THE OSTEOLOGY OF THE REPTILES

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THE OSTEOLOGY OF THE REPTILES

BY

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FOREWORD

In this book we have the chief results of Williston's half-century of exploration and research in the field of vertebrate palaeontology. Here we find the gist of his earlier researches upon the mosasaurs, plesiosaurs, and pterosaurs of the marine Cretaceous of Kansas, the substance of his later and fundamental discoveries among the primitive reptiles of the Permian of Texas, and the epitome of his last, comprehensive survey of the evolution of the Reptilia as a whole. The writing of this book was thus the culminating effort and achievement of his inspiring career.[1] Death overtook him before the final revision and completion of this work, but happily not before he had finished the greater part of the text and had made for it with his own pen a large series of new and excellent line-drawings.

In accordance with Williston's wishes the writer undertook to put his last work in shape for the publisher and to see it through the press. For the long delay since 1918 there have been too many causes to be profitably set forth in detail. The University of Chicago Press, which had published Williston's earlier books, repeatedly found itself unable to accept this one notwithstanding its good will, and private publishers proposed conditions that were not acceptable, either to the Williston Memorial Committee, or to Professor Williston's family. After much unsuccessful correspondence in various directions, the sad plight of Williston's still unpublished work came to the notice of Professor Thomas Barbour of Harvard University, and through his good offices the Harvard University Press now has the honor of publishing the "Osteology of the Reptiles."

The new drawings that Williston made for this book have been supplemented by many other illustrations, mostly from Williston's earlier works, which were needed to illustrate the present text. The University of Chicago Press has courteously loaned many of these cuts, while others have been copied from the original publications of the authors to whom they are credited. The American Museum of

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[1] For an excellent account of Williston's life and work see Henry Fairfield Osborn's article, "Samuel Wendell Williston, 1852–1918," *Journal of Geology*, Vol. xxvi, 1918, pp. 673–689.

Natural History, with the cordial approval of President Osborn, has at all times given indispensable support in the work of making ready this book for the press. Special acknowledgment is due to Mrs. E. H. Fink and Mrs. C. P. Meadowcroft of the Museum. Dr. G. K. Noble, Curator of Herpetology, has supplied critical notes on the sections dealing with recent reptiles.

Every effort has been made to keep intact the spirit and letter of the original text, and in the few places where corrections or emendations seemed necessary they have been placed in square brackets, as have also the footnotes that record some of the more conspicuous discoveries and advances since 1918.

W. K. G.

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PART I

THE SKELETON OF REPTILES

INTRODUCTION

THE PRIMITIVE SKELETON OF REPTILES

That the reptiles were evolved from the Amphibia, and more specifically from that order known as the Temnospondyli, seems now assured. The earliest as also the most primitive reptiles that we know belong to the order called the Cotylosauria. With the exception of *Eosauravus* from the middle Pennsylvanian of Ohio, of which, unfortunately, the skull is unknown, our knowledge of them goes no further back than the late Carboniferous and early Permian. At that time there was a considerable diversity of known forms, belonging to at least four well-differentiated groups and twenty or more families; from which we may very properly conclude that their earliest ancestors, the beginning of their stock, lived much earlier, certainly at the beginning of the Upper Carboniferous, and very probably in Lower Carboniferous times. We therefore never can expect to find in the rocks of the Permian any real connecting link between the two classes.

Both the reptiles and the amphibians had changed in this interval, an interval perhaps of millions of years, retaining in varying degrees their ancestral characters, while losing or adding others in various ways. The reptiles, by the acquirement of a new mode of life, the loss of gills in their youth and entire emancipation from the water, became more progressive than the amphibians, and their evolution was more rapid. Characters that are common to many amphibians became more and more rare among the reptiles, and the amphibians, handicapped by inherited habits, were restricted more and more to subordinate rôles, and only a few of the more progressive continued to develop. They, for the most part, lost those characters and adaptations that brought them into immediate competition with the reptiles, and by the close of Triassic times had become restricted to habits and habitats no longer invaded by them. The modern toads, frogs, salamanders, and blindworms differ far more from the higher amphibians of Paleozoic times than did the latter from their contemporary reptiles.

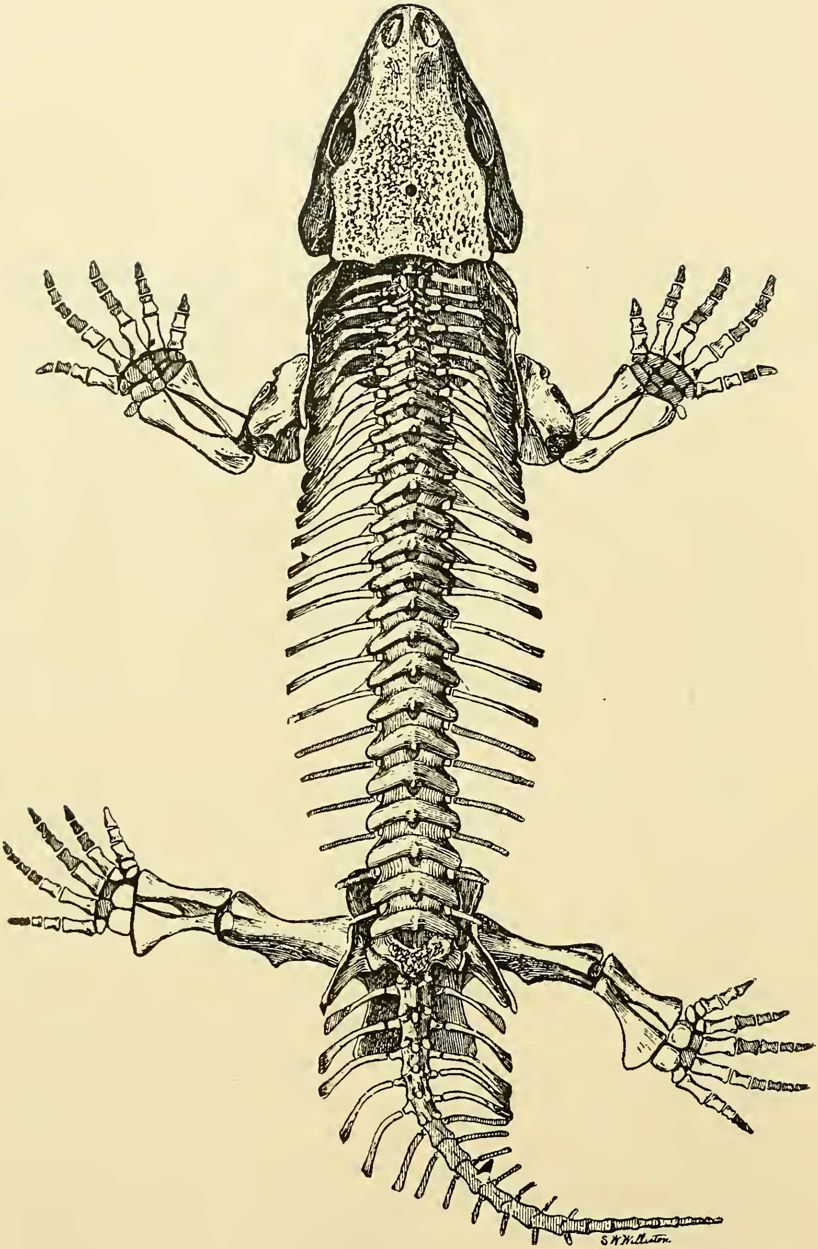

FIG. 1. Primitive Cotylosaur *Seymouria*, from nearly complete specimen, from above. A little less than one third natural size.

Nevertheless, there were still so many inherited characters among both the amphibians and reptiles of early Permian times that nothing distinctive of either class can be found in the skeleton, except in the atlas and feet, with a considerable gap in the structure of their vertebrae. In the vertebral column there was a general change among the Temnospondyli from the embolomerous to the rhachitomous type, that is, from the more simply divided centrum of two disks to the tripartite centrum composed of wedges; while all reptiles had acquired a reduced embolomerous form with one disk, the centrum, and one wedge, the intercentrum. Doubtless all amphibians of Lower Carboniferous times had embolomerous vertebrae, but only a very few of their stock persisted as late as the Permian. In general literature the Amphibia are distinguished from the Reptilia by the possession of two occipital condyles. The earliest amphibians doubtless all had a single occipital condyle, an inheritance from their ancestral fishes — all that we know from the Lower Carboniferous had—of which only one known descendant with that character survived to the Permian. The reptiles, however, retained the single condyle until the beginning of their evolution into mammals, when they too developed a double condyle. We relied, until recently, upon the widely open palate of the Amphibia as a final distinguishing character of their class, but we now know that some, if not all, of the earliest amphibians had a [closed] palate like that of the [earliest] reptiles, but of these none is known at the beginning of Permian times. In other words, a single condyle and a closed palate are more primitive characters of the tetrapods than those we had assumed as characteristic of the Amphibia. We know no amphibians with as many bones in the digits as the early reptiles possessed, and no reptiles with as many bones in the tarsus as the early amphibians had,

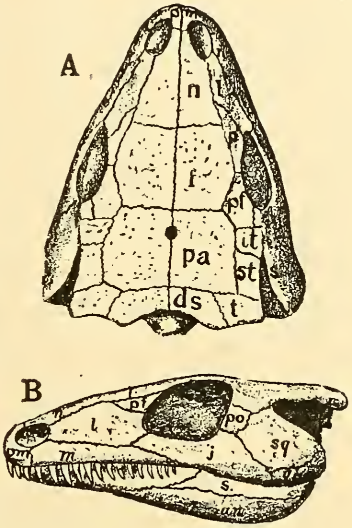

FIG. 2. *Seymouria* (Cotylosauria). A, from above; B, from side. One third natural size.

but doubtless when we discover the feet of the earliest reptiles we shall find them not different from the feet of the contemporary amphibians.

Every known bone in the skull of the Temnospondyli, except the interfrontal of a very few, has been found in the skull of early reptiles, and all, indeed, in a single genus *Seymouria* (Figs. 1, 2) from the Lower Permian of Texas. And there is no bone in the skeleton of reptiles that is not known in these same amphibians, except the preparietal of the Anomodontia, the supraorbitals of various Squamata and the predentary and rostral bones of certain dinosaurs, and doubtless the last two, if not all, are simply dermal bones which became temporarily attached to the skull. The girdles and limbs of the two classes are distinguishable only by minor characters. And thus, while we do not know from these later rocks, and probably never shall from rocks later than the Lower Carboniferous, all of the characters common to the two classes in any one animal, from the comparison of all it is not difficult to decide what were the primitive characters of the reptilian skeleton in almost every detail. They may be summarized as follows:

The Primitive Skull of the Reptilia

Rugose, with five openings in roof:
  A. Paired, divided, terminal nares.
  B. Paired orbits beyond middle [*i.e.*, in front of the middle of the skull].
  C. Median parietal (pineal) foramen.

An emargination of the occipital border, between tabular and squamosal, for the ear [the "otic notch"].

Seventeen pairs of roof bones; four pairs of palatal bones; eight pairs of cranial bones; eight pairs of mandibular bones; three unpaired cranial bones; one unpaired palatal bone — seventy-eight in all.

A. Paired Bones

1. Premaxillae (*px*)	Dentigerous
2. Maxillae (*mx*)	
3. Septomaxillae (*sx*)	Nasal bones
4. Nasals (*na*)	Median roof bones
5. Frontals (*fr*)	
6. Parietals (*pa*)	
7. Interparietals (*ip*)	

8. Lacrimals (*la*)	Surrounding orbits
9. Prefrontals (*pr*)	
10. Postfrontals (*pf*)	
11. Postorbitals (*po*)	
12. Jugals (*j*)	
13. Intertemporals (*it*)	Temporal bones
14. Supratemporals (*st*)	
15. Tabulars (*t*)	
16. Squamosals (*sq*)	
17. Quadratojugals (*qj*)	
18. Dentaries (*d*)	Mandible
19. Coronoids (*cor*)	
20. Splenials (*sp*)	
21. Postsplenials (*psp*)	
22. Angulars (*an*)	
23. Prearticulars (*pa*)	
24. Surangulars (*sa*)	
25. Articulars (*art*)	
26. Prevomers (*pv*)	Palatal bones, dentigerous
27. Palatines (*pl*)	
28. Pterygoids (*pt*)	
29. Ectopterygoids (*ec*)	
30. Quadrates (*qu*)	Articulation of mandible
31. Exoccipitals (*eo*)	Cranial bones
32. Paroccipitals (*poc*)	
33. Proötics (*pc*)	
34. Postoptics (*al*)	
35. Stapes (*stp*)	
36. Epipterygoids (*ep*)	
37. Ethmoids (*se*)	

AA. Unpaired Bones

38. Parasphenoid (*ps*)	Palate
39. Supraoccipital (*so*)	Cranial bones
40. Basioccipital (*bo*)	
41. Basisphenoid (*bs*)	

The Primitive Postcranial Skeleton

A. Membrane Bones, Exoskeletal

1. Sclerotic plates in orbits.
2. Paired clavicles, cleithra and elongate interclavicle
3. Dermal plates or scutes.

AA. Cartilage Bones, Endoskeletal

1. Notochordal vertebrae; two or three cervicals, about twenty-three presacral; one sacral; moderately long tail; proatlas; atlas embolomerous; all vertebrae to tenth or twelfth caudal with free, holocephalous ribs, articulating continuously with intercentrum and diapophysis.
2. Intercentra between all vertebrae.
3. Slender and numerous parasternal ribs.
4. Scapular girdle composed of paired scapulae, procoracoids and metacoracoids, fused in adult life, the three forming the glenoid socket; a supracoracoid and a supraglenoid foramen.
5. No sternum.[1]
6. Pelvis plate-like with small obturator foramen only; acetabulum formed by the three bones, closed.
7. Legs short and stout.
8. Humerus dilated at extremities, with entepicondylar foramen.
9. Carpus with four bones in proximal row; two (three?) in middle row; five in distal row; all well ossified.
10. Hand pentadactylate, the fourth finger strongest and longest; phalangeal formula 2, 3, 4, 5, 3.
11. Tarsus composed of nine bones: two in first row[2]; two in second; five in distal row; all well ossified.
12. Feet pentadactylate, the fourth toe strongest and longest; phalangeal formula 2, 3, 4, 5, 4.

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[1] [But see footnote 1, on page 122 below. — Ed.]

[2] [But see footnote on page 187 below. — Ed.]

CHAPTER I

THE SKULL OF REPTILES

External Appearance, Excrescences, and Chief Openings

The skull of reptiles, as of other vertebrates, has undergone many changes in adaptation to food, offensive and defensive habits. It has lost not a few bones in various forms, and others have united or formed new associations; to such an extent, indeed, that there are several in later reptiles about whose homologies there has been and yet is dispute. It has developed excrescences or horns for defense or offense, or has been covered at times with a solid armor of skin bones; but it has gained permanently no new bones, though a few have been added temporarily from the exoskeleton. The skull of carnivorous reptiles (Figs. 33, 45) is more or less elongate, like that of a wolf; insectivorous reptiles may have a more slender skull (Fig. 52 b); while those reptiles using the jaws to crush invertebrates always have a short and powerful skull (Fig. 49). The face of aquatic, fish-eating reptiles (Fig. 58) is always long, sometimes very long (Fig. 67), as in the modern gavials.

Excrescences or horns on the skull have been developed in not a few. The earliest known is that of the cotylosaurian *Chilonyx*, with excrescences, and the theromorph *Tetraceratops*, with large protuberances. Some of the later Cotylosauria, like *Elginia*, had horny protuberances at the back part. A few carnivorous dinosaurs have a median facial and supraorbital rugosities, as though for the support of horns or spines. In the Ceratopsia (Fig. 70 a) the development of horns and spines was carried to a remarkable degree, not only on the face but also along the posterior margin of the greatly extended skull. Perhaps of all reptiles none has surpassed some of the modern chameleons in the development of facial horns (Fig. 55 d), though not a few other lizards, like the horned lizards and moloch lizards, have many sharp protuberances and horny excrescences, which, were they magnified to the size of dinosaurs would be equally imposing. Even some turtles, like the southern *Miolania*, have horns upon the skull. Usually the median unpaired facial horn is borne by the nasals, as in the mammals, but in the chameleons it is formed by the maxillae. The paired facial horns are borne by the prefrontals or postorbitals. The frontals and parietals are sometimes developed into enormous crests in the dinosaurs, the supraoccipital in pterosaurs. Doubtless all such horns or protuberances were covered in life with a horny sheath.

The *external nostrils* (*external nares*) vary greatly in position. Primitively located near the extremity of the face (Figs. 2, 3, etc.), each was surrounded by the premaxilla, maxilla, nasal and lacrimal, and they almost always have the same relations with the first three of these bones, wherever located. Well separated by the premaxillae and nasals in the older reptiles, they are often confluent in later ones (Figs. 31, 32, 59, 68). They are surrounded by the maxillae in the chameleons (Fig. 55), by the nasals in the phytosaurs (Fig. 66); the nasals are often excluded from them, and the lacrimals have lost all relations with them since Permian times. In most aquatic reptiles they have receded toward the orbits, or rather the face has grown away from them, often for a long distance, as in the ichthyosaurs (Fig. 50), plesiosaurs (Fig. 46 A), proganosaurs, thalattosaurs (Fig. 61), and phytosaurs (Fig. 67). In the very slender-faced amphibious Crocodilia (Fig. 68) and Choristodera (Fig. 63), however, the nostrils retain their primitive position at the extremity of the face. They are located far back from the extremity in the volant pterodactyls (Figs. 71, 72) as in most birds.

The *internal nares*, or *choanae*, normally situated almost immediately below the external (Fig. 55), are carried back by a respiratory canal, formed by the undergrowth of the maxillae and palatines as a secondary palate, to a greater or less extent in the Cynodontia and Crocodilia (Fig. 69); in the former and in the early kinds of the latter, to the posterior border of the palatines; in the later crocodiles even into the pterygoids. A similar respiratory canal, probably separated from the cavity of the mouth by a membrane only, is characteristic of the Phytosauria (Figs. 66, 67). A partial secondary palate, formed by the union of the palatines or maxillae, with the opening only a little way back, occurs in some Chelonia and Anomodontia. In those reptiles in which the external nares are situated posteriorly, the internal nares are also (*e.g.*, Figs. 61, 66). In the plesiosaurs only (Fig. 46), there may be a partial reversion of the respiratory canal, with the internal opening in front of the external. The internal nares, primitively (Figs. 6, 21, 47) divided by the prevomers and surrounded by the premaxillae, maxillae and palatines, may sometimes (Figs. 49, 71 C) lie between the prevomers and palatines.

The *parietal* or *pineal foramen*, very large in certain shell-eating cotylosaurs (Fig. 22), had become inconstant even in that order. It is present, so far as known, in all the Theromorpha (Figs. 33–42), and in the Therapsida (Figs. 43–45), with the exception of a few forms; in the Proganosauria, Ichthyosauria (Fig. 50), Sauropterygia (Fig. 48), the Diaptosauria (Figs. 60–62), and most lizards (Figs. 55 A, 56), but is absent in some true lizards, the chameleons, and all snakes (Fig. 59). It has been reported in certain doubtful Pseudosuchia and more or less doubtfully in a few phytosaurs and dinosaurs, but with these possible exceptions appears to be absent in all the Archosauria (Figs. 65 B, 66 B, 68, etc.) as also the Chelonia (Figs. 30, 31, 32). Usually located between the parietals anteriorly (Figs. 22, 33, 43, 44, 45, 46, etc.), it may occur between the frontals posteriorly (Fig. 55). In the Anomodontia and Gorgonopsia (Fig. 43) there is a separate bone, the preparietal, a small unpaired element of doubtful homologies, absent in other reptiles, in front of or surrounding the foramen.

The *orbits*, directed upward sometimes in aquatic animals (Fig. 32), but usually laterally, were primitively (Figs. 2, 3, 22, 23, 33, 43, 44, 65) surrounded by the prefrontal, postfrontal, postorbital, jugal, and lacrimal. The frontal usually forms a part of the upper margin, the maxillae sometimes below (Figs. 30, 48, 49, 55, 56, 59). In snakes (Fig. 59), only the prefrontal and postorbital may be left. Sometimes the postorbital bar is incomplete in lizards (Fig. 56), snakes (Fig. 59), and therapsids (Fig. 45 D). The prefrontal is excluded in some dinosaurs, the postorbital in *Araeoscelis* (Fig. 52) and *Hyperodapedon* (Fig. 62 D), leaving not a single element invariably associated with the orbit. *Antorbital* or *preorbital vacuities* are very characteristic of the Archosauria, occurring in all phytosaurs (Figs. 66 B, 67 A) and true pseudosuchians (Fig. 65 B, D), most Saurischia (Fig. 70 A, B) and Pterosauria (Fig. 71) and some Crocodilia. Usually there is but one, but there may be two or even three on each side in certain Theropoda (Fig. 70 A).

Openings through the skull roof,[1] back of the orbits, are characteristic of all reptiles save the Cotylosauria (Figs. 2, 4, 19, 22) and Chelonia. The upper opening, the *supratemporal,* arose primitively by the separation of the postorbito-squamosal bar (Fig. 33 A) from the parietal (Fig. 53 C). The lower or *lateral temporal* opening appeared primitively (Figs. 33, 53 A) between the squamosal and the jugal. It is bounded above by the postorbito-squamosal arch, below by the jugal, to which was added, in some of the double-arched forms, the quadratojugal (Figs. 62, 64, 65, 70 A, B). Either the upper or the lower opening may occur independently, or both together. In the Cynodontia (Fig. 45) and some other Theriodontia, with a lower temporal opening (Figs. 44 F, 45 D), the squamosal may fail to meet the postorbital above the opening, permitting the parietal to form the upper boundary in part; and this is the condition in mammals. In not a few of the Therapsida, the Dinocephalia especially (Fig. 44 B), the jugal is excluded from the lower margin by the union of the squamosal and postorbital.

All known forms of the Sauropterygia (Figs. 46, 47, 48) and Placodontia (Fig. 49) have the single opening bounded below by the squamosal and postorbital, above by the sides of the parietal, that is, it is like the upper one of those reptiles with two temporal openings. It is usually considered to be what it really appears to be, the upper temporal opening only; and its certain nature will not be determined until more is known of their terrestrial antecedents.

The *intertemporal vacuity.* The single temporal opening of the Squamata (Figs. 55, 54), when complete, the Ichthyosauria (Fig. 50), and certain other forms here grouped under the Parapsida, lies between the postorbito-squamosal arch and the parietal, but has, in most if not all, an additional bone helping to form its posterior or outer border, the supratemporal or tabular, for there is doubt as to its real homology. (See pages 61–69 below.)

