646
4. *Ateles* sp.
Amer. Mus. No. 6336
1. *Notharctus osborni*
Amer. Mus. No. 11466
2. *Propithecus diadema*
Amer. Mus. No. 31253

In *Ateles* the malleus shows the following processes: (1) processus longus, a very large sharply pointed process on the manubrium near the caput mallei; (2) processes brevis, a well defined, blunt process distal to the processus longus and lying in a plane almost at right angles to it; (3) processus muscularis, a low projection on the opposite side of the manubrium and distal to the processus brevis.

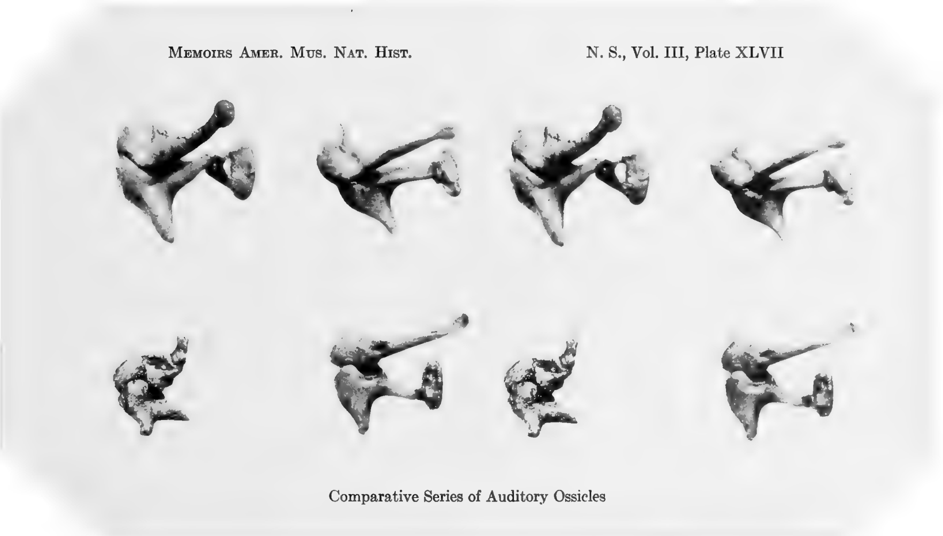
Lower (steroscopic) figure: The same series seen from below.

3

4

1

2



Memoirs Amer. Mus. Nat. Hist. N. S., Vol. III, Plate XLVII

Comparative Series of Auditory Ossicles

PLATE XLVIII

Plate XLVIII

Inner and Middle Ear of *Propithecus diadema*, for Comparison with the Corresponding Parts in *Notharctus*. After Milne Edwards

1. Vertical anteroposterior section of the left bulla, mastoid and attic, seen from the medial side. Showing the malleus (*m*) and incus (*e*), the tympanum (*t*) and tympanic annulus (*c*). The chorda tympani is seen passing between the malleus and the incus. Four times natural size.

2. Vertical section (medial to the last) of the left bulla and periotic, lateral aspect. Showing the auditory prominence (*ro*), the fenestra rotunda (seu cochleæ, *a*), the malleus (*m*), incus (*e*), and outer part of the stapes (*et*); behind the incus is the large subarcuate fossa (*st*) while above is another large sinus (*st*) which, as shown in an American Museum specimen (No. 31255), is merely a dorsal prolongation of the tympanic attic or recessus epitympanicus. In *Notharctus osborni* (Amer. Mus. No. 12659) the fossa subarcuata was smaller and the epitympanic recess did not extend dorsad in front of it.

3. Vertical anteroposterior section of the inner ear of the right side, viewed from the encephalic side. Three times natural size. Showing the expanded fossa subarcuata (*f*), the superior (*s*), external (*s''*), and posterior semicircular canals, the fenestra ovalis with the foot plate of the stapes (*o*), the fenestra rotunda (*r*), the cochlea (*l*) and the cavum bullæ or hypotympanic sinus of the bulla (*b*).