The *post-temporal* opening is situated on the occipital aspect of the skull, a vacuity between the parietal, or parietal and squamosal, and the paroccipital on each side. It is present in some Cotylosauria

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[1] [In addition to the openings noted by the author, paired *subtemporal openings* occur in all reptiles in the palatal aspect of the skull; they are bounded medially by the pterygoids and the basis cranii, laterally by the lower temporal bar, if present, or by the dermal covering of the temporal region, as in Squamata. — ED.]

(Fig. 21 B), and Theromorpha (Fig. 45 G), and is generally present in later reptiles though absent or vestigial in the Crocodilia.

The cranial region thus exposed by these various openings has been exposed to a greater or less degree in most Chelonia (Figs. 30–32) in a different way: by the emargination of the roof bones from behind or from behind and below, until, in some forms like the terepenes, the whole temporal roof is lost.

Posterior palatine or *suborbital openings* occur in most reptiles (Figs. 55, 63, 66, 69, 72) since the Theromorpha, but are absent in some turtles. They are situated between the palatines and maxillae posteriorly, and are usually also bounded in part by the ectopterygoids. They do not occur in the Cotylosauria (Figs. 6, 21 A, 24, 29) or Theromorpha (Figs. 40 C, 42 C), though present in many Therapsida.

THE SKULL ELEMENTS

The primitive relations of the skull elements may be discussed seriatim, with their chief modifications in later reptiles.

Premaxillae (*px*). Primitively short (Figs. 2, 3, 4, 19, 22, 33, 43), articulating with maxillae, nasals and prevomers, the posterior process forming a partial division between the nasal chambers. They form the anterior boundary of the external and internal nares. Four or five teeth in each.

Elongate in the strictly aquatic reptiles (Figs. 46, 47) and in the Pterosauria. In the plesiosaurs (Figs. 46, 47), pterosaurs (Fig. 72 A), some lizards (Fig. 56), and thalattosaurs (Fig. 61), a median prolongation separates the nasals, articulating directly with the frontals, in the first group (Fig. 46) sometimes directly with the parietals, separating the frontals. Edentulous in the chameleon lizards (Fig. 55), they take no part in the boundary of the nares. They are also edentulous in the turtles (Figs. 30–32), anomodonts (Fig. 44 C), some dromasaurians, the later pterodactyls (Fig. 72), most ornithischians (Fig. 70 C, D), the chameleon lizards, and many snakes. Teeth, when present, are in a single row and rarely exceed five or six in number in each, though there are as many as twenty-three in some phytosaurs (Fig. 66) and even more in ichthyosaurs, where the dentigerous border is greatly elongated. The dentigerous part is short in the long-faced plesiosaurs (Fig. 48 C). They are often fused (Fig. 72), and sometimes united with the nasals (Fig. 54 C).

Maxillae (*mx*). Primitively (Figs. 2 B, 3, 4, 6, 19, 21, 22, 33, 43), articulating anteriorly with premaxillae, above with septomaxillae and lacrimals, posteriorly with the jugals, ectopterygoids, and postorbitals internally, forming the outer boundary of both external and internal nares in part.

In most reptiles since Permian times they also articulate with the nasals above (*e. g.*, Figs. 33, 43, 44); in the crocodiles (Fig. 69 B) with each other on the palate, as also in many Anomodontia and Theriodontia. They are edentulous in the Chelonia (Figs. 30–32), later Pterosauria (Fig. 72), some Anomodontia (Fig. 44 C), Dromosauria, Ophidia, *Saphaeosaurus*, *Ornithomimus*, etc. The teeth may be in single or numerous rows.

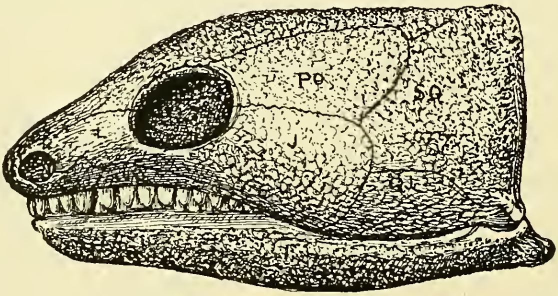

FIG. 3. *Pantylus* (Cotylosauria), from side. Three fourths natural size.

Septomaxillae (*sx*). Small bones, the so-called turbinals of reptiles, located partly within the nasal chamber, but appearing more or less on the outer side at the back part of the external nares. (Figs. 33, 44 A, B, F, 45.) Present probably in all the earliest and most early reptiles, and in most Squamata (Fig. 59); they are absent in the Chelonia (Figs. 28–32) and Crocodilia (Figs. 68, 69). In some Dromasauria they extend back on the face to meet the lacrimals. Little can be said about them in other extinct reptiles.

Nasals (*na*). Articulating with premaxillae, frontals, prefrontals, and lacrimals, forming more or less of the partition between the external nares.

Except in most Cotylosauria (Figs. 2, 3, 22, 23, etc.), some Theromorpha and Therapsida, they also articulate with the maxillae on the sides. They are absent in many Chelonia (Figs. 28–32); either absent or fused with the premaxillae in the Mosasauria (Fig. 54 C); separated by the premaxillae in the plesiosaurs, pterosaurs (Fig. 72), and some lizards (Fig. 56), and probably absent in some of the former (Fig. 46). They do not enter into the formation of the nares in the Rhiptoglossa (Fig. 55 D), but surround them in the Phytosauria (Figs. 66, 67). Very large in the Ichthyosauria (Fig. 50), they also articulate with the large postfrontals. They are often fused in the midline.

Frontals (*fr*). Primitively (Figs. 2, 4, 22, 23, etc.) articulating with nasals, prefrontals, postfrontals, parietals, and ethmoids, often forming the middle of the upper margin of the orbits.

Always present and not varying much in their relations. In the plesiosaurs (Fig. 46), pterodactyls (Fig. 72), and some lizards, they articulate directly with the premaxillae (Fig. 56), and in some of the former are separated externally in the middle. Often fused in midline (Figs. 68, 69).

Parietals (*pa*). Primitively (Figs. 2, 4) articulating with frontals, postfrontals, intertemporals, supratemporals, tabulars, and interparietals; below with the supraoccipital, epipterygoids, postoptics, and proötics.

In the absence (*e. g.*, Figs. 31 B, 33, 44, 45, etc.) of the intertemporals and supratemporals, the parietals articulate directly with the squamosals and postorbitals; in the Chelonia (Fig. 30) and Crocodilia, also directly with the pterygoids. Fused in most late reptiles (*e. g.*, Figs. 69, 72).

Interparietals (*ip*). Primitively (Figs. 2 A, 4, 22) back of the parietals on the superior surface of the skull, articulating with parietals, tabulars, and supraoccipital.

In the later Cotylosauria (Fig. 9), most if not all Theromorpha (Figs. 33, 42 D), some Therapsida (Figs. 44 A, D, G), they are situated on the occipital surface and are usually unpaired. A vestige, supposed to be these bones, occurs in some Crocodilia, originally named dermosupraoccipitals. They do not help form any part of the cerebral wall. Unknown or doubtful in other reptiles.

Lacrimals (*la*). Primitively (Figs. 2 B, 3, 22, 23, etc.) large, extending from orbit to nares, articulating with prefrontals, nasals, septomaxillae, maxillae, and jugals.

In the latest Cotylosauria (*Procolophon*), most Theromorpha

(Fig. 33) and Therapsida (Figs. 43, 44, 45), and all other reptiles, they are excluded from the narial margin. They are small or vestigial in the Squamata, and absent in most Chelonia and in *Sphenodon* (Fig. 60 A). They are of extraordinary size in some Theropoda (Fig. 70 A), articulating posteriorly with the postorbitals. It has been urged by Jaekel and Gaupp that these bones are not the homologues of the mammalian lacrimal, and should be called by another name, for which postnasal and adlacrimal have been proposed.[1]

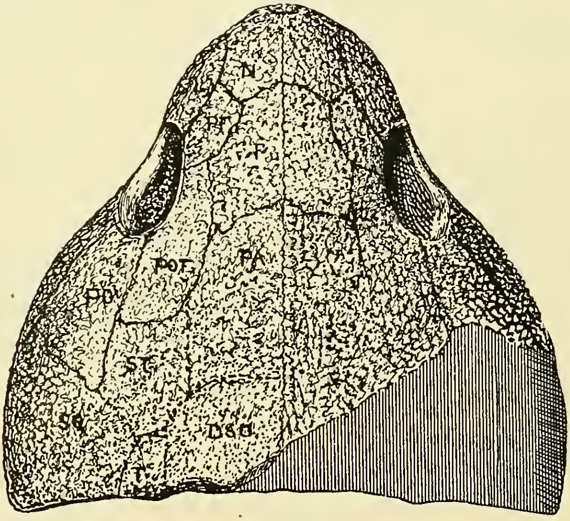

FIG. 4. *Pantylus*, from above. Three fourths natural size.

Prefrontals (*pr*). Primitively (Figs. 2, 4, 22) at the upper anterior border of the orbits, articulating with lacrimals, nasals, frontals, and postfrontals, and by a descending process with the palatines.

Never absent, though much reduced and excluded from the orbital margin in the Theropoda (Fig. 70 A). Sometimes (Fig. 70 C) they articulate with the postorbitals or postfronto-orbitals when the postfrontals are absent as discrete bones. Below, they articulate with the prevomers in the Chelonia (Fig. 30 B), with the palatines and pterygoids in the Crocodilia (Fig. 69 D). Excluded from the frontals in the

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[1] [The cumulative evidence against the views of Gaupp and Jaekel, with regard to the reptilian homologue of the mammalian lacrimal, has been set forth in the *Bulletin* of the American Museum of Natural History, vol. XLII, pp. 99, 131–135. — ED.]

Ichthyosauria (Fig. 50). Thought by some to be the homologues of the mammalian lacrimals, and so called.

Postfrontals (*pf*). Primitively (Figs. 2, 4, 22) at the upper posterior border of the orbits, articulating with prefrontals, frontals, parietals, the intertemporals or supratemporals when present, and with the postorbitals.

In the Chelonia (Figs. 30 A, 31 B, C, 32 A), Crocodilia (Figs. 68, 69), many mosasaurs (Fig. 54), lizards (Fig. 56) and the snakes (Fig. 59), the Pterosauria (Figs. 71, 72), Dinosauria (Fig. 70), and many Therapsida (Figs. 44 D, 45), they are absent or fused with the postorbitals which take their place. Sometimes they (Fig. 46 C, 49 A) help form the anterior boundary of the upper temporal opening. They extend forward to the nasals in the Ichthyosauria (Fig. 50).

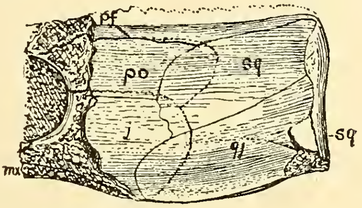

FIG. 5. *Pantylus.* Cotylosaur skull: left temporal region, from without. Three fourths natural size.

Postorbitals (*po*). Primitively (Figs. 2, 3, 4, 5, 22) at the upper back part of the orbits, articulating with postfrontals, jugals, and squamosals. A descending process also articulates with the maxillae or ectopterygoids.

In the absence of the intertemporal and supratemporal, the postorbital also articulates with the parietal (Figs. 28, 30, 33, 43). In the absence of the postfrontal it takes its place, often extending forward to meet the prefrontal (Figs. 30, 45 B), or even the lacrimal (Fig. 70 A) in the Theropoda. It still retains its connection with the maxillae [sic][1] in certain Chelonia (Fig. 31 B) and most snakes (Fig. 59), but not in most other reptiles. Rarely in the lizards (Fig. 56) it does not meet the squamosal. In the Crocodilia (Fig. 69) it is large, and may articulate with frontal, parietal, jugal, quadratojugal, and squamosal. It extends far back in the Chelonia (Figs. 30, 31 A), forming a large part of the temporal roof, articulating with the quadratojugal, the latter also in the Ichthyosauria (Fig. 50). It is extensive also in some of the Dinosauria (Fig. 70), supporting the paired horns of the Ceratopsia (Fig. 70 D).

Jugals (*ju*). Primitively (Figs. 2 B, 3, 5, 22, 33) large, forming the under boundary of the orbits, articulating in front with lacrimals

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[1] ["Maxillae" — a *lapsus calami* for "parietal"?—ED.]

and maxillae, above with postorbitals, and, by an extensive overlapping suture, with the squamosals and quadratojugals; on the inner side perhaps with the ectopterygoids.

Absent in some Ophidia (Fig. 59 B) and some lizards (Fig. 56). In the lizards (Fig. 55) they may not articulate with the squamosals.

Intertemporals (*it*). An amphibian bone known only in *Seymouria* (Figs. 2, 19) of the Cotylosauria, intercalated between the postfrontal, parietal, supratemporal, and postorbital.

Supratemporals (*st*). Primitively (Figs. 2, 4, 19) articulating at the sides of the parietals with the postfrontal and postorbital anteriorly, the tabulars behind, and the squamosals on the outer side; interrupted by the otic notch in *Seymouria* (Figs. 2, 19).

Absent in the more specialized Cotylosauria, probably all Theromorpha, and all other reptiles save possibly the Ichthyosauria (p. 62) and Squamata (p. 65). Generally known as the posterior bone of the arch in the Squamata (Fig. 55 A, *ta*). [But see tabular below.]

Tabulars (*t*). Primitively (Figs. 2, 4, 22) on the dorsal surface of the skull in the Cotylosauria, as in the Amphibia, at the outer side of the interparietals, articulating with the squamosals and supratemporals, with the upper end of the quadrates and the outer end of the paroccipitals, whence the name "paroccipital plates" given to them by Baur. They are known to be absent in but a single genus of Cotylosauria; are probably present in most Theromorpha (Figs. 33 B, 42 D) and Therapsida (Fig. 44 G), and some "Pseudosuchia" (Fig. 65 C). The tabular has been identified by the author as the posterior bone of the arch in the Squamata (p. 62), and Ichthyosauria (p. 62), usually and perhaps correctly called the supratemporal. It is unknown in other reptiles.

Squamosals (*sq*). Primitively (Figs. 2, 4) articulating with tabulars and supratemporals above, in the absence of the latter directly with the parietals (Figs. 33 A, 53 A). Below, they cover the posterior part of the temporal region, extending back of the quadrate to articulate with the pterygoids (Fig. 7), overlapping extensively the quadratojugals on the sides (Fig. 33 A), and articulating in front with jugals and postorbitals.

In later reptiles the squamosal has undergone many changes, but is always present, though sometimes vestigial in the Chelonia, Squamata, and Ichthyosauria. Only in the Cotylosauria and some Theromorpha does it articulate with the pterygoids. In later forms it articulates with the paroccipital to a limited extent, supporting the head of the quadrate. In many Therapsida (Figs. 43, 44 B), but not in the more primitive Theromorpha (Fig. 33 A), it may articulate with the postorbital below as well as above the temporal opening. Its relations with the quadratojugal are also inconstant, lost in the Crocodilia (Fig. 69 C) and Predentata (Fig. 70 C). On the other hand, it may extend forward to unite with the maxillae in some plesiosaurs (Fig. 46 B). In the Squamata (Fig. 55 A), as most recent authors identify the squamosal, it articulates with the bones usually called the supratemporal and the postorbital (rarely excluded from it) and usually with the jugal.

Quadratojugals (*qj*). At the outer posterior side of the temporal region (Figs. 2 B, 3, 22, 33), overlapped by the squamosals, articulating in front narrowly with the jugals, behind with the quadrates.

The quadratojugals are relatively large in the primitive skull, sometimes forming a part of the articular surface for the mandible (Fig. 21 B). In the single-arched skull the quadratojugal tends to disappear. It is probably present in all Theromorpha, but is often confined chiefly to the posterior side of the quadrate (Fig. 42 D). It is absent in most Therapsida,[1] the Sauropterygia and the Squamata. It enters into the boundary of the lower temporal opening only in the Crocodilia (Fig. 69), Phytosauria (Fig. 66 B), Pseudosuchia (Fig. 65), Pterosauria, Theropoda (Fig. 70 A), and some Predentata (Fig. 70 D), excluded in many Predentata (Fig. 70 C), as in all the other double-arched reptiles. It is very large in some Chelonia (Fig. 30 A), articulating with the postorbitals, as is also the case in the Crocodilia (Fig. 69 C).

Prevomers (*pv*). Paired bones on the palatal surface, articulating with the premaxillae in front, the pterygoids and palatines behind separating the internal nares; dentigerous (Figs. 6, 40 C).

Only in the Chelonia (Fig. 32 B) are the prevomers single, though sometimes fused in the Rhiptoglossa, Theropoda, and Theriodontia (Figs. 43 C, 44 E). They are edentulous in all known reptiles except the Cotylosauria (Fig. 6), some Theromorpha, perhaps, certain "Pseudosuchia," Diaptosauria (Fig. 63), and Squamata. Poste-

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[1] [But see footnote, p. 52. — Ed.]

riorly in the Squamata (Figs. 55 C, 56 B) they articulate with the palatines only, as also in some Chelonia (Figs. 31 A, 32 B) and Plesiosauria (Fig. 46 B). Generally believed not to represent the unpaired vomer of the mammals.

Palatines (*pl*). Primitively (Figs. 6, 21) forming the posterior boundary of the internal nares, articulating with the prevomers and pterygoids on their inner sides, the maxillae on their outer, and with the descending process of the prefrontals above. More or less dentigerous.

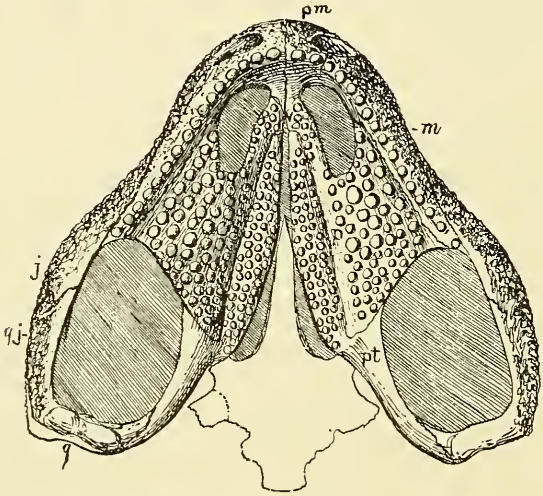

FIG. 6. *Pantylus.* Cotylosaur skull: from below. Three fourths natural size.

Teeth are still present in the Theromorpha (Figs. 40 C, 42 C) and some Therapsida, but are lost in other reptiles except the Rhynchocephalia (Figs. 62 E, 63 B) and most Squamata (Fig. 54 B). They may join in the middle in the Chelonia (Figs. 31 B, 32 B) and in the Crocodilia (Fig. 69 B) below the prevomers.

Pterygoids (*pt*). (Figs. 6, 7, 21, 40 C.) Bones of the posterior part of the palate, articulating with the prevomers in front, the palatines and ectopterygoids laterally, the basisphenoids on the inner sides, the quadrates and squamosals posteriorly. Dentigerous.

As stated above they do not articulate with the prevomers anteriorly in the Squamata and many Chelonia and Plesiosauria, but do articulate with the parietals in many Chelonia. Their connection with the prevomers is lost in some Cynodontia (Fig. 43 C) and Rhiptoglossa. Teeth are generally present in the Theromorpha, Rhynchocephalia, and Squamata, and in some Therapsida and "Pseudosuchia." In the early reptiles (Figs. 6, 21, 24 C, 40 C) they are more or less loosely articulated with the basipterygoid process of the basisphenoid, as in most modern reptiles, but are fixed in the Therapsida (Fig. 43 C) and not a few others. There is an interpterygoidal space between them partly filled with the parasphenoid rostrum in the early reptiles (Figs. 6, 21 A), as in the Plesiosauria (Fig. 47 F), Rhynchocephalia, most Squamata (Fig. 55 C), etc. In some Therapsida (Fig. 43 C), Nothosauria (Fig. 47 E), Placodontia (Fig. 49 B), they unite along the whole middle line. There is a theory that the pterygoids are the real homologues of the mammalian alisphenoids.[1]

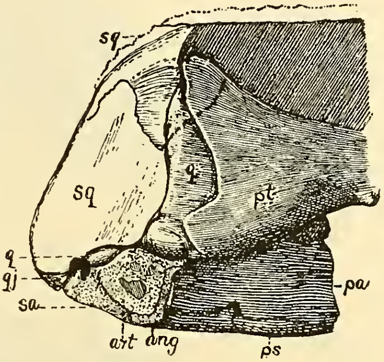

FIG. 7. *Pantylus.* Cotylosaur skull: left quadrate region, with section of mandible through condyle. Enlarged one half.

Ectopterygoids (*ec*). The ectopterygoids (transpalatines) have not yet been certainly demonstrated in the early Cotylosauria, though perhaps present; they are certainly absent in some of the Temnospondyli. They have been recognized in all other orders except the Ichthyosauria and Chelonia, connecting the pterygoids with the posterior end of the maxillae, back of the palatines; sometimes also with the jugals in the Squamata (Fig. 55 C). Most remarkable are their relations in *Pteranodon* (Fig. 72 C) of the Pterosauria, where they pass *above* the palatines to unite with the pterygoid. The ectopterygoids are believed by some to be the homologues of the pterygoid process of the alisphenoid of the mammals.

Epipterygoids (*ep*). A pair of bones articulating below with the pterygoids, above with the parietals (Fig. 8). They have been observed in the Temnospondyli, various genera of the Cotylosauria, Theromorpha, and Therapsida, and are probably generally present in reptiles, though absent in the Crocodilia, many Chelonia, the

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[1] [Watson has shown that this view is untenable. — ED.]

Ophidia, Amphisbaena, Rhiptoglossa of the Squamata. In the Chelonia (Fig. 30 B) they have been identified with a plate of bone intercalated between the descending plate of the parietal and the basisphenoid of many forms. Their real homologues are yet doubtful; by some they have been identified with the alisphenoid of the mammals.

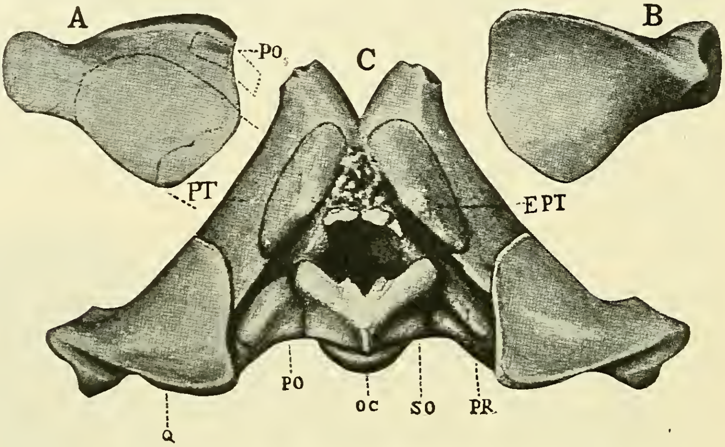

Fig. 8. *Labidosaurus hamatus* Cope. Cotylosaur skull: A, right quadrate from below; B, the same from above; C, posterior basicranial bones from above.

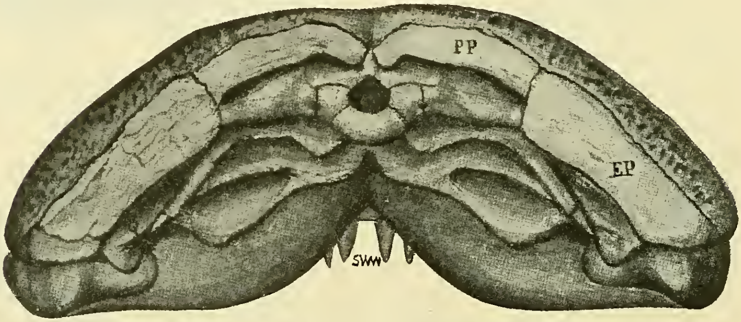

Fig. 9. *Labidosaurus hamatus* Cope. Cotylosaur skull: from behind.

Supraoccipital (*so*). (Figs. 9, 21 B, 42 D.) Unpaired, articulating with the parietals and interparietals above, the exoccipitals, paroccipitals, and proötics, and including a part of the semicircular canals formerly believed to be in a separate bone called the epiotic, but which has never been demonstrated in any air-breathing animal. Primitively more or less excluded from the margin of the foramen magnum.

Only in certain plesiosaurs is the supraoccipital paired, by the extension of the large foramen magnum to the parietal roof. In most reptiles save the Ophidia and Crocodilia, it enters more or less into the boundary of the foramen magnum.

Exoccipitals (*eo*). Primitively (Figs. 21 B, 42 D) small, forming the larger part of the boundary of the foramen magnum, approximated to each other both above and below, closely articulated with the basioccipital only.

Primitively the exoccipitals took but little part in the formation of the occipital condyle, but in many later reptiles they form a large part, as in the Chelonia (Fig. 31 B), or even the whole, as in the Amphisbaenia (Fig. 56 B); or, by the recession of the basioccipital, the double condyles of the Cynodontia and mammals.

Paroccipitals (*po*). (Figs. 9, 21 B.) Only in the Cotylosauria primitively do the paroccipitals exist as distinct bones in the adult, articulating with the exoccipitals, supraoccipital, proötics, stapes, tabulars, and quadrates. On the inner side they help form, with the supraoccipital and proötics, the otic capsule. In the Theromorpha, so far as known, the paroccipitals are fused with the supraoccipital, suturally or loosely articulated with the exoccipitals. In the Chelonia (Fig. 31 B, *op*), only of modern reptiles, are they separate bones in the adult, intercalated between the exoccipitals, supraoccipital, proötics, squamosal, and supporting the head of the quadrate. Among other reptiles they are known to be free only in the Ichthyosauria (Fig. 51), articulating with the basioccipital, exoccipitals, stapes, and so-called supratemporal. In other reptiles they are indistinguishably fused with the exoccipitals in the adult.

Proötics (*pc*). The proötics (Figs. 8, 10, 11, 30, 59, 69) are a conspicuous part of the brain-case, intercalated between the supraoccipital, paroccipitals, basioccipital, basisphenoid, and, when present, the postoptics, and containing a part of the internal organ of hearing. Their relations are yet poorly known in the primitive reptiles. They usually have foramina perforating them for the passage of the third and sixth nerves, and form the posterior boundary of the foramen for the fifth nerve; posteriorly for the eighth, ninth, and tenth nerves. They form a large part of the brain-case exteriorly in the snakes (Fig. 59) and amphisbaenian lizards; in the mosasaurs (Fig. 57) their outer extremity extends to the outer extremity of the paroccipital, articulating with the so-called supratemporals, or, as the author believes, the tabulars.

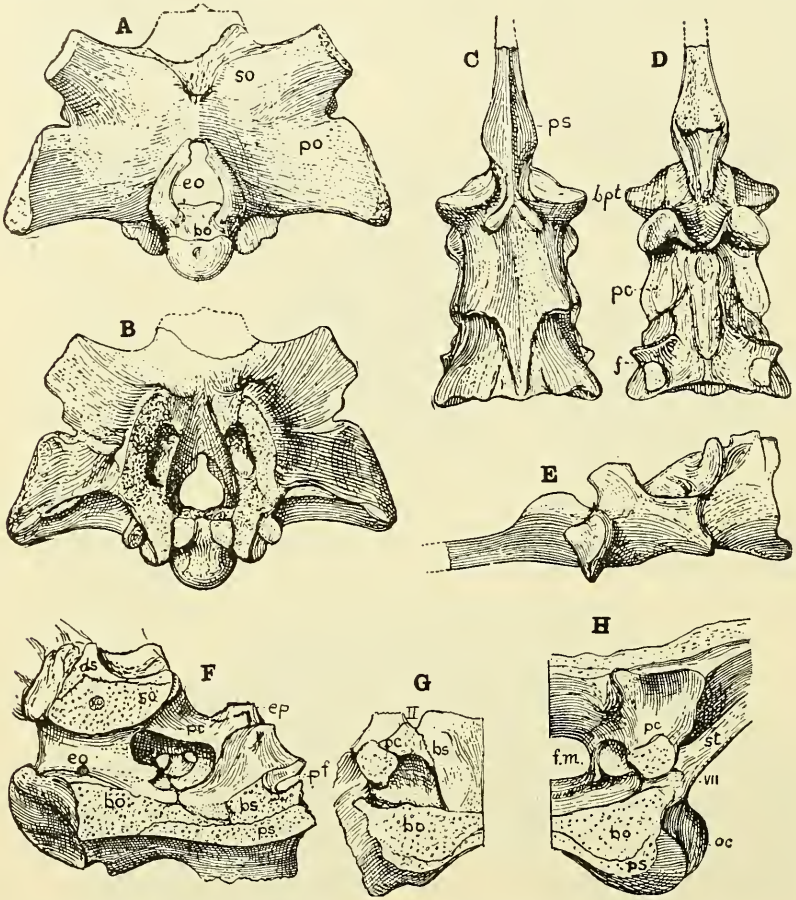

Fig. 10. A, B, *Edaphosaurus.* Theromorph skull: occipital complex, from without and within, natural size; C, genus indet. basisphenoid, from below; D, the same from above; E, the same from side, natural size. F, G, H, *Eryops.* Temnospondyl skull: basicranial bones, longitudinal and transverse sections; *so*, supraoccipital; *po*, paroccipital; *eo*, exoccipital; *bo*, basioccipital; *pc*, proötic; *bs*, basisphenoid; *ps*, parasphenoid; *st*, stapes; *ep*, epipterygoid.

Postoptics (*as*, *al*), (laterosphenoids, otosphenoids, "alisphenoids"). Variable and yet doubtful bones in the reptiles, apparently not homologous with the mammalian alisphenoid, though usually so called. Imperfectly known in the early reptiles, they have been recognized in the Temnospondyli, Cotylosauria, and Theromorpha, articulating as in the Crocodilia (Fig. 69) below with the basisphenoid, above with the parietal, back of the optic foramen, whence the name postoptics given to them by Cope. Between them and the proötics is the foramen for the fifth nerve. They form the lateral brain-case in the Crocodilia, but are absent in the Chelonia and snakes. In the lizards they are imperfectly ossified, and are usually lost in prepared specimens. They are present in the Rhynchocephalia and most other reptiles.

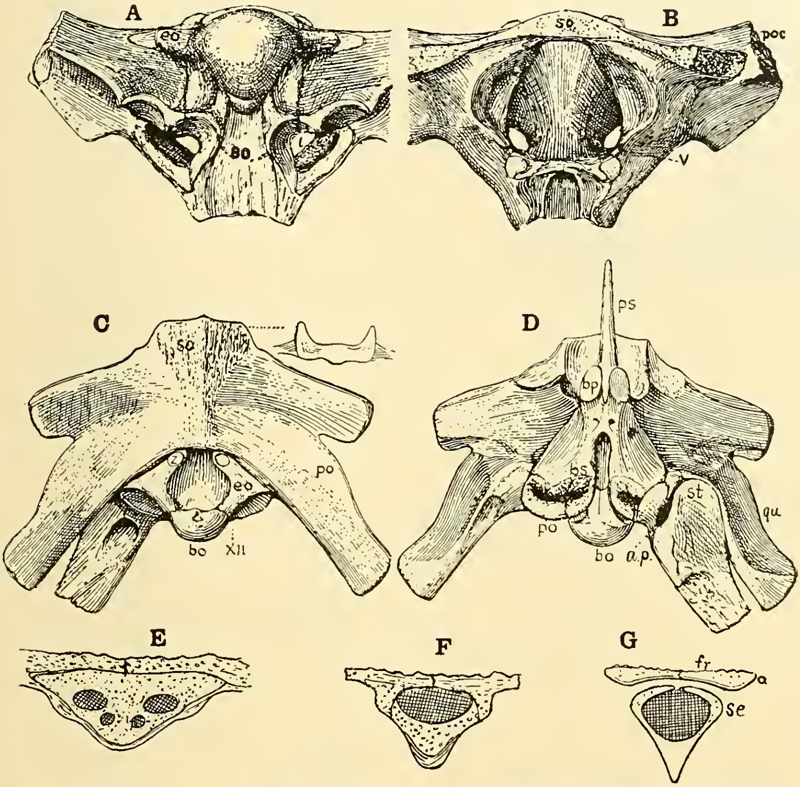

Fig. 11. A, B, C, D, *Dimetrodon*. Pelycosaur skull: occipital complex: A, from below; B, the same from above; C, obliquely from behind; D, the same from in front. Temnospondyl skulls: E, *Eryops*, section through parasphenoidal rostrum, near front part of orbit; F, *Eryops*, section through parasphenoidal rostrum near base; G, *Cacops*, section through parasphenoidal rostrum at middle of orbit.

Basisphenoid (*bs*). (Figs. 10, 11 D, 30.) Forming the floor of the brain-case in front of the basioccipital, continuous with the parasphenoid in front (Fig. 12), which is closely fused with its under side, articulating in front above with the postoptics (Fig. 69 D), behind above with the proötics (Figs. 30, 69 D), externally above with the stapes (Fig. 11 C), and externally below with the pterygoids. It lodges in front the fossa or depression for the pituitary body (Fig. 69 D).

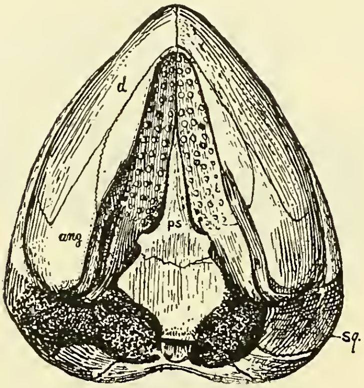

FIG. 12. *Pantylus.* Cotylosaur skull and mandible: immature animal, from below. Natural size.

Stapes (*st*). (Fig. 11 C, D.) The stapes in all early reptiles is a large bone, articulating over the auditory opening, or foramen ovale, between the paroccipital and basisphenoid, and extending toward or touching the quadrate. It is perforated near its proximal end by the foramen for a perforating artery. It is also large in the Ichthyosauria and Plesiosauria, but in most other reptiles is slender, without a perforating foramen. It is stout and short in the Amphisbaenia (Fig. 56).

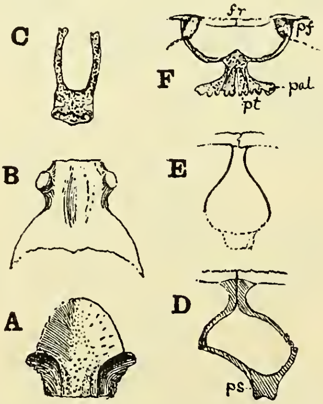

FIG. 13. *Pantylus.* Cotylosaur skull: internal cranial bones. Natural size. A, basioccipital; B, basisphenoid; C, section at front of basisphenoid; D, section of rhinencephalic chamber opposite hind margin of orbits; E, outline of same at extreme front end of parietals; F, same in front of orbits; *pal*, prevomer.

Parasphenoid (*ps*). (Figs. 6, 10 C, D, 21 A.) A membranous, unpaired bone, firmly fused in the adult with the under side of the basisphenoid, and never a separate bone.[1] It extends far forward as a narrow rostrum in the temnospondyls (Fig. 11 E–G) and some cotylosaurs (Figs. 6, 21 A) quite to the prevomers, forming the floor to the ethmoidal cavity. This seems to be the rule in the early reptiles, though in some (*Labidosaurus sp*) it

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[1] [It is separate in at least some geckos. — G. K. N.]

may not extend in front of the basisphenoid. It has been homologized by Broom with the median vomer of mammals, whence the name prevomers for the paired bones in front, the so-called vomers.

Ethmoid (*eth*) or *Sphenethmoid*. In the temnospondyl amphibians (Fig. 11 E–G), between the orbits and in front of the optic foramina, there is a pair of thin bones lying closely below the frontals and united with the parasphenoid below, enclosing an undivided cavity for the olfactory lobes, opening into the nasal and paranasal cavities in front of the orbits. Similar bones have been observed in various cotylosaurs (Fig. 13) and theromorphs, and are probably constant among early reptiles. They have been called sphenethmoids, though they have no immediate relation to the sphenoid. Probably the median ethmoidal plate arose from the fusion of these bones. There was no median ossified interorbital septum in these reptiles, and not probably any median septum. A cartilaginous interorbital septum is present in most modern reptiles but is ossified in none.

Skull Elements — Synonyms

Ectopterygoid = Transpalatine, Transverse.
Interparietal = Dermosupraoccipital, Dermoöccipital, Postparietal.
Postoptic = Laterosphenoid, Otosphenoid, "Alisphenoid."
Paroccipital = Opisthotic.
Proötic = Petrosal.
Prearticular = Goniale.
Postsplenial = Preangular.
Splenial = Opercular.
Supratemporal = Supramastoid, Suprasquamosal.
Squamosal = Prosquamosal.
Tabular = "Epiotic," Postparietal [sic][1].

THE MANDIBLE

The mandible of reptiles was composed primitively of eight, possibly nine, separate bones, differing from that of their temnospondyl antecedents (Figs. 14, 15) only in the loss of one or two slender bones along the inner margin of the teeth, the precoronoid and intercoronoid. All of these, except the postsplenial, known in a single cotylosaur (Fig. 18), have persisted to modern times, though never all in the same reptile, none having more than six, and some but five.

The relations of these bones will be seen in the accompanying

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[1] [Possibly "paroccipital plate" was intended. — Ed.]

figures (16–18) and do not require a detailed description. The *dentary* (*d*) is always present and dentigerous, except in all Chelonia (Fig. 31 B, E), some Anomodontia (Fig. 44 C) and Dromasauria, some Theropoda, and the late Pterosauria (Fig. 71 E), *Saphaeosaurus*, etc.

The *coronoid* (*cor*), extending along the inner margin of the teeth from near the symphysis to the hind end of the dentary on the inner side, possibly composed of two bones in some of the earliest reptiles (Fig. 18), has been restricted to a place at the posterior end of the dentary in later forms (*e. g.*, Fig. 55 B), and may in some cases be absent. In the Plesiosauria (Fig. 25 A) it still retains its ancient character, even entering into the symphysis in some cases. In the Dinosauria, or some of them at least, it also extends far forward, or there may perhaps be a distinct bone in front, the intercoronoid

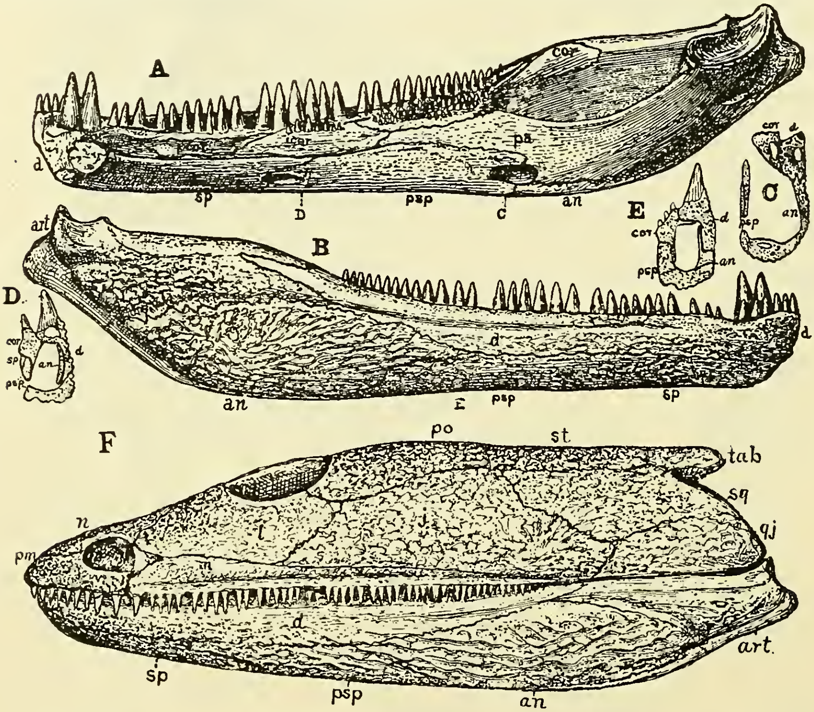

Fig. 14. *Trimerorhachis alleni* Case. Temnospondyl skull and mandible: A, right mandible, inner side; B, the same, outer side; C, D, E, sections of mandible as designated; F, skull and mandible, left side; *psp*, postsplenial; *cor*, coronoid; *icor*, intercoronoid; *pcor*, precoronoid.

or precoronoid. Primitively (Fig. 18) it often bore teeth, as in many temnospondyls, but no such teeth are known in later reptiles.

The *surangular* (*sa*), always present in reptiles, though sometimes indistinguishably fused with the articular, forms the upper margin of the mandible back of the coronoid, and the outer margin of the Meckelian orifice (Figs. 15–18). In some it may take part in the articular surface for the quadrate.

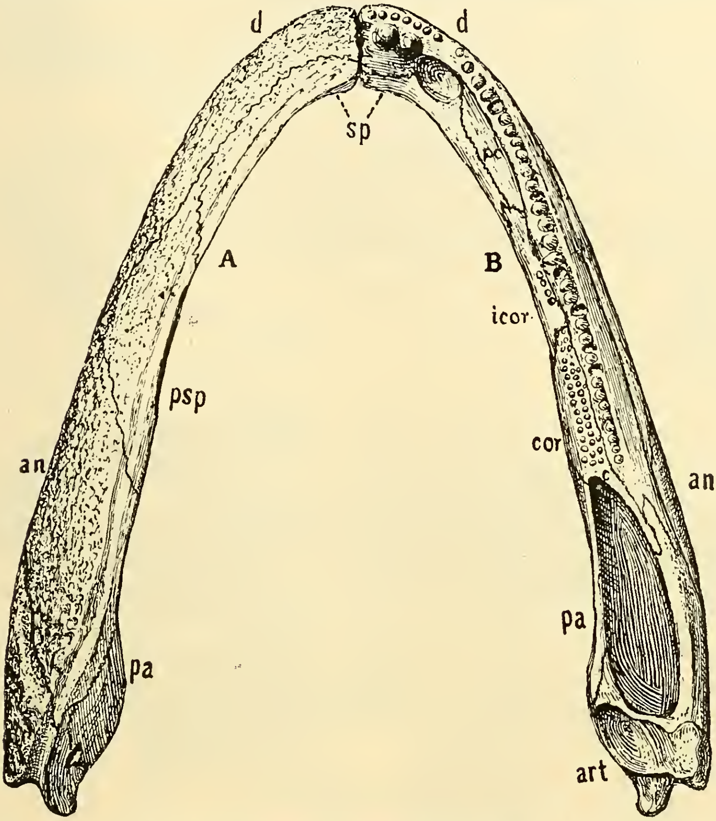

Fig. 15. *Trimerorhachis insignis.* Temnospondyl mandible: A, right ramus from below; B, the same from above.

The *angular* (*an*), on the inferior border posteriorly, articulating with the dentary in front, the prearticular, articular, and surangular behind, and extending to the hind angle of the jaw, is always present (Figs. 15–18). In the crocodiles (Fig. 69 c, d) it helps form the inner border of the Meckelian orifice.

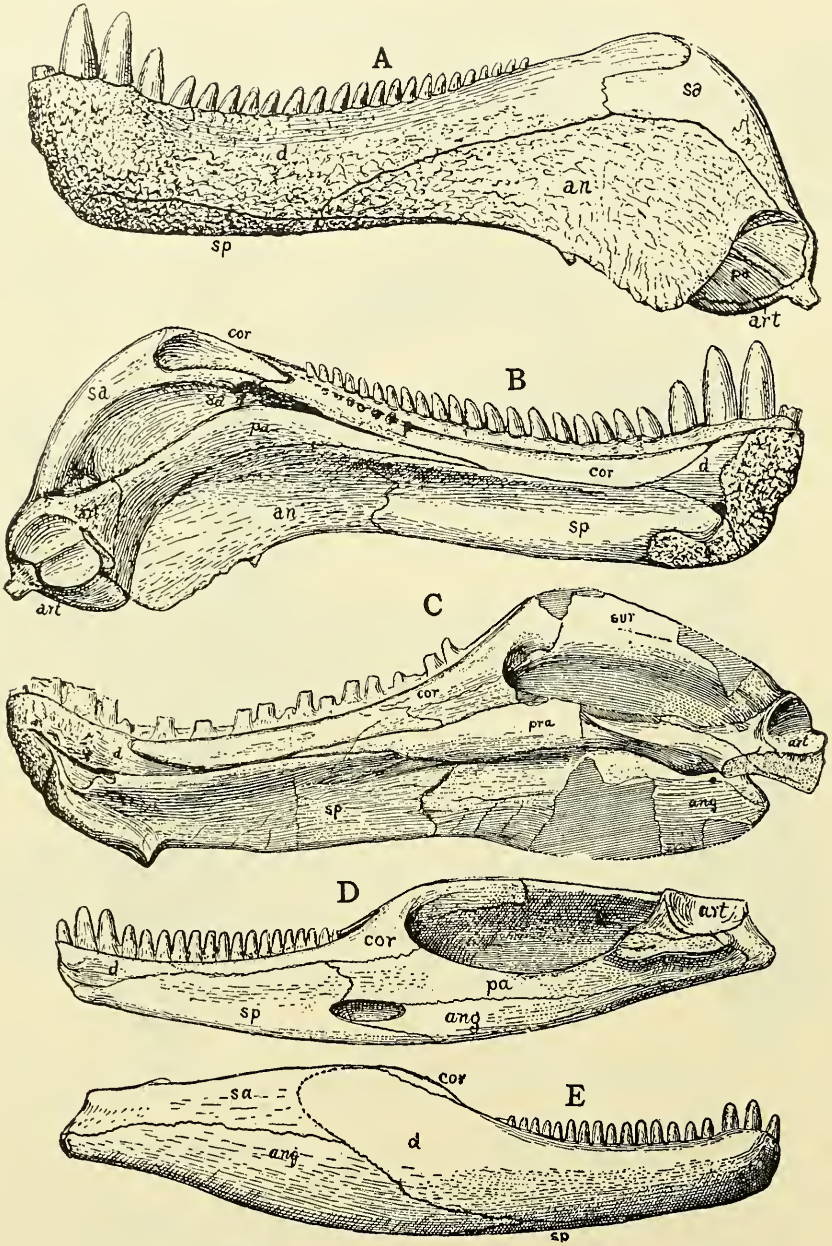

Fig. 16. A, *Dimetrodon incisivus* Cope. Pelycosaur: left mandible, outer side. B, *Dimetrodon incisivus* Cope. Pelycosaur: left mandible, inner side. C, *Dimetrodon incisivus* Cope. Pelycosaur: right mandible, inner side. D, *Labidosaurus hamatus* Cope. Cotylosaur: right mandible, inner side. E, *Labidosaurus hamatus* Cope. Cotylosaur: right mandible, outer side.