4. Vertical transverse section of the right periotic, viewed from in front, passing through the middle of the fossa subarcuata (*f*), the vestibule and internal auditory meatus (*a*). Three times natural size. Showing sinus lateralis (*sl*), superior semicircular canal (*s*), bottom of the subarcuate fossa (f^1), surrounded by the posterior semicircular canal; s^1 external semicircular canal, *so*, so^1 openings of the semicircular canals into the vestibule.

5. Horizontal section of the left auditory bulla viewed from below. Three times natural size. Showing the auditory prominence or cochlea (*l*), the carotid canal (*tc*), the tympanic annulus (c^1), the Eustachian tube (*te*), and the foramen lacerum posterius (*td*).

6. Left malleus (*m*) and incus (*e*), mesal aspect. Eight times natural size.

7. Left malleus, lateral aspect. Eight times natural size.

7a. The same, viewed from in front.

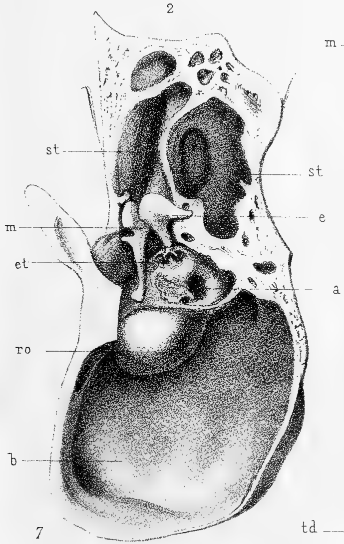
8. Left incus, lateral aspect. Eight times natural size.

9. Stapes (*et*) surmounted by os lenticulare (*le*) *in situ* in the fenestra ovalis and traversed by the osseous canal for the stapedial artery (*ti*).

10. Stapes (*et*) and lenticulare (*le*). Eight times natural size.

11. Foot plate of stapes.

2



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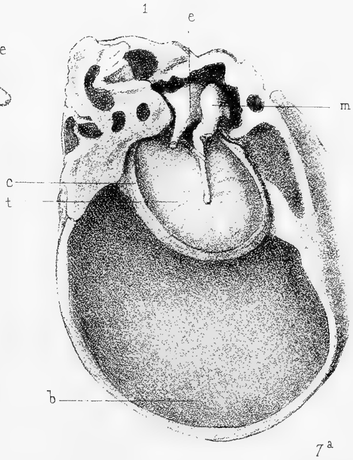

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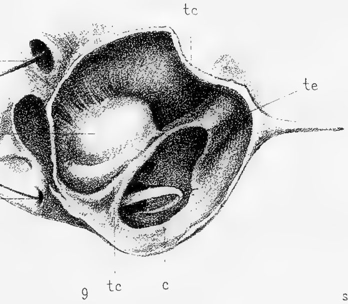
7^a

5



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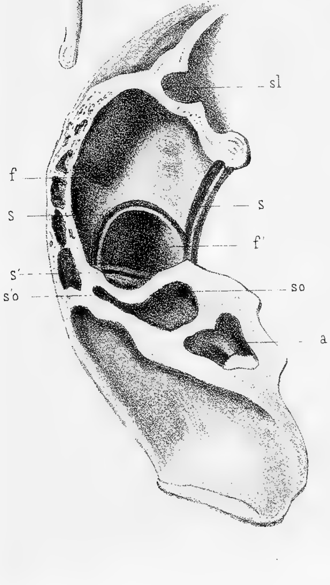

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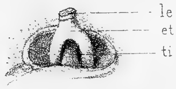