The *splenial* (*sp*), entering into the Meckelian symphysis primitively (Figs. 15–18), extending back to the posterior inferior Meckelian foramen, articulating with the dentary, coronoid, prearticular, and angular, is not infrequently absent. In *Pantylus* (Fig. 18) only, so far as known, the *postsplenial* corresponds to its posterior part as in the known Stegocephalia (Fig. 15). It [the splenial] never bears

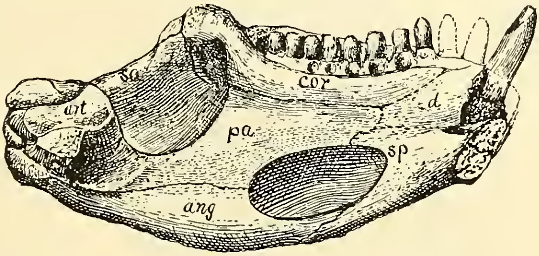

Fig. 17. *Diadectes* (*Nothodon*). Cotylosaur: left mandible, from within. One half natural size.

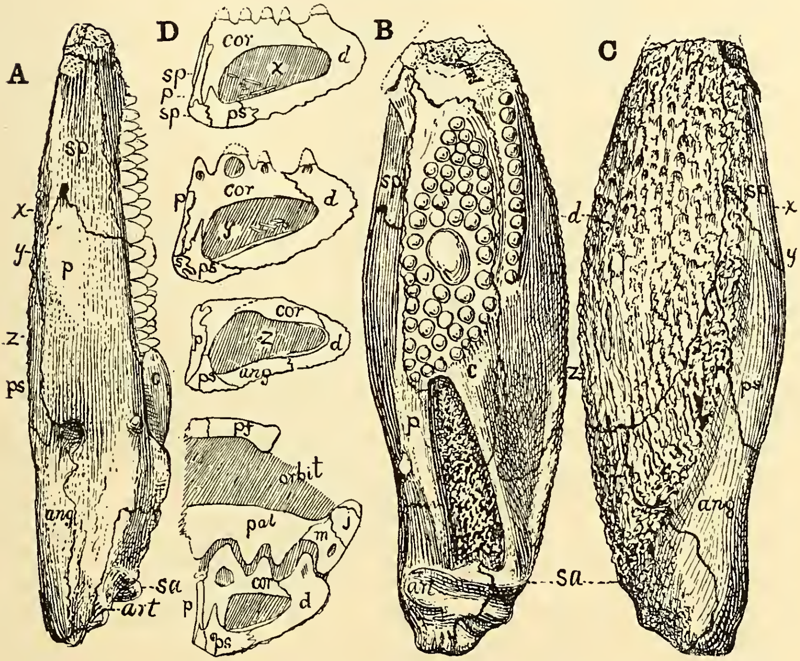

Fig. 18. *Pantylus.* Cotylosaur: A, right mandible from inner side; B, the same from above; C, the same from below; D, sections corresponding to letters.

teeth and is more or less inconstant, absent in *Sphenodon* and most Chelonia. It is a thin bone and forms the cover to the Meckelian groove, whence the name *opercular* often given to it. Primitively (Figs. 15–18) it formed a large part of the inferior border of the mandible anteriorly, appearing on its outer face, but in all late reptiles it is restricted to the inner side. It enters into the mandibular symphysis in most long-jawed reptiles, probably an acquired character.

The *prearticular* (goniale) (*pa*), recognized only within recent years, is a thin bone, articulating with the articular behind, the angular below, the coronoid and splenial in front, forming the hind border of the posterior inferior foramen and the lower margin of the Meckelian orifice. It was present in all early reptiles (Figs. 16–18), and remains a separate bone in the modern turtles (Fig. 31 E) and young *Sphenodon* (Fig. 60). It was present in the Dinosaurs, Plesiosauria (Fig. 25 A), where it was first named, Ichthyosauria, and doubtless many other extinct reptiles. It is fused with the articular in the Squamata (Fig. 55 B), extending far forward in the mosasaurs (Fig. 58), ensheathed by the united angular and coronoid, splenial and dentary. It is apparently wholly absent in the Crocodilia (Fig. 69).

The *articular*, the only cartilage bone of the mandible, forms the cotylus, in whole or part. Distinct in all early (Figs. 16–18) and many later reptiles, it may be indistinguishably fused with the prearticular or surangular. Believed to be the malleus of the mammalian ear.

Openings in the mandible

Aside from the large opening for the entrance of nerves and blood-vessels [and jaw muscles] at the posterior upper part of the mandible (Figs. 16–18), there are in the early reptiles one or two smaller openings through the inner wall: the posterior one just in front of and below the anterior end of the large orifice, between the coronoid, angular, prearticular, and splenial, is still present in the crocodilians (Fig. 69 D). A large perforation of the outer wall of the mandible, between the angular, surangular, and dentary, is very characteristic of most Crocodilia (Fig. 69 C), Theropoda (Fig. 70 A), Phytosauria, and Pseudosuchia (Fig. 65 A, E).

A foramen posteriorly, between the prearticular and angular, is for the passage of a track of the chorda tympani nerve.

THE SKULL OF THE COTYLOSAURIA

(Figs. 1–9, 12, 13, 16 D, E, 17–24, 25 B, C, 26–29)

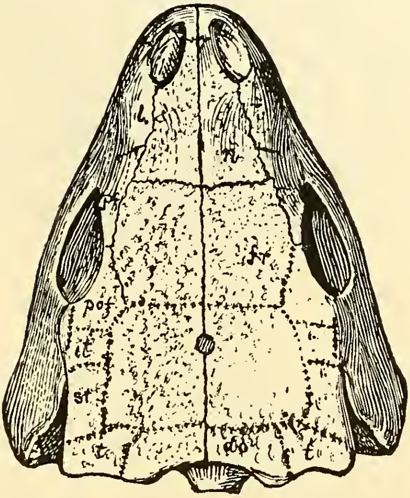

FIG. 19. *Seymouria baylorensis.* Cotylosaur skull: from above. One half natural size. *n*, nasal; *l*, lacrimal; *pf*, prefrontal; *pof*, postfrontal; *fr*, frontal; *it*, intertemporal; *st*, supratemporal; *do*, dermoöccipital; *t*, tabulare.

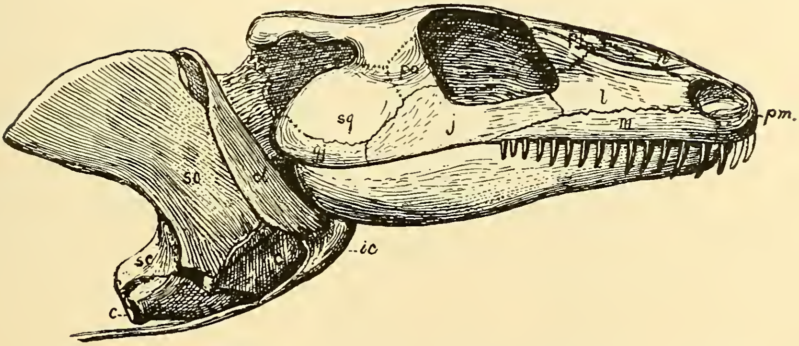

FIG. 20. *Seymouria baylorensis.* Skull and pectoral girdle: from the side. One half natural size. *pm*, premaxilla; *m*, maxilla; *l*, lacrimal; *n*, nasal; *pf*, prefrontal; *j*, jugal; *po*, postorbital; *sq*, squamosal; *qj*, quadratojugal; *cl*, clavicle; *ic*, interclavicle; *sc*, scapula; *c*, coracoid.

But few modifications of the primitive characters of the skull are known in this order. The parietal foramen is absent in one or two genera, the supratemporals and tabulars in a few others. Teeth may occur on the coronoids. The postsplenial occurs in but one known genus [*Pantylus*], as also the intertemporal [*Seymouria*]. The interparietals are reduced and posteriorly placed in a few, and in the latest genera may be vestigial. The lacrimal in *Procolophon* is small, not reaching the nares. The teeth are usually conical throughout; in some genera they are obtuse and cuspidate; in the Diadectidae the posterior ones are transversely molariform; in no known forms are they sectorial. Doubtless with future discoveries other modifications of the primitive structure will be found.

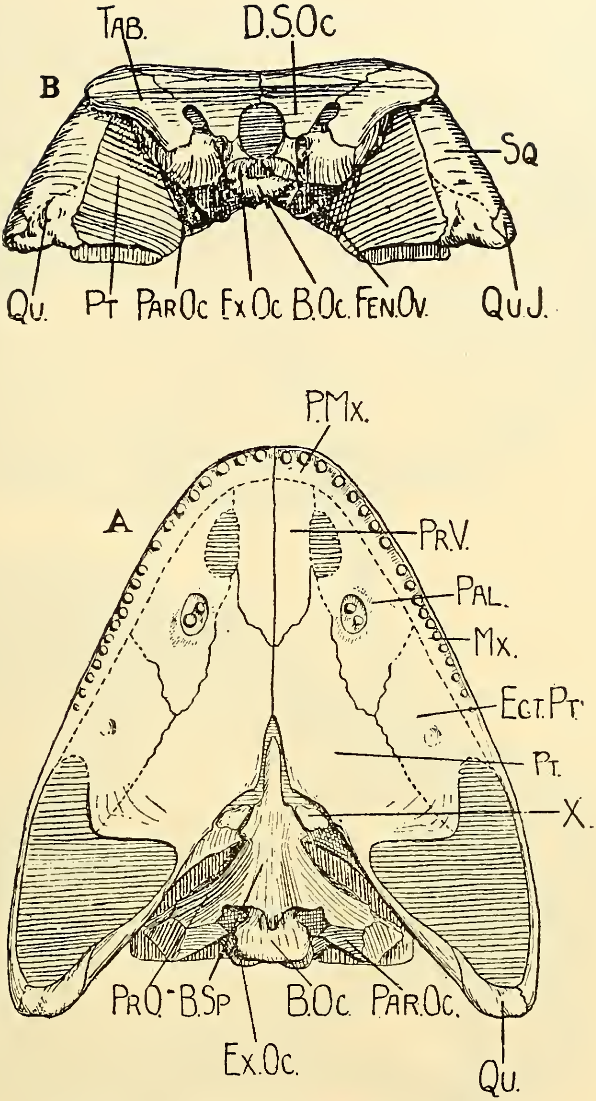

Fig. 21. Cotylosaur skull: *Seymouria*. After Watson. A, from below. Two thirds natural size. B, occipital view. Two thirds natural size.

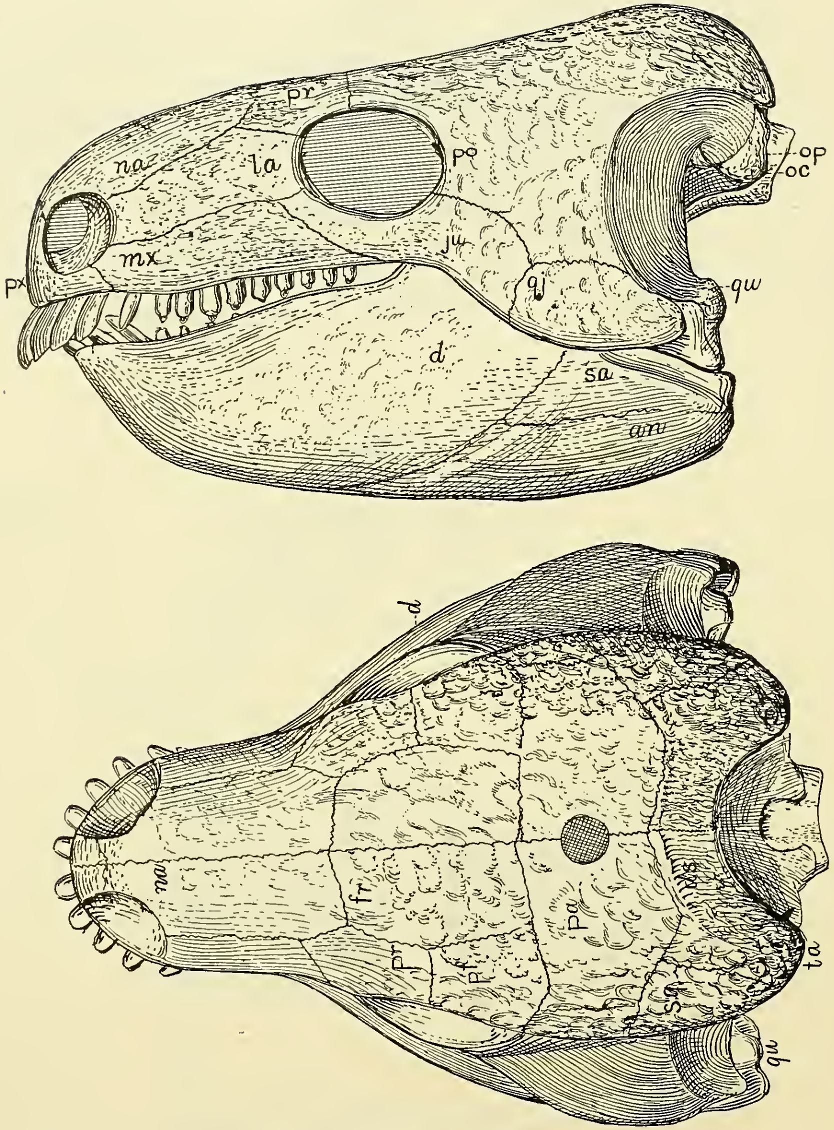

FIG. 22. Cotylosaur skull: *Diadectes*, from the side and above. One half natural size.

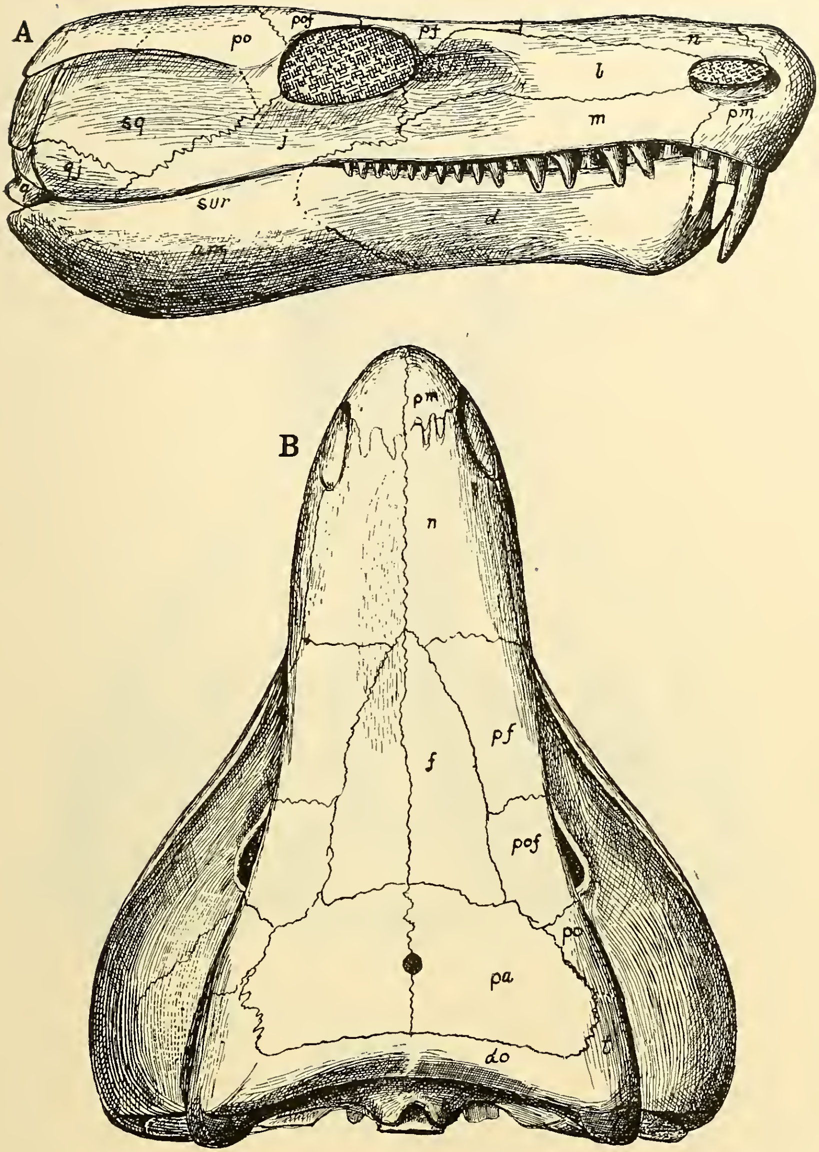

Fig. 23. *Limnoscelis paludis.* Cotylosaur skull: A, from the side; B, from above. *pm*, premaxilla; *n*, nasal; *l*, lacrimal; *m*, maxilla; *f*, frontal; *pf*, prefrontal; *pof*, postfrontal; *po*, postorbital; *pa*, parietal; *do*, dermoöccipital; *t*, tabulare; *j*, jugal; *sq*, squamosal; *qj*, quadratojugal; *q*, quadrate; *d*, dentary; *sur*, surangular; *ang*, angular.

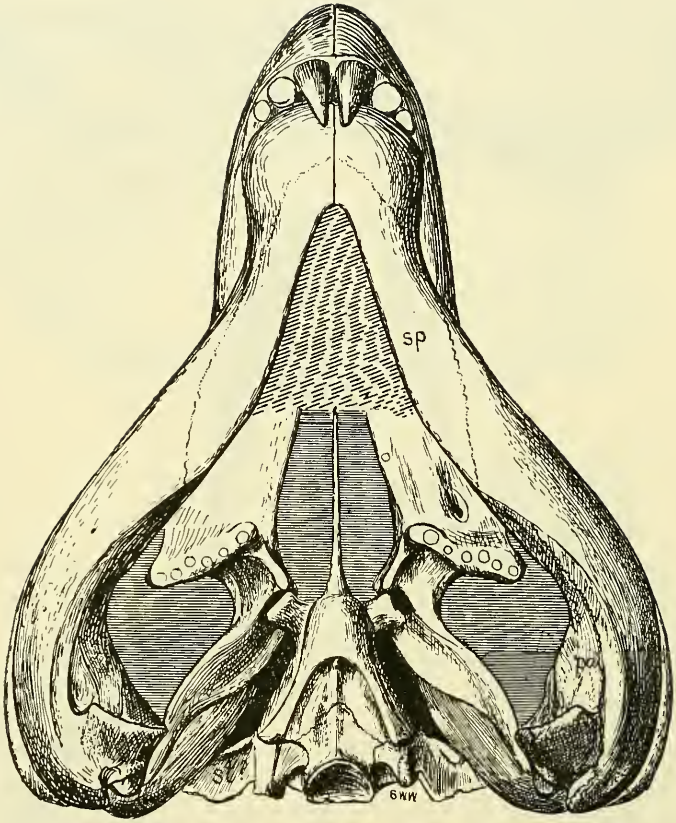

Fig. 24. *Limnoscelis paludis.* Cotylosaur skull: from below. Two fifths natural size. *sp*, splenial; *pa*, prearticular; *st*, stapes (?).

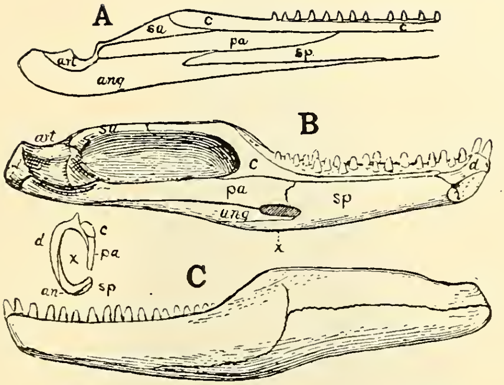

Fig. 25

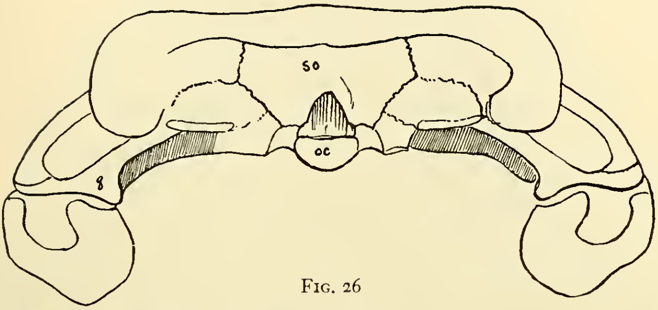

Fig. 26

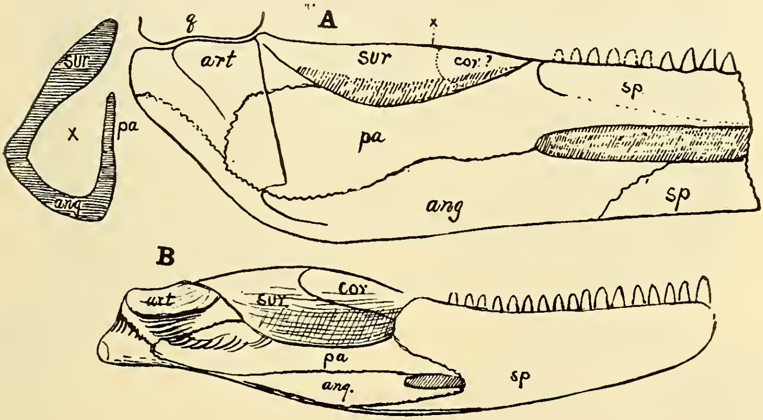

Fig. 27

Fig. 25. A, *Trinacromerum osborni* Williston. Plesiosaur: left mandible to symphysis, inner side, after Williston, 1903; B, *Captorhinus aguti* Cope. Cotylosaur: left mandible, from within; C, the same, outer side.

Fig. 26. *Limnoscelis paludis*. Cotylosaur. Outline of back of skull. Two fifths natural size.