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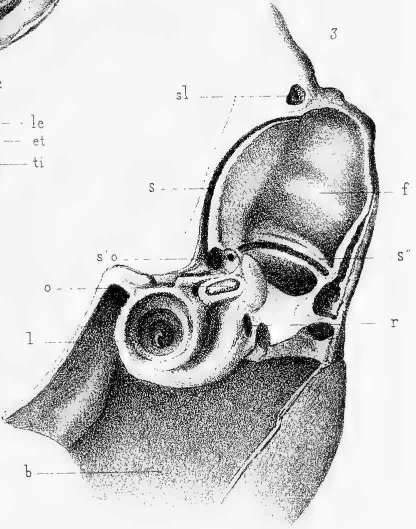

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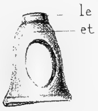


PLATE XLIX

Plate XLIX

Comparative Series: Under side of the skull of various Primates to show the Form and Relations of the Auditory Bulla and the Position of the Internal Carotid Foramina

All figures natural size.

Lemur varius. Amer. Mus. No. 14024. The bristle shows the course of the internal carotid canal through the bulla.

Notharctus osborni. Amer. Mus. No. 11466. The bullæ of both sides are broken, showing the cochlea, the carotid canal, the Eustachian tube of the left side. For details see Plates XLIV, XLV.

Propithecus coquerelli. Amer. Mus. No. 31255. The lower part of the bulla has been removed, showing the tympanic annulus and part of the external auditory meatus, the internal carotid canal and the cochlea. For details see Plates XLVI, XLVIII.

Perodicticus potto. Amer. Mus. No. 15972. The bristle indicates the foramen on the posteromedial face of the bulla, through which enters a branch (art. stapedia?) of the internal carotid artery. The prominent foramen (for. lacerum medium) in front of the bulla transmits the anterior branch of the internal carotid (art. promontorii?). The left bulla is sectioned and shows the cellulæ petrosæ and the large sinus in the mastoid.

Necrolemur sp. Princeton Univ. Mus. On the right side, between the large bulla and the basioccipital, is a prominent foramen probably for the internal carotid artery. The external auditory meatus is indicated by a bony tube lateral to the bulla.

Alouatta sp. Amer. Mus. No. 14660. The expanded tympanic annulus forms the lateral part of the bulla, the latter being filled with cellulæ petrosæ. The internal carotid foramen is on the posteromedial surface of the bulla. Compare Plate XLVI.

Perodicticus
Lemur

Necrolemur
Notharctus

Alouatta
Propithecus

PLATE L

PLATE L

Comparative Series: Interior of the Brain-case of Primates seen from above, to show especially the Endocranial Openings of the Internal Carotid Artery

All figures natural size.

Lemur varius. Amer. Mus. No. 14024. The anterior end of the tunnel for the arteria promontorii is indicated by the bristle at the left side of the sella turcica. The endocranial course of the arteria stapedia is indicated by the bristle on the right side on the medial wall of the brain-case. (See page 174).

Propithecus coquerelli. Amer. Mus. No. 31255. The courses of the arteria promontorii and art. stapedia are indicated by the bristles. (See page 175).

Perodicticus potto. Amer. Mus. No. 15972. The anterior branch (art. promontorii?) enters the brain-case through the prominent foramen in front of the bulla.

Alouatta sp. Amer. Mus. No. 14660. The internal carotid enters the brain cavity through the carotid groove on the anteromedial extension of the periotic. The bristle leads through the hiatus Falopii to the canalis facialis (aqueductus Falopii).