Fig. 27. Cotylosaur. Inner side of mandibles. A, *Limnoscelis paludis;* B, *Labidosaurus hamatus*. One half natural size. *art*, articular; *q*, quadrate; *sur*, surangular; *cor*, coracoid; *pa*, prearticular; *ang*, angular; *sp*, splenial.

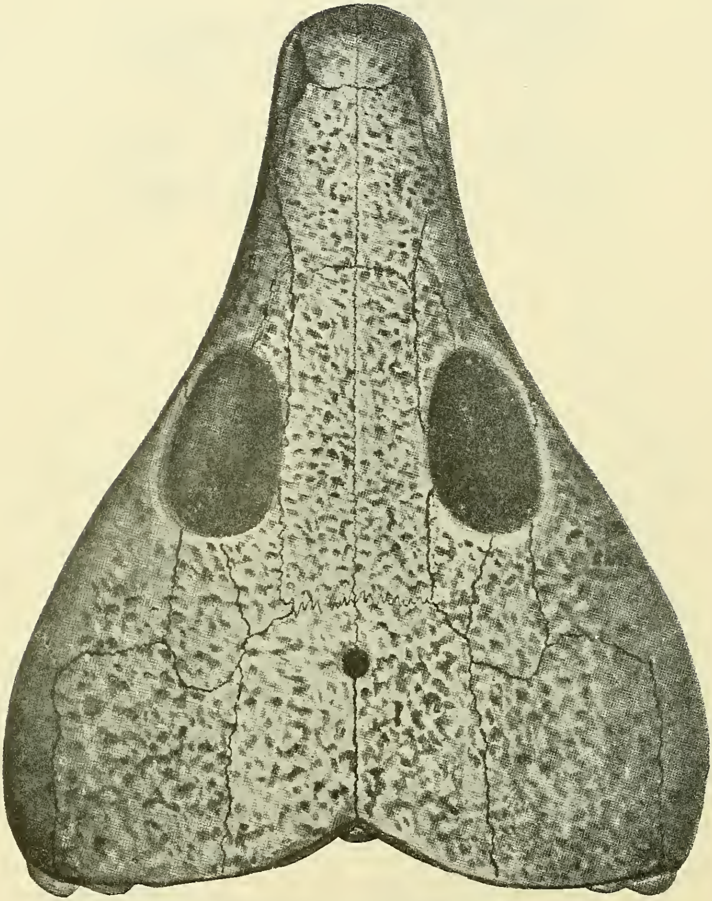

Fig. 28. *Labidosaurus hamatus* Cope. Cotylosaur skull: from above. Two thirds natural size.

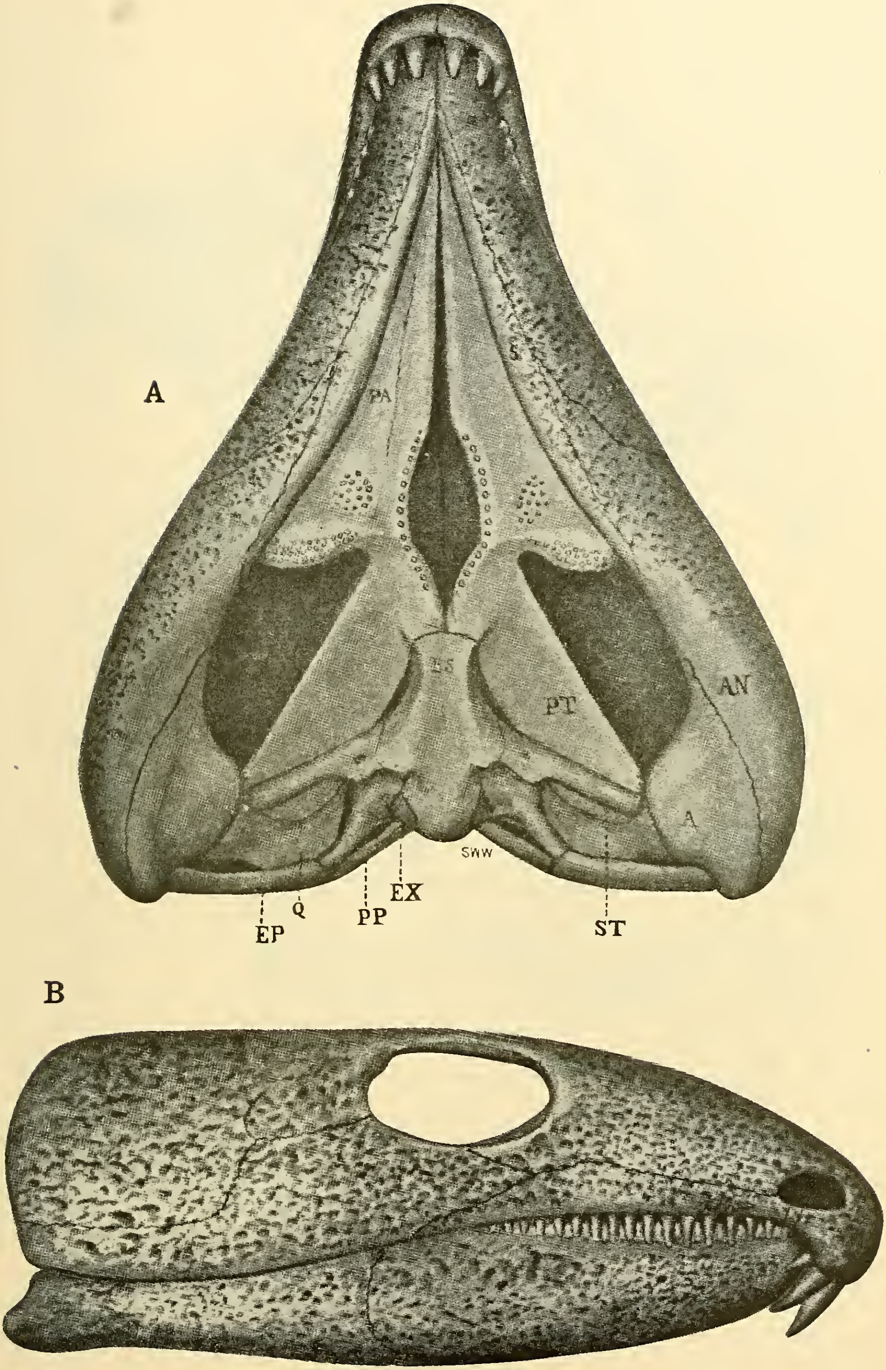

FIG. 29. *Labidosaurus hamatus* Cope. Cotylosaur skull: A, from below, B, from the side. Two thirds natural size. *a*, articular; *an*, angular; *bs*, basisphenoid; *ep*, epiotic; *ex*, exoccipital; *pp*, postparietal; *pt*, pterygoid; *q*, quadrate; *st*, stapes.

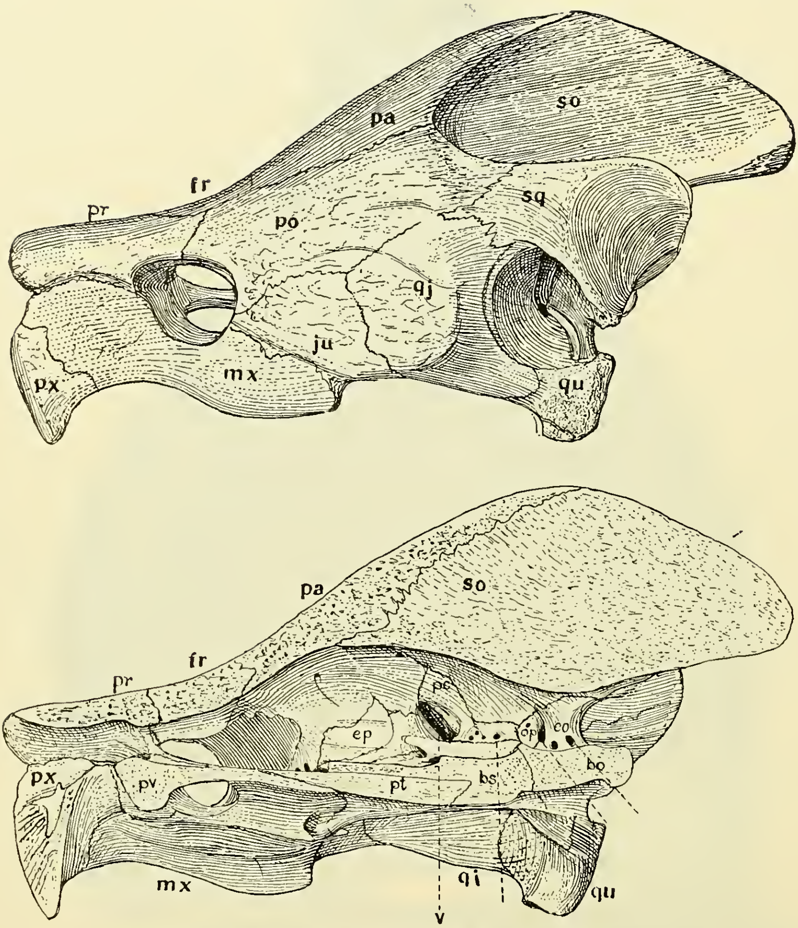

Fig. 30. Pleurodiran skull: *Macrochelys*, from the side and hemisection. One half natural size.

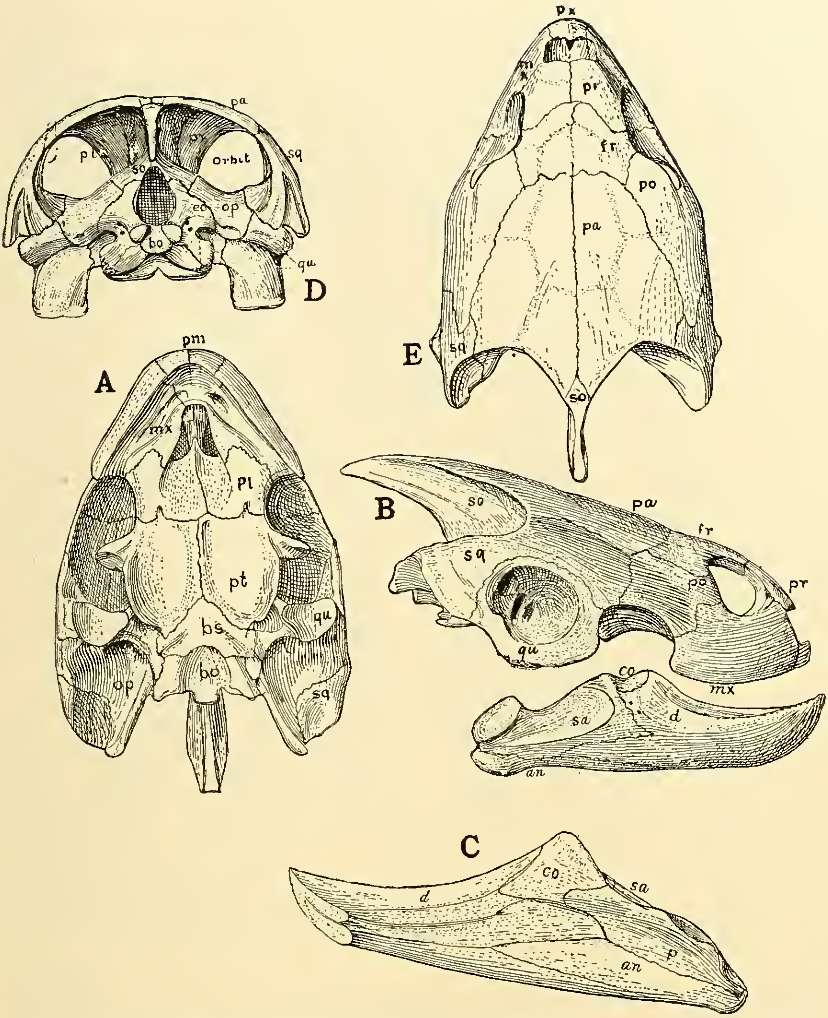

Fig. 31. A, Pleurodiran skull: *Podocnemis*, from below. B, the same, from the side. One half natural size. C, Trionychoid mandible *Platypeltis*, from the inner side. Three halves natural size. D, Cryptodiran skull, *Thalassochelys*, occiput. One half natural size. E, Cryptodiran skull, *Colpochelys*, from above. One half natural size.

The Skull of the Chelonia

(Figs. 30–32)

The skull of the Testudinata or Chelonia is never elongate, though relatively slender in some of the more predaceous kinds. It always lacks the septomaxillae, postfrontals, supratemporals, dermosupraoccipitals, tabulars, ectopterygoids, ethmoids, and the parietal foramen. The nasals are usually absent, and the lacrimals are present only in some ancient forms. The prefrontals are large, meeting in the middle line. The prevomers are single and sometimes obsolete; they usually articulate above with the prefrontals. The parasphenoid has been lately recognized as a distinct bone in certain forms. There is no postoptic, but its place is taken, except in *Dermochelys*, by descending plates from the parietals to the pterygoids, sometimes with an intercalated epipterygoid, which, however, is usually absent. The quadrate may or may not reach the basisphenoid. The palatines often meet in the middle line between the pre-

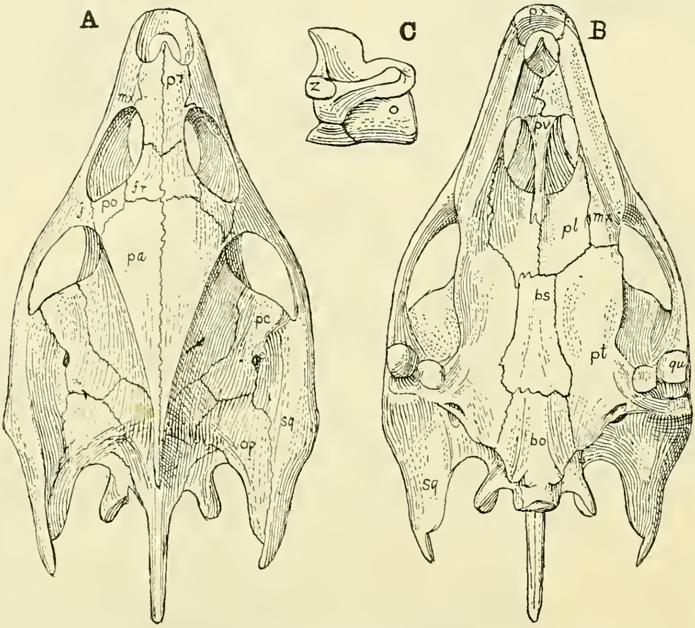

Fig. 32. Trionychoid skull: *Platypeltis*. Natural size. A, from above; B, from below; C, atlas of same from the side. Note abnormal proatlas.

vomer and the pterygoids. The pterygoids also usually meet in the middle, though separated in the Trionychoidea by the basisphenoid. The palatines also often meet for a short distance below and in front of the internal nares, forming a rudimentary secondary palate.

The temporal region primitively was wholly roofed over, and yet is, in some marine turtles, by the large postorbital, quadratojugal, and squamosal. Usually it is more or less exposed by the emargination of the roof from behind or below, or from both sides; and the squamosals and quadratojugals may even become vestigial in the process as in the terapenes. The quadrate is always large, its ear-cavity sometimes wholly surrounded by bone. The stapes is slender. The condyle is largely formed by the exoccipitals, in some wholly so. It remains cartilaginous in the Dermochelyidae, as in some cotylosaurs. The paroccipital remains free throughout life.

The mandibles have a large, free prearticular, usually but incorrectly called the splenial; the splenial is rarely present (*Emydura*, *Toxochelys*, etc.). Both upper and lower jaws are encased in a cutting horny sheath, and are without teeth. Small teeth on the palatal bones are known to occur only in *Stegochelys*, a Triassic genus.

THE SKULL OF THE THEROMORPHA

(Figs. 10 A–D, 11 A–D, 16 A–C, 32–42)

More modifications of the skull structure are found in this order than in the Cotylosauria, as would be expected. The interparietals and tabulars are probably sometimes absent, and they are always confined to the occipital surface when present, the former usually, if not always, unpaired. The supratemporals are doubtfully present in any. The quadratojugal is smaller and never extends far forward.

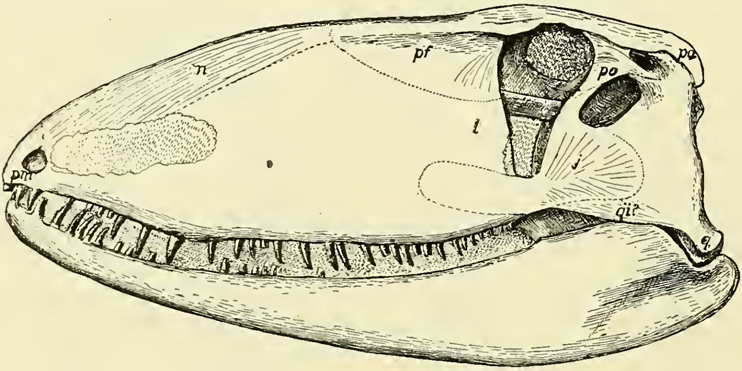

FIG. 32 *bis*. Theromorph skull: *Ophiacodon mirus* Marsh, lateral view. *pa*, parietal; *po*, postorbital; *pf*, prefrontal; *l*, lacrimal; *j*, jugal; *qj*, quadratojugal; *q*, quadrate.

The lacrimals seldom extend to the nares. The teeth are often wanting on the prevomers and are sometimes present on the coronoids. There is a lower temporal opening, bounded by the jugal, postorbital, and squamosal. In the Edaphosauridae only may it possibly extend to the parietal. The teeth of jaws and mandibles are more variable, often markedly anisodont, conical, obtuse, or compressed and sectorial.

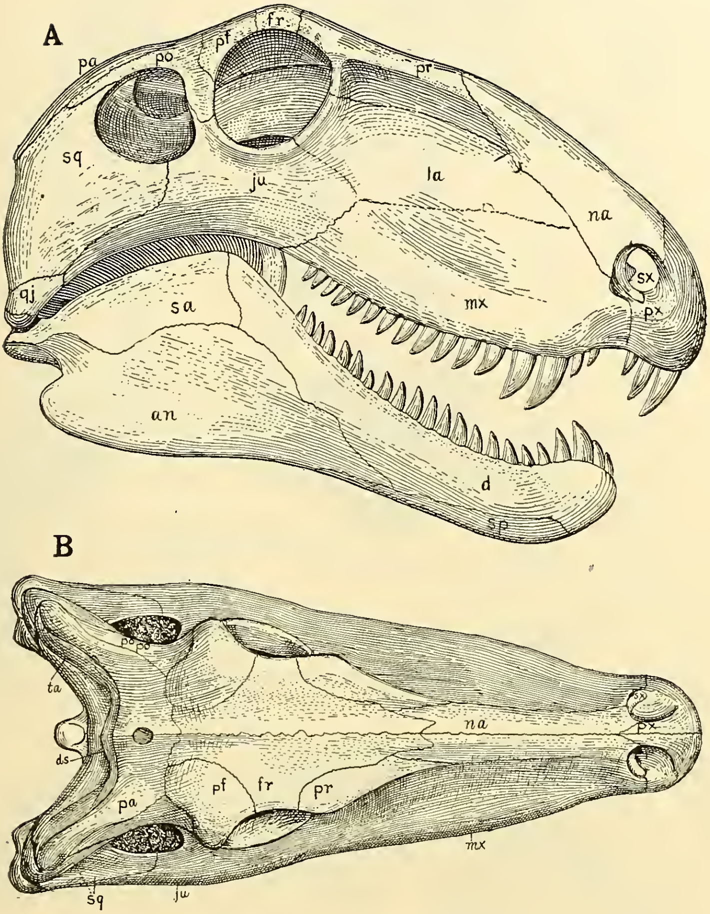

FIG. 33. Theromorph skull: *Sphenacodon.* A, from the side; B, from above. One third natural size.

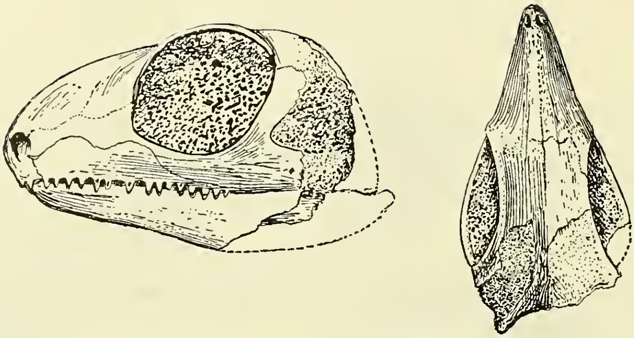

Fig. 34. Theromorph skull: *Glaucosaurus megalops*, from the side and from above. Natural size.

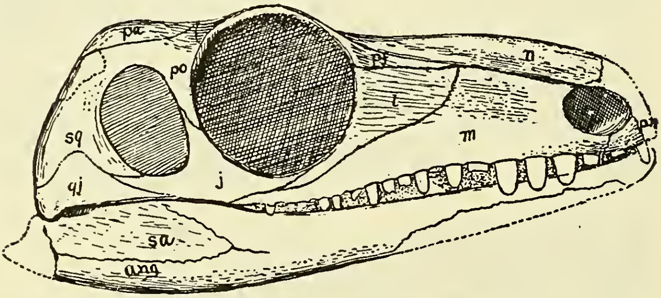

Fig. 35. Theromorph skull: *Mycterosaurus*, from the side. Natural size.

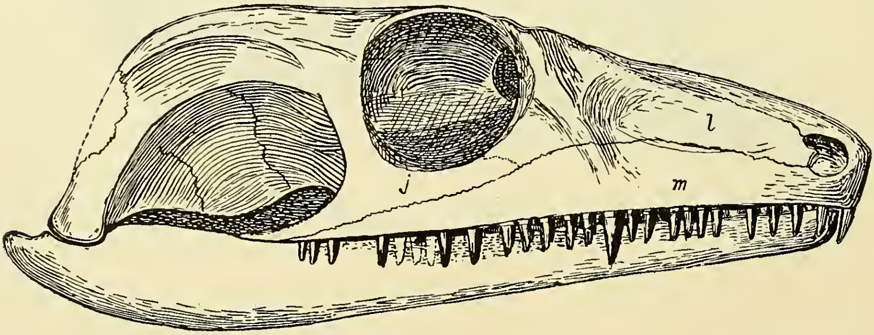

Fig. 36. Theromorph skull: *Varanosaurus brevirostris* Williston, from the side. Two thirds natural size.

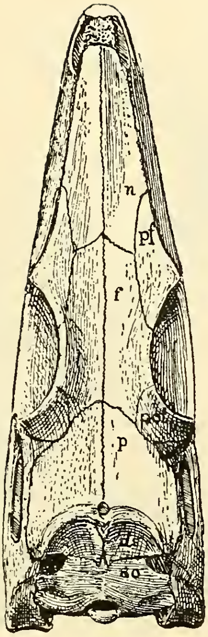

Fig. 39

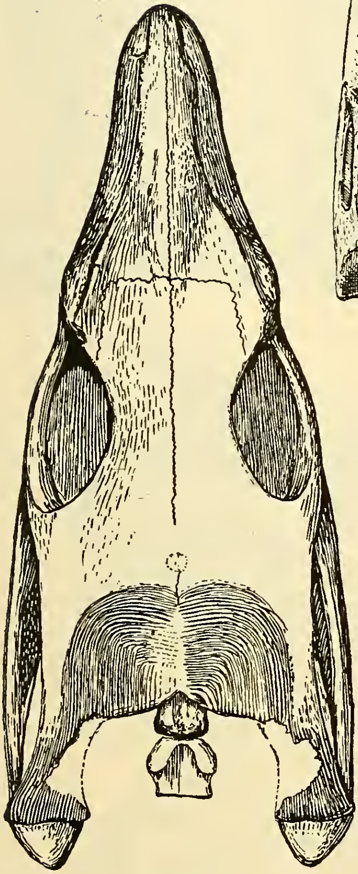

Fig. 37

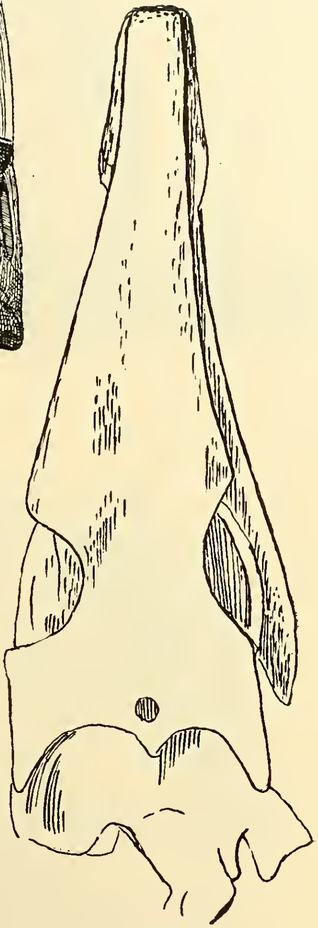

Fig. 38

Fig. 37. Theromorph skull: *Varanosaurus brevirostris* Williston, from above. Two thirds natural size.
Fig. 38. Theromorph skull: *Varanosaurus acutirostris* Broili, from above. Two thirds natural size. After Broili.
Fig. 39. Theromorph skull: *Mycterosaurus*, from above. Natural size.

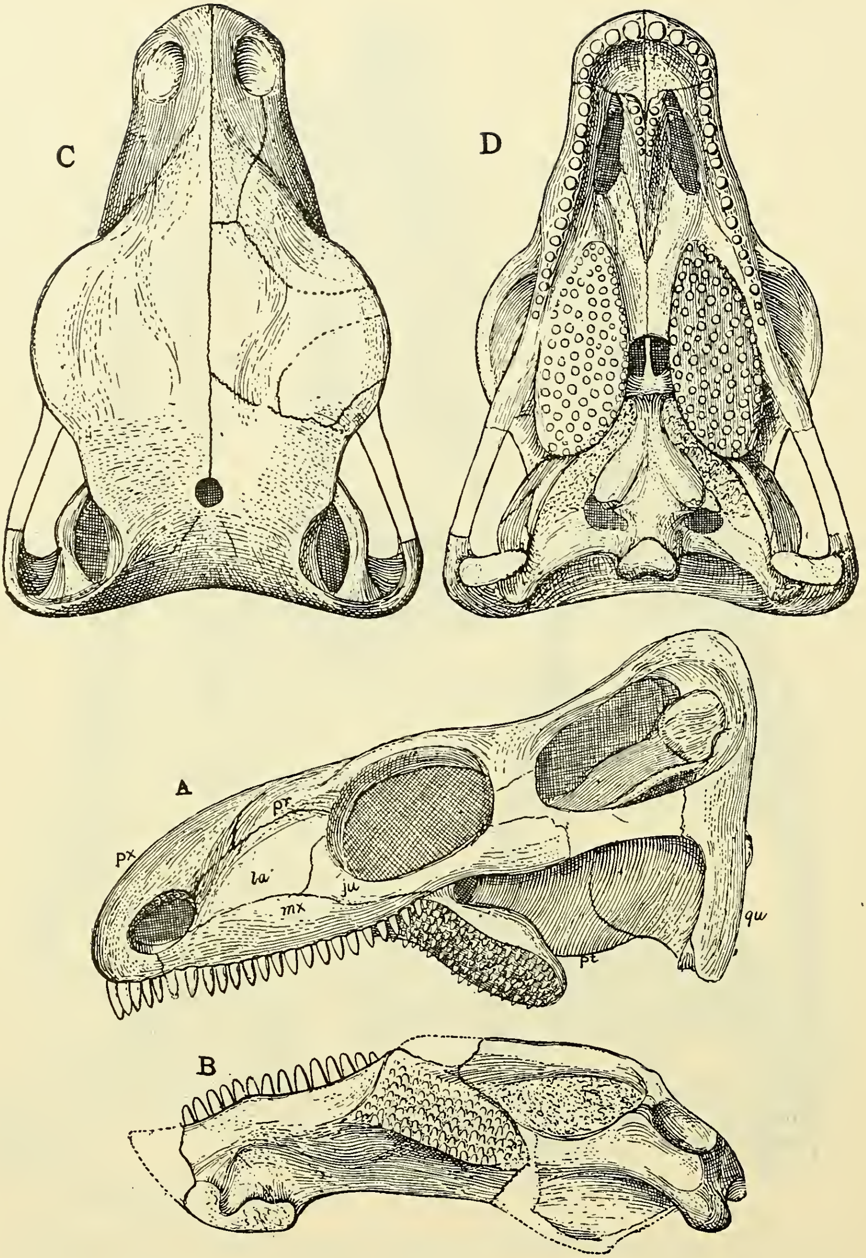

Fig. 40. Theromorph skull: *Naosaurus claviger.* A, from the side; B, right mandible, from inner side; C, skull from above; D, the same from below. Two fifths natural size.

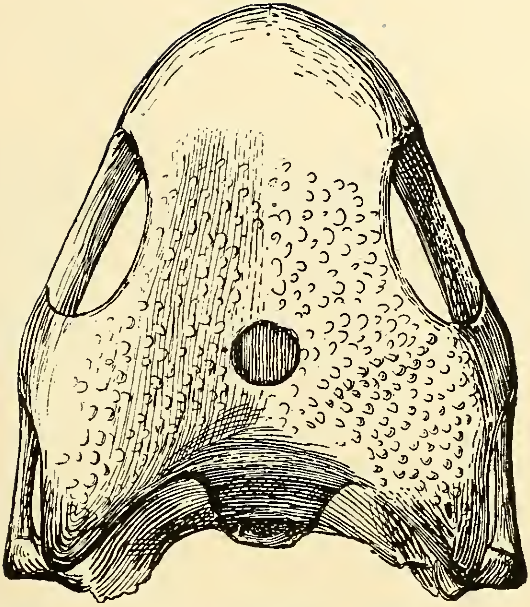

Fig. 41. Theromorph skull: *Casea broilii* Williston, from above. Natural size.

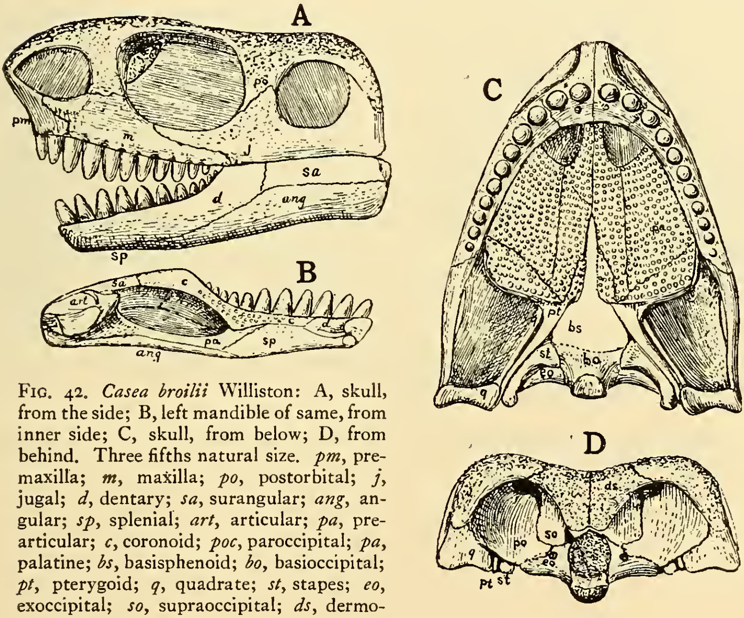

Fig. 42. *Casea broilii* Williston: A, skull, from the side; B, left mandible of same, from inner side; C, skull, from below; D, from behind. Three fifths natural size. *pm*, premaxilla; *m*, maxilla; *po*, postorbital; *j*, jugal; *d*, dentary; *sa*, surangular; *ang*, angular; *sp*, splenial; *art*, articular; *pa*, prearticular; *c*, coronoid; *poc*, paroccipital; *pa*, palatine; *bs*, basisphenoid; *bo*, basioccipital; *pt*, pterygoid; *q*, quadrate; *st*, stapes; *eo*, exoccipital; *so*, supraoccipital; *ds*, dermosupraoccipital.

THE SKULL OF THE THERAPSIDA

(Figs. 43–45)

Many more modifications of the skull are found among the reptiles grouped under the name Therapsida or Anomodontia *sens. lat.* The supratemporals are never present. The postfrontals are often absent; the quadratojugals are present only in the Dinocephalia and are small.[1] Only in some of the Dromasauria do the lacrimals and septomaxillae exclude the maxillae from union with the nasals. There is a separate bone in front or surrounding the parietal foramen in the Anomodontia and Gorgonopsia. The parietals may be united in some of the Bauriasauria. The interparietal or dermosupraoccipital is always on the occipital surface of the bone and is unpaired; it is generally present, as also the tabulars. The temporal foramen, usually bounded above as in the Theromorpha, reaches the parietal in the Therocephalia and Theriodontia, the postorbitals and squamosals not meeting. The vomers are fused into a single bone in the Gorgonopsia, Bauriasauria, and Cynodontia. The pterygoids and palatines meet in the middle line in the Dinocephalia. There is a partial false or secondary palate formed by the union of the maxillae in front of the nares in the Anomodontia, a well-formed secondary palate in the Bauriasauria and Cynodontia. The ectopterygoids may be absent or present. Only in some of the Therocephalia are there teeth on the palatal bones. The pterygoids do not meet the small quadrates in the Cynodontia. In the Cynodontia the condyle is essentially dicondylar. The parietal foramen is usually absent.

Some Dromasauria and the females of some Anomodontia are edentulous. Other anomodonts may have a single caniniform tooth in each jaw, or canines and molars. The Therocephalia have anisodont sectorial teeth, the Cynodontia with real heterodont dentition, the molars sectorial or cuspidate.

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[1] [Broom, Sollas, Watson, and von Huene have observed a distinct quadratojugal in various Therapsida. — Ed.]

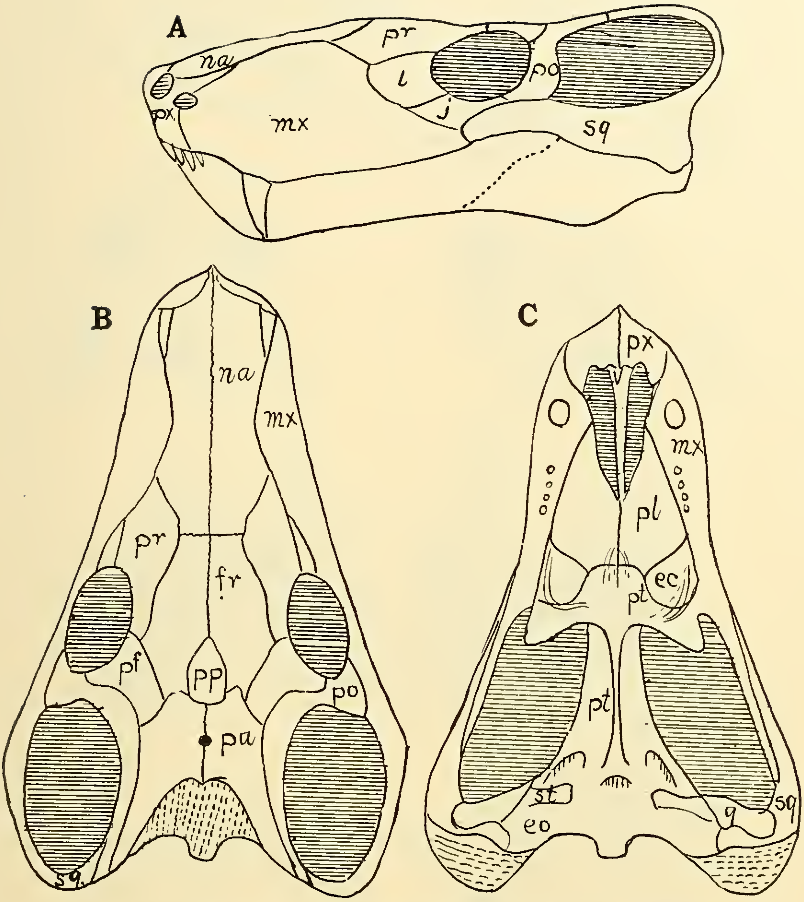

FIG. 43. Gorgonopsian skull: *Scylacops capensis*. A, from the side; B, from above; C, from below. One half natural size. After Broom.

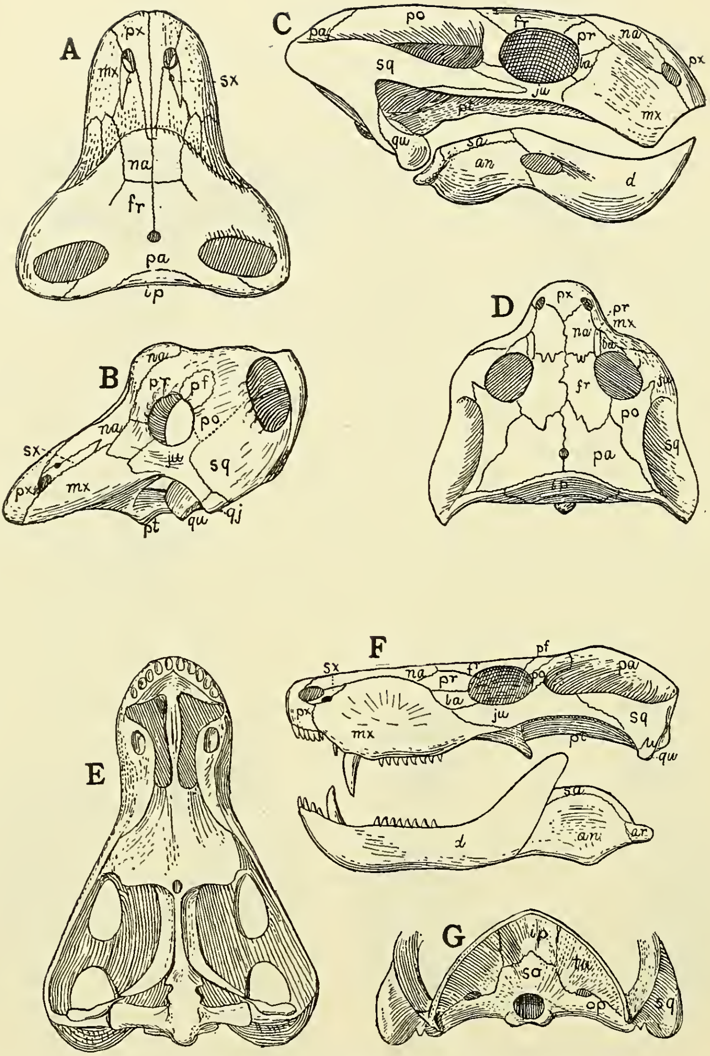

Fig. 44. Therapsid skulls: A, B, *Mormosaurus* (Dinocephalia) from above and from side. After Watson. One twelfth natural size. C, *Dicynodon* (Anomodontia) from the side. After Broom. One half natural size. D, *Cistecephalus* (Anomodontia), from above. After Broom. One half natural size. E, *Gorgonops* (Gorgonopsia), from below. After Watson. One fourth natural size. F, *Scylacosaurus* (Therocephalia), from the side. After Broom. Two sevenths natural size. G, *Diademodon* (Cynodontia), occiput. After Watson. One half natural size.

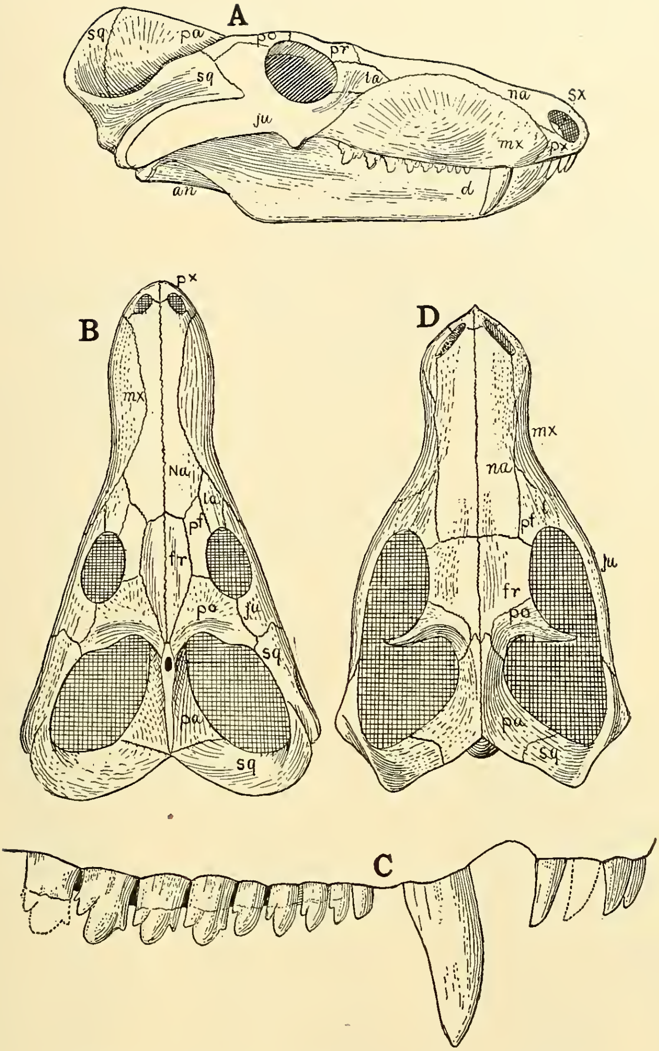

FIG. 45. Therapsid skulls: A, *Cynognathus platyceps* (Cynodontia), from the side. After Broom. One third natural size. B, the same, from above. C, *Cynognathus crateronotus*, upper teeth, from the side. D, *Bauria* (Bauriasauria), from above. After Broom. One half natural size.

THE SKULL OF THE NOTHOSAURIA

(Fig. 47)

[No manuscript. See pages 211, 246, 247]

THE SKULL OF THE PLESIOSAURIA

(Figs. 46–48, 25 A)

The extreme aquatic adaptations of the plesiosaurs have caused certain modifications in the structure and relations of the bones of the skull that are unique among reptiles.

The general shape of the skull seems to bear a definite relation to the length of the neck, always shorter in the long-necked forms, slender, sometimes very slender in the short-necked types. The premaxillae are always greatly elongated, extending back at least as far as the front part of the orbit, in the long-faced kinds even to articulate with the parietals, above or between the frontals. The alveolar border also is [short?] shut. The maxillae are much more elongate than in the icthyosaurs and phytosaurs. There are no teeth in the palate. The nasals have never been certainly determined; possibly they are fused with the frontals, which extend as far forward as the external nares, forming the inner border. The prefrontals are small; the lacrimals have been identified in a few forms only; they appear to be absent in some. The postfrontals are probably present in all. The orbits are bounded below by the jugals and maxillae. The quadratojugals are conceded to be absent in all plesiosaurs. The single large temporal opening is bounded below by the postorbitals and squamosal, above by the parietals, which are more or less elevated in the middle in a crest. There is a pineal foramen. The squamosals, in some at least, join each other back of the parietals on the upper surface of the skull. There are no interparietals, tabulars, or supratemporals.

On the occipital surface the supraoccipital is excavated more or less by the foramen magnum, which may extend to the roof, dividing the bone. The paroccipitals are always fused with the exoccipitals. The brain-case is more or less open in front on the sides, the postoptics either reduced or absent. The stapes is large and stout.

Very great also, are the modifications of the palate. The anterior nares are situated either between the prevomers and the maxillae,

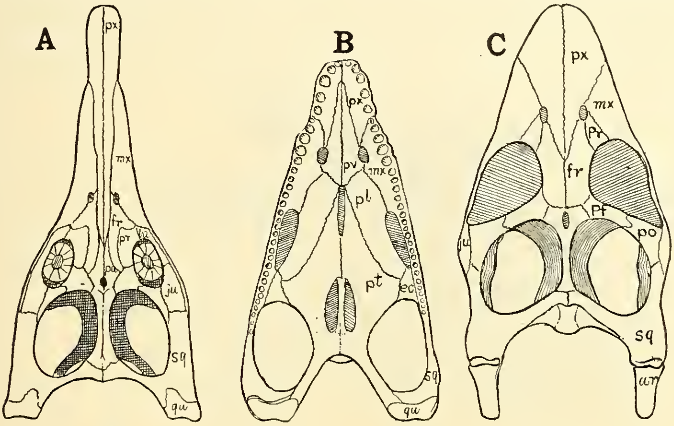

Fig. 46. Sauropterygian skulls: A, *Peloneustes*. After Linder. One ninth natural size. B, *Plesiosaurus*. After Andrews. One sixth natural size. C, *Muraenosaurus*. After Andrews. One sixth natural size.