Perodicticus
Lemur

Alouatta
Propithecus

PLATE LI

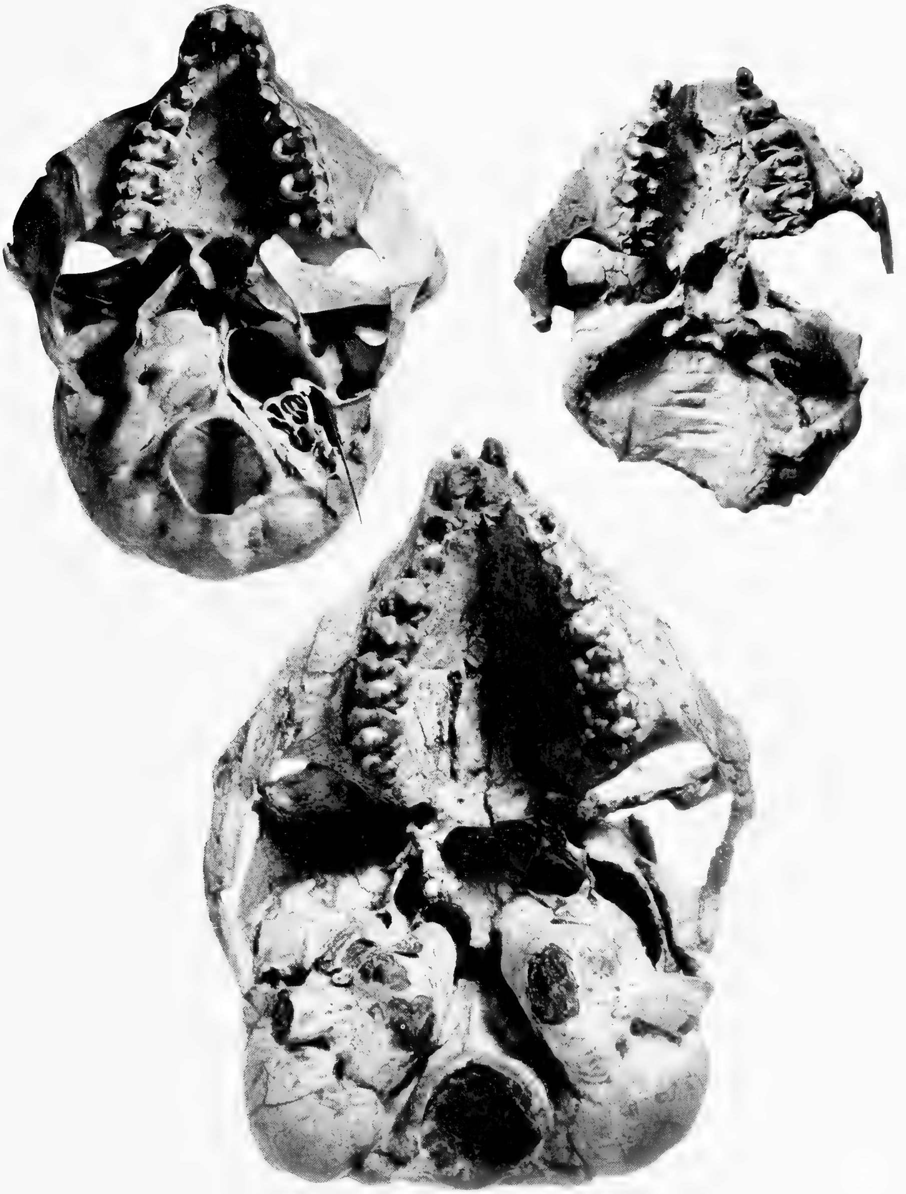
PLATE LI

Comparative Series: Norma Basalis of the Skull of *Tarsius*, *Tetonius*, and *Necrolemur*

Tarsius spectrum. Amer. Mus. No. 64. The prominent foramen for the internal carotid artery is shown perforating the middle of the inferior surface of the greatly expanded bulla. On the left side the lower part of the bulla has been removed and the cochlea is shown in section. At the apex of the cochlea is a section of the carotid canal. (The lumen of this canal does not show in the plate.) The bristle indicates the position of the cavum tympani and Eustachean foramen. Three times natural size.

Tetonius ("*Anaptomorphus*") *homunculus* (Cope). Amer. Mus. No. 4194. Lower Eocene, Gray Bull beds, Bighorn Basin, Wyoming. On the left side is shown the auditory prominence, or cochlea, which is much smaller than that of *Tarsius*. Adhering to the cochlea is the remnant of the septum bullæ and possibly of the carotid canal. In front of the cochlea is the cavum tympani. The bullæ were evidently greatly expanded and extended anterointernally toward the midline, pressing against the alisphenoid laterally and against the basisphenoid anteriorly. Three times natural size.

Necrolemur antiquus. Peabody Mus. Comp. Zool., Harvard Univ. The greatly inflated bullæ extend far forward and inward and are overlapped by the alisphenoid. The carotid foramen is on the medial wall of the bulla near its junction with the basioccipital and just in front of the slit-like foramen lacerum posterius. Four times natural size.



Tarsius *Necrolemur* *Tetonius homunculus*

PLATE LII

PLATE LII

Comparative Series: Norma Lateralis of the Skulls of *Notharctus, Chirogale, Lemur, Myoxicebus*

Chirogale sibreei. Brit. Mus.[1] No. 97, 9, 1, 160. × $\frac{3}{2}$.
Lemur catta. Brit. Mus. No. 75, 7, 20, 10. × $\frac{1}{1}$.
Notharctus osborni. Amer. Mus. No. 11466. × $\frac{1}{1}$.
Myoxicebus (Hapalemur) simus. Brit. Mus. Nos. 84, 10, 21, 4. × $\frac{1}{1}$. The mandible is incorrectly placed in front of the articular eminence, causing the subcaniform p_2 to appear in front of the upper canine instead of behind it as it should be.

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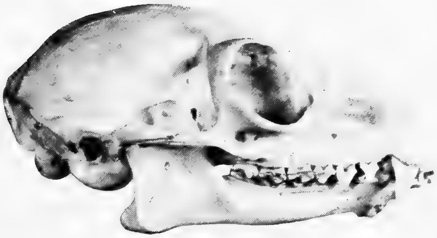
[1] Figures of British Museum specimens in Plates LII–LVIII from photographic negatives made for the American Museum by Mr. A. E. Anderson. These negatives were first used in the late Dr. Elliot's monograph on the Primates (1912, Monogr. Amer. Mus. No. 1, I–III). For the present work the backgrounds have been changed from black to white and some minor corrections of the shading have been made.

Chirogale



Lemur

Notharctus

PLATE LIII

Plate LIII

Comparative Series: Norma Verticalis of the Skulls Figured in Plate LII

Chirogale

Myoxicebus

Notharctus

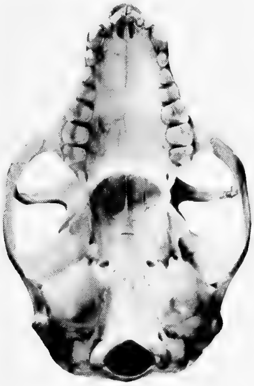
Lemur

PLATE LIV

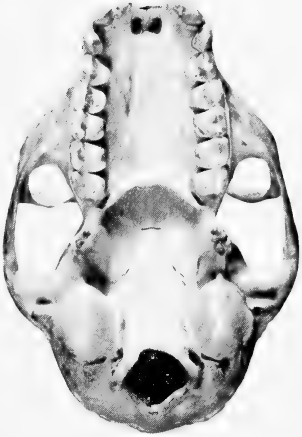
PLATE LIV

Comparative Series: Norma Basalis of the Skulls of *Notharctus*, *Lepilemur*, *Chirogale*, *Myoxicebus*

Notharctus osborni. Amer. Mus. No. 11466. × $\frac{1}{1}$.
Lepilemur mustelinus. Brit. Mus. Nos. 97, 9, 1, 24. × $\frac{3}{2}$.
Chirogale sibreei. Brit. Mus. Nos. 97, 9, 1, 160. × $\frac{3}{2}$.
Myoxicebus (“*Hapalemur*”) *simus.* Brit. Mus. Nos. 84, 10, 24, 4. × $\frac{1}{1}$.