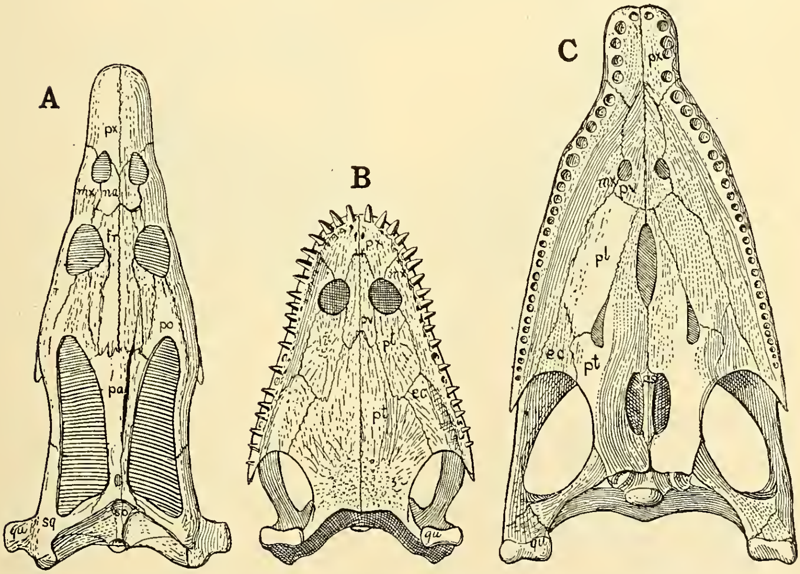

Fig. 47. Sauropterygian skulls: A, *Nothosaurus*, from above. One fourth natural size. B, *Simosaurus*, from below. After Jaekel. One fourth natural size. C, *Thaumatosaurus*, from below. After Fraas. One fourth natural size.

or between them and the palatines, and, like the external ones, are small. There is always a remarkable posterior interpterygoidal vacuity, divided in the middle throughout by the large parasphenoid, the pterygoids meeting in front of and to a slight extent behind them.

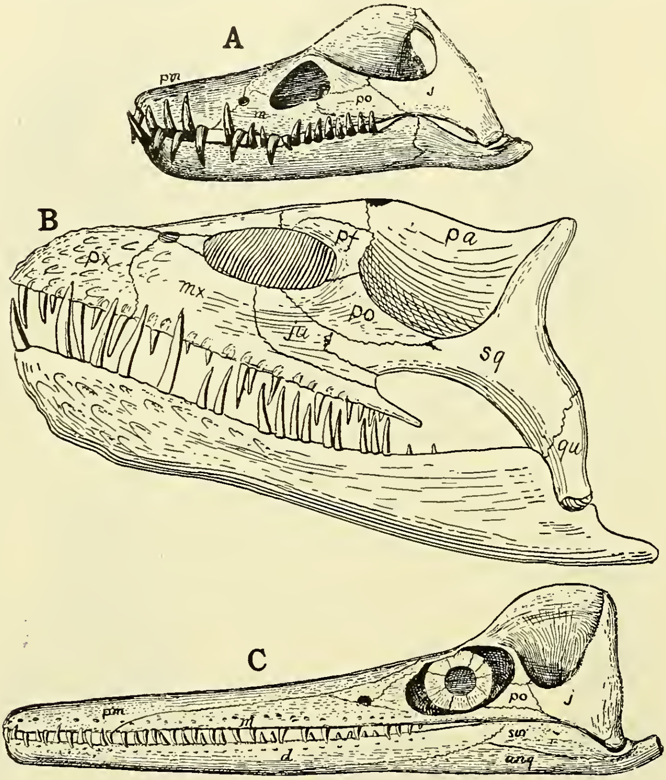

FIG. 48. Plesiosaur skulls: A, *Elasmosaurus*, from the side: *pm*, premaxilla; *m*, maxilla; *po*, postorbital; *j*, jugal. B, *Plesiosaurus*, from the side. One sixth natural size. C, *Trinacromerum*, from the side: *ang*, angular; *d*, dentary; *pm*, premaxilla; *po*, postorbital; *j*, jugal; *sur*, surangular.

An anterior interpterygoidal vacuity, as also posterior palatine and other openings in the palate, may or may not be present. The internal nares are in front, sometimes very much in front, of the external nares. The coronoids are elongate bones, extending along the sides of the teeth internally and meeting each other in some forms in a median symphysis. As usual in long-faced forms, the splenials meet in a median symphysis.

THE SKULL OF THE PLACODONTIA

(Fig. 49)

The skull of the Placodontia is almost unique among reptiles for the extraordinary development of large, flat, crushing teeth upon the

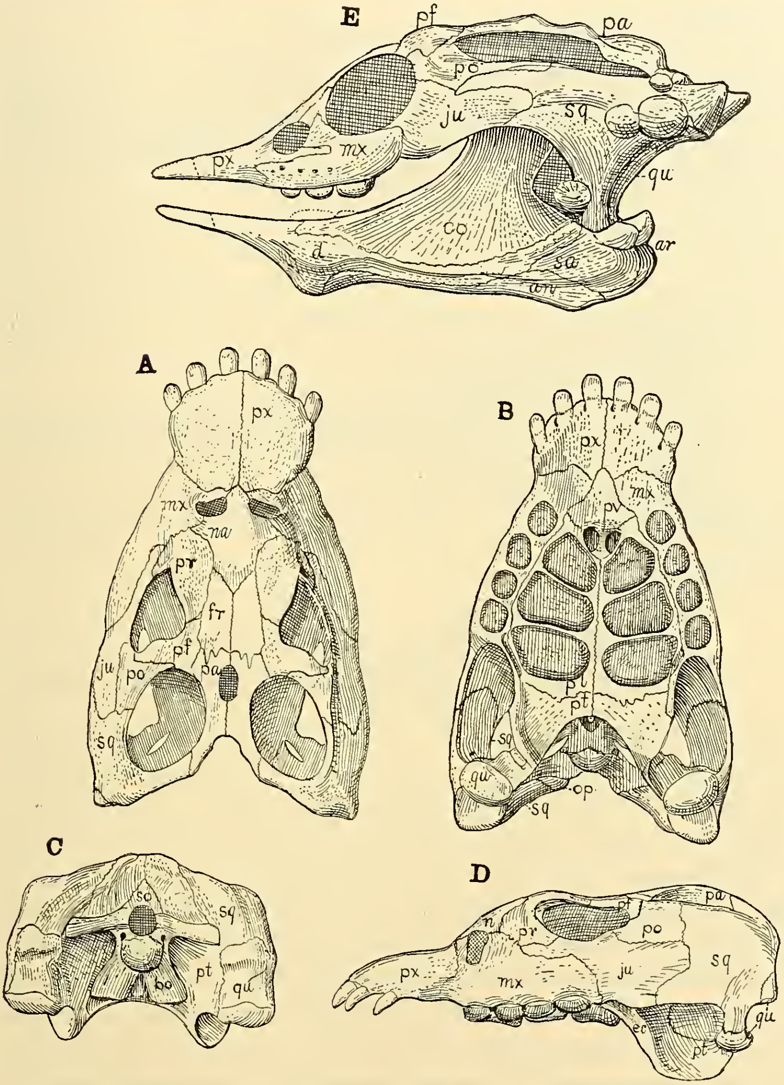

FIG. 49. Placodont skulls: A–D, *Placodus*. After Broili. One fourth natural size. E, *Placochelys*. After Jaekel. One half natural size.

jaws and palatines, in *Placodus* as few as twenty all told, in *Placochelys* still fewer. In consequence, the palatines are very large, meeting each other throughout as do the pterygoids in the median line. The ectopterygoids are very small and the pterygoids are restricted to the posterior part of the palate, widely separated from the prevomers.

The massive cranium has a large temporal opening bounded above by the parietal, below by the united postorbitals and squamosal, with the postfrontal entering into the anterior border. Except for the postfrontals, the structure here, it is seen, is like that of the Dinocephalia, and possibly has arisen in the same way. The stout lateral bar below the opening is identified by Jaekel in *Plachochelys* as composed of the squamosal and quadratojugal, by Huene as the supratemporal and squamosal; both views are probably incorrect, since Broili finds only the squamosal, which is in *Placodus* the more probable. So, also, Huene believes there is an interparietal, which Broili cannot find.

The nasal only of the roof bones is unpaired in *Placodus;* possibly the prevomers are also single. There is a large epipterygoid. No tabulars have been found. The premaxillae in *Placodus* are large, each with three incisor-like teeth. The largest skulls of *Placodus* are about ten inches long.

THE SKULL OF THE ICHTHYOSAURIA

(Figs. 50, 51)

The skull of the ichthyosaurs, while retaining not a few primitive characters, has been highly and peculiarly modified in many ways. The greatly elongated premaxilla, unlike those of other aquatic reptiles, is broadly separated above by the very large nasal, and bears numerous teeth; the maxillae are short. All bones are paired. The frontals are small. The very large orbits have the usual bounding bones, prefrontal, postfrontal, postorbital, jugal, and lacrimal, but their relations are somewhat changed. The prefrontals are long, the postfrontals are extraordinarily large, articulating in front not only with the whole extent of the frontals but also with the nasals and prefrontals, posteriorly with the so-called supratemporals. The postorbitals are long bones forming nearly the whole posterior boundary of the orbits, with their usual articulations. The jugals are long, articulating with postorbitals, quadratojugals, maxillae, and lacrimals. The relations of the bones of the palate and the boundaries of the nares are primitive; an ectopterygoid has not been recognized and is probably absent; there are no teeth on the palatal bones. On the occiput the paroccipitals, unlike all other reptiles since the primitive Cotylosauria, save the Chelonia, are separate. The stapes is a short, stout bone, possibly an acquired, more probably a primitive, character. There are no dermosupraoccipitals. The large parietal foramen is at the front end of the parietals, sometimes between the frontals.

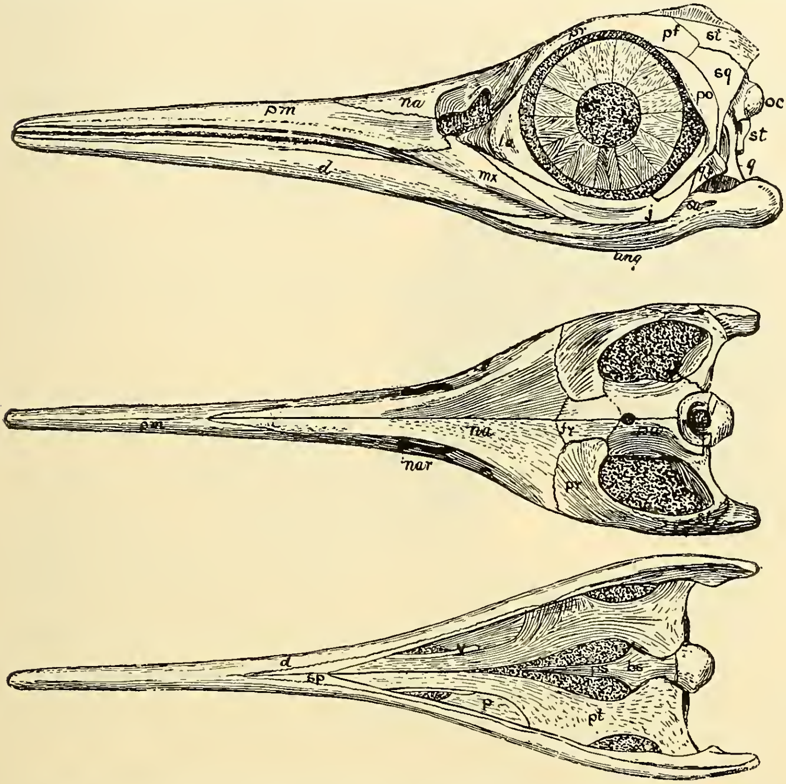

FIG. 50. Ichthyosaur skull: *Baptanodon* (*Ophthalmosaurus*), from the side, from above, and from below. After Gilmore.

Most characteristic of the ichthyosaur skull is the structure of the temporal region, about which there has been dispute from the time of

Owen to the present. The large temporal vacuity is admittedly the upper one, bounded on the inner side by the parietal, on the outer by the postfrontal and the so-called supratemporal. There is no lateral foramen, and it is quite improbable that a preëxistent one was later closed by the encroachment of the orbit. This region, as in the primitive skull, has five bones. About three, the postfrontal, postorbital, and quadratojugal, there can be no question of identity. And unless we accept the wholly improbable theory that new bones have been developed in the temporal region of the ichthyosaurs, the other two must be homologized with the supratemporal, or tabular, and the squamosal. The supratemporal bone was the first to be lost in the primitive skull, and there is no certain evidence yet forthcoming that it was retained in any reptiles after the cotylosaurs. If, however, the supratemporal was persistent in the ichthyosaurs instead of the tabular, by no possibility can it be the bone on the outer side of the squamosal, as some recent writers assert, as a comparison of the cotylosaur skull will make evident. The outer bone, sometimes obsolete in ichthyosaurs, must be the squamosal. The upper, posterior bone completing the upper border of the temporal vacuity, the author prefers to believe is the tabular and not the supratemporal, and doubtless is homologous with the bone so recognized in the skull of the Squamata. We cannot conceive of its being anything else, having as it does the same relations with paroccipital, parietal, and quadrate, rarely in the mosasaurs extending forward to articulate with the postorbital.

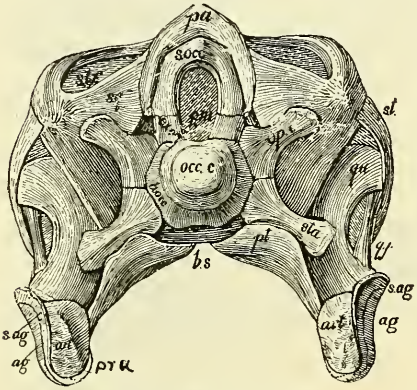

Fig. 51. Ichthyosaur skull: *Baptanodon* (*Ophthalmosaurus*), from the rear. After Gilmore. *Ang*, angular; *bs*, basisphenoid; *d*, dentary; *fr*, frontal.

The Skull of the Protorosauria

(Figs. 52, 53 c–e)

In the order here provisionally called the Protorosauria the skull is completely known in none, but best in *Araeoscelis*, the oldest certainly-known reptile with a single typical upper temporal vacuity. The roof bones are all paired in all, so far as known. In *Araeoscelis*, *Pleurosaurus*, and probably *Protorosaurus*, there is a parietal foramen, but none in *Saphaeosaurus*. The lacrimal is small or vestigial in all. The postfrontal is present in *Araeoscelis*, and only in this genus are there indications of the presence of the dermosupraoccipitals. Probably all have teeth on the palatal bones.

Their chief interest lies in the structure of the temporal region. In *Araeoscelis* the temporal opening is bounded externally by three bones, the postorbital in front, and two bones posteriorly, about which there is doubt because of their evident identity with the corresponding bones in the lizard skull, which have been the subject of more controversy than any others of the reptilian skull. Aside from the tabular, there are three recognized bones of the primitive temporal region, all present in the Cotylosauria and Ichthyosauria, to which the names mastoid, supramastoid, squamosal, suprasquamosal, prosquamosal, temporal, supratemporal, and quadratojugal have been applied in almost all possible combinations. Only two of these are present in *Araeoscelis*, *Pleurosaurus* and the Squamata, to

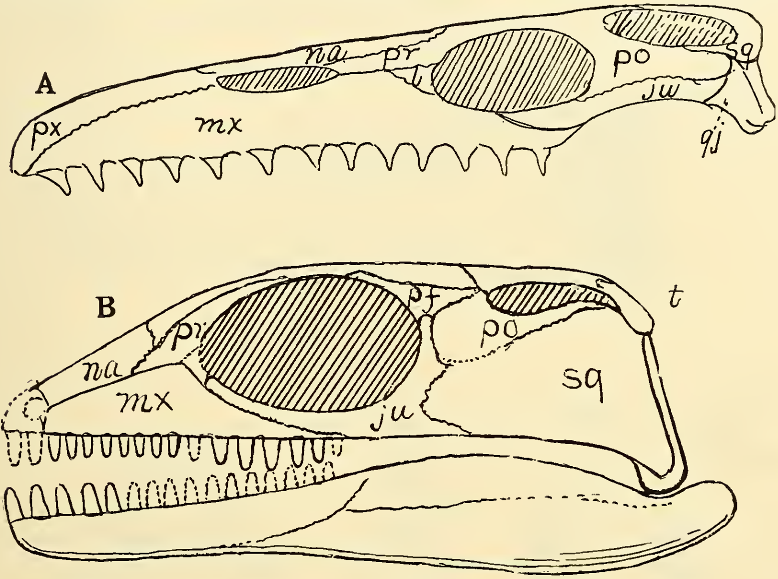

FIG. 52. Parapsid skulls: A, *Pleurosaurus*, from the side. Natural size. B, *Araeoscelis*, from the side. Twice natural size.

which all of these names have been given by different authors. The more general opinion is that the posterior one of the *Araeoscelis* and

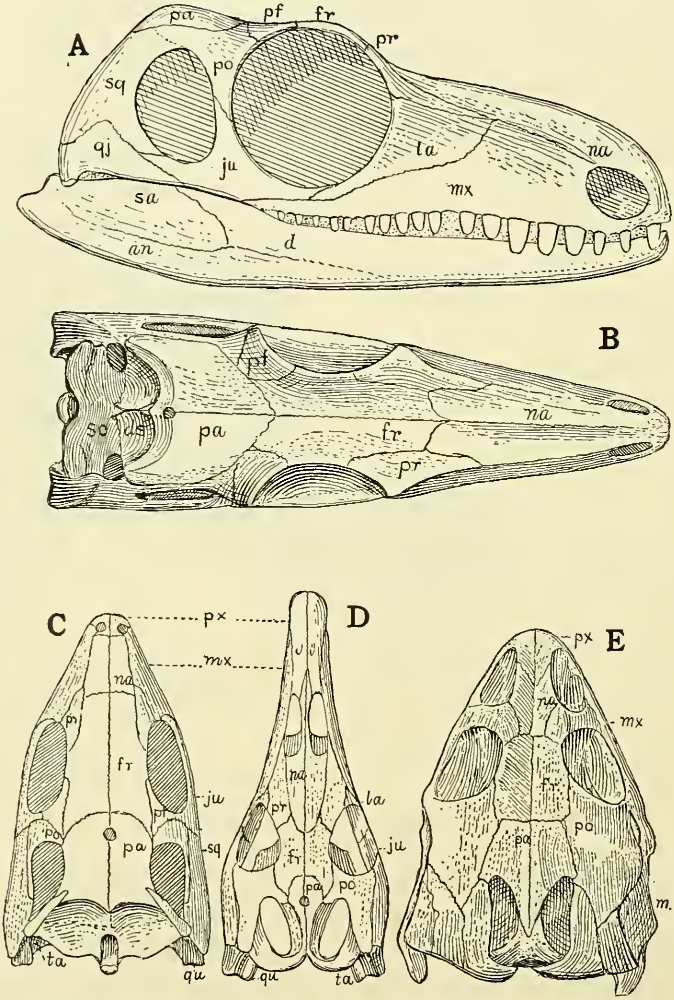

FIG. 53. Parapsid, etc., skulls: A, B, *Mycterosaurus* (Theromorpha), from the side and from above. Natural size. C, *Araeoscelis* (Protorosauria), from above. Natural size. D, *Pleurosaurus* (Protorosauria), from above. One half natural size. E, *Sauranodon* (Protorosauria), from above. Natural size.

Squamata arch is the supratemporal, the anterior and outer one the squamosal; some, however, reverse these names, calling the posterior one the supratemporal or its synonym, the prosquamosal. Yet others both in the past and the present call the outer anterior bone the quadratojugal. The author has given his reasons for believing that the posterior bone is none of these but the tabular instead, the anterior one the squamosal, the quadratojugal absent. He believes that the posterior is the tabular because it occupies the primitive position of that bone in its relations to the interparietal, paroccipital, squamosal, and quadrate. The supratemporal is the first bone to disappear in the temporal region of the Cotylosauria, and its presence has never been positively determined in the Theromorpha and Therapsida.

It is quite possible, however, that both the tabular and supratemporal have disappeared in these reptiles, and that the squamosal has usurped their position and functions; the true supratemporal, however, has no relations with the quadrate as has the bone so called in the skull of the lizards. If so, the bone articulating with it in front and forming the outer boundary of the temporal opening may be the quadratojugal, as was formerly believed and yet is by some. It is a fact, however, that the quadratojugal is a very inconstant bone in all single-arched reptiles otherwise. It is very small in the Theromorpha, is present in only a very few of the Therapsida as more or less of a vestige, and has wholly disappeared in the Sauropterygia. That it should lose its original position at the lower outer side of the quadrate, to form part of the articular surface for its upper end, seems improbable. Furthermore, in the Ichthyosauria (and ? *Saphaeosaurus*) there is a distinct bone between it and the temporal opening that must be either the squamosal or supratemporal. There is at present no certain solution of the problem.

THE SKULL OF THE SQUAMATA

(Figs. 54–59)

The skull of the Squamata is at once distinguished from that of all other reptiles by the movable, streptostylic quadrate, secondarily more or less fixed in some forms. The exoccipitals and paroccipitals are always fused; the pterygoids never reach the vomers; the interparietals and either the supratemporals or tabulars, or the quadratojugals, according to the identification, are absent. The teeth are acrodont or pleurodont; the prearticular of the mandibles is always fused with the articular. Other characters are very variable in this extensive order, which is sometimes divided into two or three distinct orders.

Sauria or Lacertilia

In the lizards (Figs. 55, 56) the quadrate articulates above normally with three bones, the squamosal, paroccipital, and a third bone whose homology is yet disputed, but which is usually called the supratemporal. The squamosal may be absent in those lizards without a temporal arch, and rarely in certain degraded burrowing lizards (Fig. 56) the "supratemporal" may also be absent, the quadrate lying against the brain-case and more or less fixed by the pterygoid. The paroccipital usually but not always helps support the quadrate.

As regards the identity of all these bones, there has been great difference of opinion, and there is by no means unanimity at the present time. The tabular, as here identified, has been called the squamosal, supramastoid, supratemporal, and even the paroccipital (opisthotic). The squamosal as here considered has been called the quadratojugal, supratemporal, paraquadrate, squamosal, and prosquamosal. The reasons for their identification as the tabular and squamosal will be found in the discussion of the skull of the Protorosauria.

Below, the quadrate articulates with the pterygoid on the inner side by a rather free joint in most lizards, in some, like the Amphisbaenia (Fig. 56) by a close sutural joint. On the inner side the usually slender stapes abuts against the quadrate (Fig. 55 C). In the mosasaurs there is an elongated suprastapedial process arching backward and often extending to the lower end, enclosing the auditory meatus, as in some turtles.

The tabular (Fig. 55 A, *ta*), or supratemporal, at the distal and under side of the parietal process, forming more or less of the boundary of the temporal opening, articulates with the squamosal, paroccipital, and quadrate. In the mosasaurs (Fig. 54 C) only, it has a long internal process, firmly wedged in between the paroccipital and proötic, extending nearly or quite to the semicircular canals. In some lizards the tabular has suffered reduction or has become indistinguishably fused with the squamosal.

The squamosal normally articulates with the tabular and quadrate posteriorly, anteriorly with the postorbital, and often, both in the lizards and mosasaurs, by a slender prolongation with the tip of the jugal; very rarely, as in *Uromastix,* with the jugal only. In some lizards it has suffered reduction, and is absent in the Geckonidae, *Anniella,* and Amphisbaenidae, vestigial in the Helodermatidae.