Chirogale



Myoxicebus

Notharctus

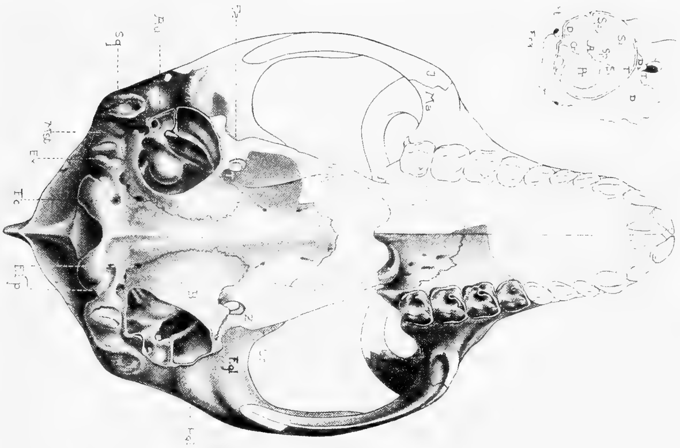
Lepilemur

PLATE LV

PLATE LV

Comparative Series: Norma Basalis of the Skulls of *Adapis, Megaladapis, Lepilemur*

Adapis parisiensis var. *Schlosseri.* After Stehlin. Scale not given. The lower parts of the bullæ have been removed.
Megaladapis grandidieri. After Standing. Much reduced.
Lepilemur mustelinus. Brit. Mus. No. 97, 9, 1, 24. $\times \frac{3}{2}$.



Adapis

Megaladapis

Lepilemur

PLATE LVI

Plate LVI

Comparative Series: Norma Lateralis of the Skulls of *Notharctus*, *Propithecus*, *Indris*, *Lichanotus* (*Avahis*)

Notharctus osborni. Amer. Mus. No. 11466. × $\frac{1}{1}$.
Propithecus diadema. Amer. Mus. No. 31253. × $\frac{1}{1}$.
Indris indris. Brit. Mus. No. 48, 10, 28, 1. × $\frac{1}{1}$.
Lichanotus (*Avahis*) *laniger*. Brit. Mus. No. 1512 d. × 2.

Indris

Lichanotus (Avahis)

Notharctus

Propithecus

PLATE LVII

PLATE LVII

Comparative Series: Norma verticalis of the Skulls of *Notharctus, Propithecus, Indris, Lichanotus* (*Avahis*)

The same specimens as in Plate LVI.

Lichanotus (Avahis)

Propithecus

Indris

Notharctus

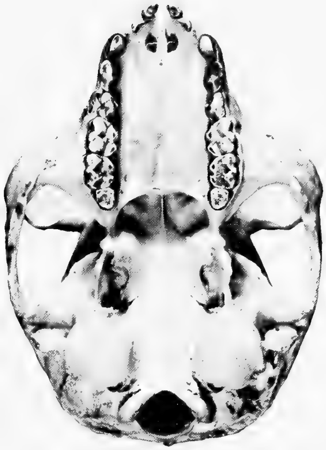
PLATE LVIII

Plate LVIII

Comparative Series: Norma basalis of the Skulls of *Notharctus*, *Propithecus*, *Indris*, *Lichanotus* (*Avahis*)

The same specimens as in Plate LVI.

Lichanotus (Avahis)



Propithecus

Indris

Notharctus

PLATE LIX

Plate LIX

Comparative Series: Upper and Lower Teeth of *Notharctus* and *Alouatta* ("*Mycetes*")

1. *Notharctus crassus.* Amer. Mus. No. 11982. Middle Eocene (Upper Bridger). Right upper premolar-molar series and canine. × $\frac{3}{1}$.
2. *Alouatta* ("*Mycetes*") sp. Amer. Mus. No. 14660. Right upper tooth-row. × $\frac{3}{1}$.
3. *Notharctus crassus.* Amer. Mus. No. 11982. Middle Eocene (Upper Bridger). Right ramus of mandible with teeth. × $\frac{3}{1}$.
4. *Alouatta* ("*Mycetes*") sp. Amer. Mus. No. 14660. Right ramus of mandible with teeth. × $\frac{3}{1}$.

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