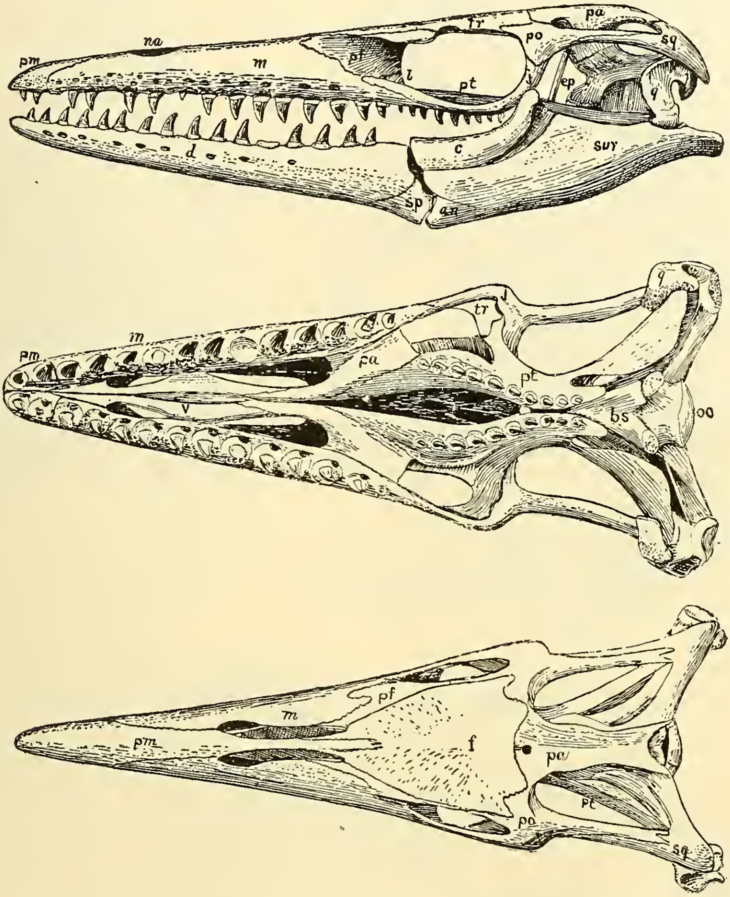

FIG. 54. Mosasaur skulls: Upper figure, *Clidastes,* from the side; middle figure, *Platecarpus,* from below; lower figure, *Tylosaurus,* from above. *an,* angular; *bs,* basisphenoid; *c,* coronoid; *ep,* epipterygoid; *fr,* frontal; *j,* jugal; *l,* lacrimal; *m,* maxilla; *na,* nasal; *oc,* occipital condyle; *pa,* parietal, palatine; *pm,* premaxilla; *pf,* prefrontal; *pt,* pterygoid; *po,* postorbital; *q,* quadrate; *sp,* splenial; *sq,* squamosal; *tr,* transverse; *v,* vomer.

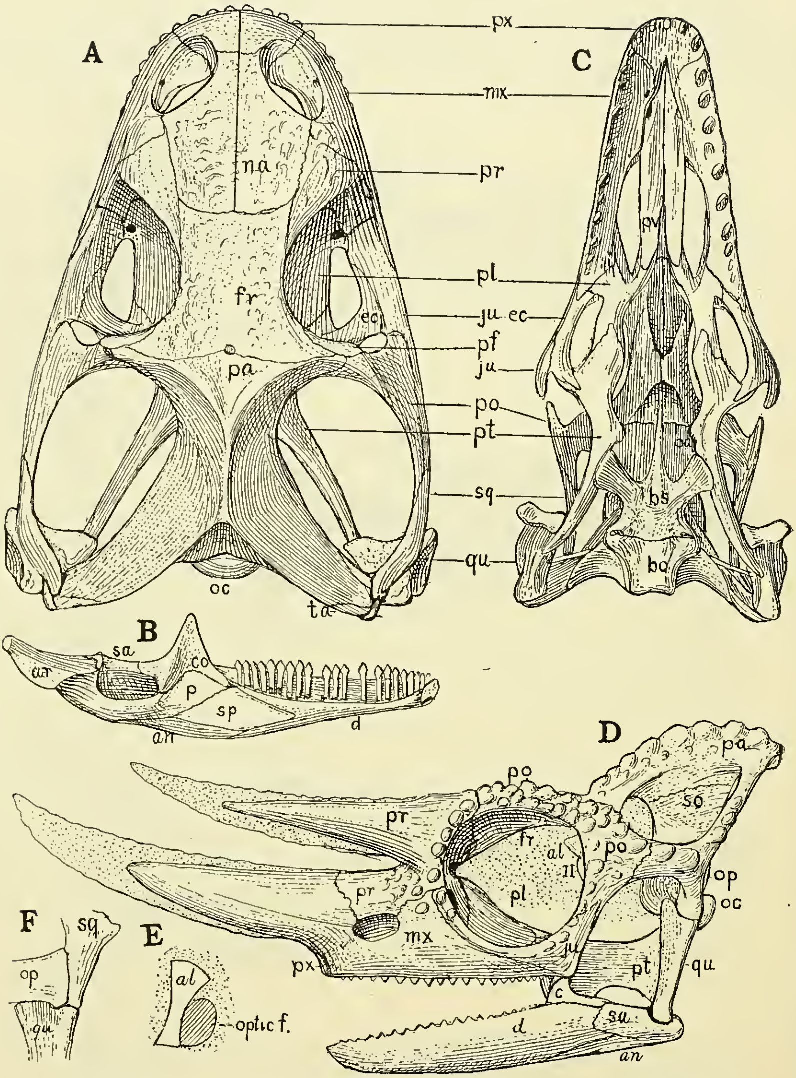

Fig. 55. Lacertilian skulls: A, *Conolophus*, from above. Natural size. B, the same, left mandible. Three fourths natural size. C, *Varanus*, from below. Natural size. D, E, F, Chameleon, from the side, the postoptic, and the upper end of quadrate.

The temporal fossa, normally (Fig. 55 A) bounded above by the parietal, below by the tabular, squamosal, and postorbital, may be wholly absent, as in the Amphisbaenidae (Fig. 56 A), completely roofed over by dermal bones, or obliterated by the union of the temporal arch with the parietal.

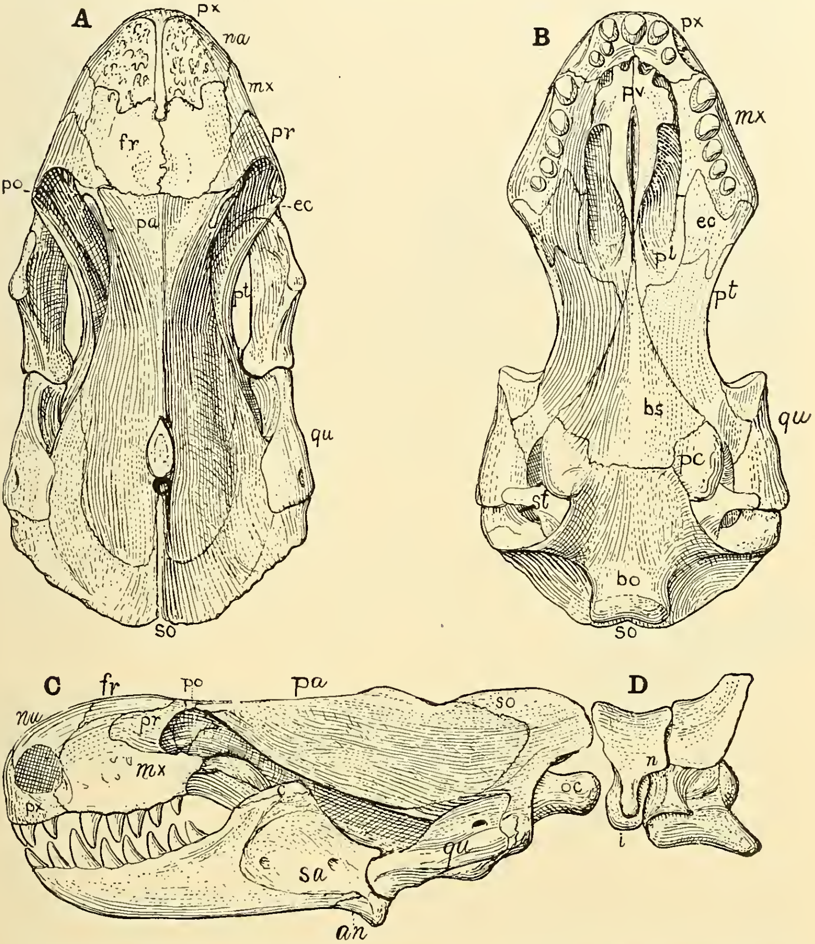

Fig. 56. Lacertilian skull: A, B, C, *Amphisbaena*, from above, below, and the side. Five halves natural size. D, side view of atlas and axis.

The premaxillae may be paired or fused; in the mosasaurs (Fig. 54 C) the united bone is fused with the nasals posteriorly, or the latter may be absent or vestigial. The lacrimals are always small, sometimes vestigial or absent. The prefrontals are always large, entering into the formation of the nares in the Varanidae and Mosasauridae (Fig. 54 A). They articulate with the palatine by a descending process. The nasals, usually paired, are sometimes fused with the premaxillae or with each other; they are separated from the nares in the Rhiptoglossa (Fig. 55 D). The postfrontals are rarely large in lizards and are often absent; when absent the postorbitals take their place, sometimes (Fig. 55 D) ending forward over the orbit to meet the prefrontal. The postfrontal and postorbital are not rarely found united by suture in the mosasaurs; usually, however, the two bones are indistinguishably fused or the postfrontal is absent. Posteriorly the postorbitals articulate as usual with the squamosal; below with the jugals. The postorbito-jugal and the postorbito-squamosal arch may be absent in various terrestrial lizards.

The jugal is a slender bone bordering the orbit below and extending forward to meet the lacrimal when that bone is present. It articulates with the maxilla, ectopterygoid, postorbital, and often with the tip of the squamosal. It may be vestigial or even entirely absent in lizards.

The maxilla articulates normally with the premaxilla, sometimes with the nasal and prefrontal, with the jugal, prevomer, palatine, ectopterygoid. It always bears a single row of acrodont or pleurodont, pointed or obtuse teeth.

On the palate the prevomers are paired or partially fused in the Rhiptoglossa. They articulate in front (Fig. 55 C) with the premaxillae, laterally usually with the maxillae, posteriorly with the palatines only. They very rarely bear small teeth.

The palatines (Fig. 55 C), unlike those of most other reptiles, are intercalated between the prevomers and pterygoids, articulating on the sides with the maxillae and more or less with the ectopterygoids. They sometimes bear teeth. The pterygoids have the normal articulations except that in front they articulate with the palatines only. The posterior palatine opening is usually large. They usually bear teeth.

The epipterygoid, a slender rod, is present so far as known in all lizards except the Amphisbaenia and Rhiptoglossa,[1] articulating in a

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[1] [Also Dibamidæ. — G. K. N.]

pit on the upper side of the pterygoids and extending to or toward the parietals.

The frontals usually and the parietals always are fused in the midline (Fig. 55 A).[1] The parietal foramen, usually present, is absent in many terrestrial lizards and in the Rhiptoglossa. The frontals and parietals may be either paired or unpaired. The frontals in the Varanidae, Helodermatidae, and some others have descending processes of the frontals which meet in the middle below, enclosing a rhinencephalic chamber, very much like the primitive one of the early reptiles.

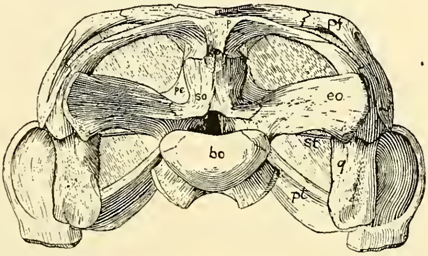

FIG. 57. *Platecarpus*, occipital view. *bo*, basioccipital; *eo*, exoccipital; *pf*, postfrontal; *st*, stapes; *pt*, pterygoid; *q*, quadrate.

The brain-case of lizards, as of other reptiles, is formed by the supraoccipital, exoccipitals, paroccipitals, basioccipital, basisphenoid, proötics, and postoptics, but is more or less membranous in front on the sides. The postoptics (Fig. 55 D, *al*) are small ossifications in the wall membrane, usually lost in maceration. In the Amphisbaenia (Fig. 56 C) and Mosasauria the sides of the parietals are partially decurved, forming incomplete cerebral walls, but they do not reach, as in the snakes (Fig. 59 B), to the basisphenoid.

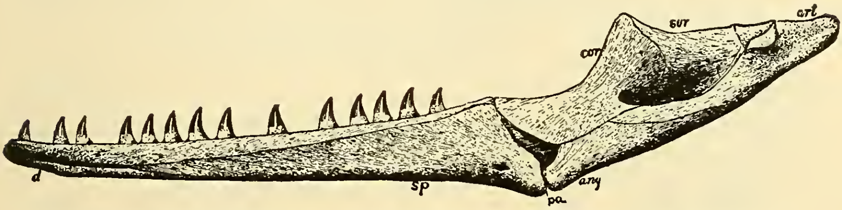

FIG. 58. Mosasaur mandible: *Clidastes*, inner side of right mandible. *ang*, angular; *art*, articular; *cor*, coronoid; *pa*, prearticular; *sur*, surangular.

The mandibles (Figs. 55 B, 58) are composed of the dentary coronoid, surangular, articular, angular, and splenial, with a long fused prearticular, which in the mosasaurs is more or less ensheathed by the union of the coronoid and angular, strengthening the peculiar

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[1] [Some geckos have them separate. — G. K. N.]

joint between the angular and splenial; a similar joint, though less well developed, is found in the monitor lizards. The mandibles are usually united in front by suture but are ligamentously connected in the mosasaurs and some land lizards.

As is seen, there are many variations in the skull of the lizards, more than in many other groups of reptiles called orders.

Ophidia or Serpentes

(Figs. 59 A–E)

The skull of snakes differs from that of lizards, especially in the complete closure of the brain cavity in front by descending plates from the parietals and frontals, the former always meeting the basisphenoid below, the latter sometimes interrupted by the coalesced optic foramina; in the constant absence of the postoptics, epipterygoids, and squamosals, the quadrate articulates proximally with the tabular only, which may also be absent. The parietals are always fused; there is no parietal foramen. There is no temporal arch, and, rarely, no ectopterygoid. The premaxillae are small and often edentulous, the maxillae rarely edentulous. The pterygoids and palatines usually bear long teeth. The postorbitals may meet the maxillae below, and there is no jugal.

The vipers (Fig. 59 E) have but one functional tooth attached to the maxilla. It is hollow, with an opening at its base and another near its apex for the passage of venom. Only the dentary is freely articulated in the mandible, the posterior bones closely fused; the two mandibles are usually united in front by ligament only. There is no ossified interorbital septum, and the proötics are largely exposed on the side of the skull.

The mandible of Ophidia has the primitive structure, except that the coronoid appears to be absent or fused, the bone usually so called being clearly the prearticular. The long splenial, as usual in reptiles with a long median symphysis of the mandibles, enters into the symphysis.

The conical teeth of the premaxillae, maxillae, and dentaries primitively were inserted in sockets, but in the more specialized types are rather loosely lodged in grooves.

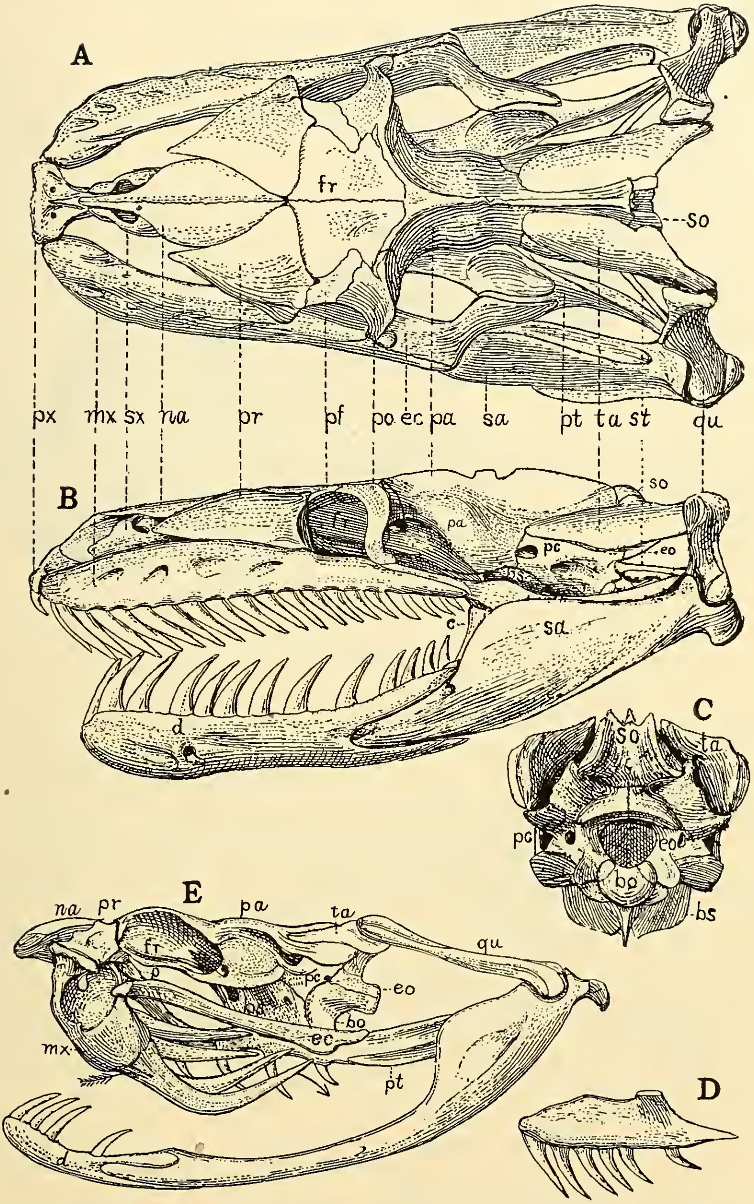

Fig. 59. Ophidian skulls: A, B, C, D, *Python*, from above, and from the side, occiput, and palatine bone with teeth. Natural size. E, *Crotalus*, from the side. Natural size.

THE SKULL OF THE RHYNCHOCEPHALIA

(Figs. 60–63)

[No manuscript. Some skull characters are noted on pages 20, 21, 25, 213, 279.]

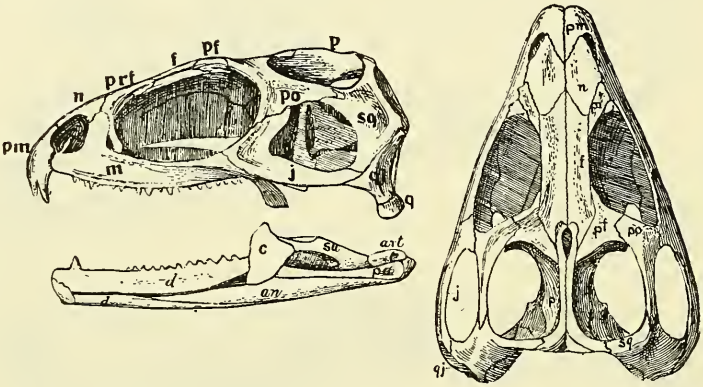

FIG. 60. Rhynchocephalian skull: *Sphenodon* (Tuatera), from the side and above. *pm*, premaxilla; *n*, nasal; *prf*, prefrontal; *f*, frontal; *pf*, postfrontal; *p*, parietal; *po*, postorbital; *sq*, squamosal; *m*, maxilla; *j*, jugal; *qj*, quadratojugal; *q*, quadrate; *c*, coronoid; *sa*, surangular; *art*, articular; *pa*, prearticular; *d*, dentary; *an*, angular.

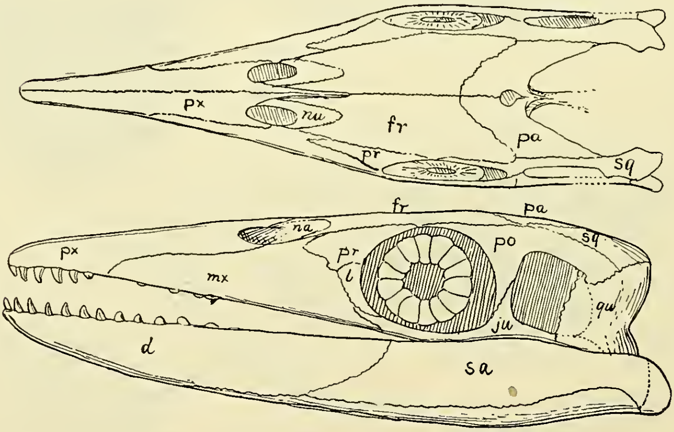

FIG. 61. Thalattosaur skull: *Thalattosaurus*, from above and from the side. After Merriam. One eighth natural size.

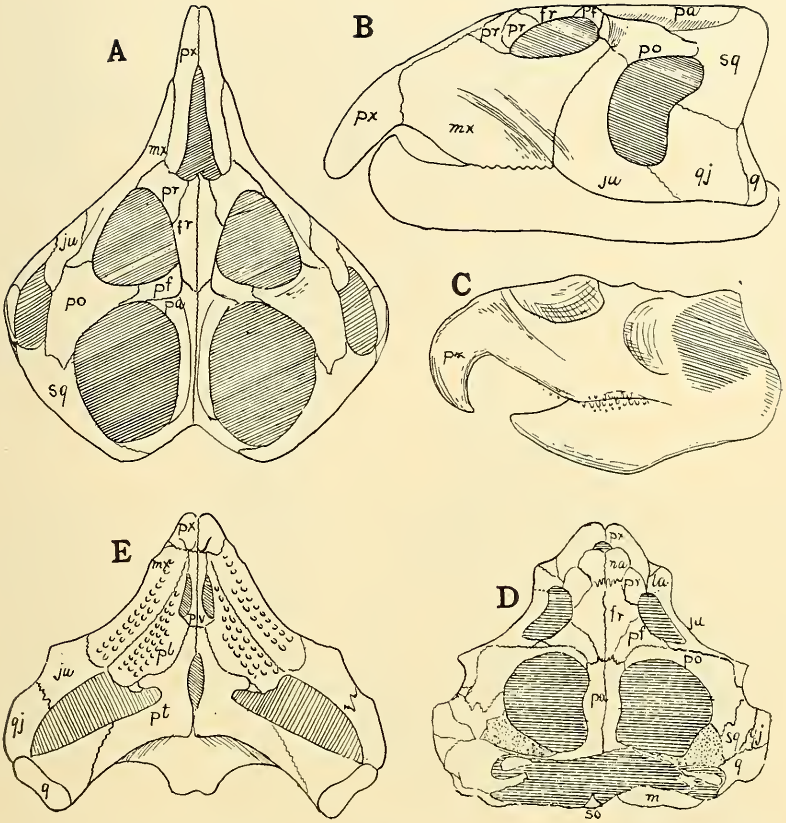

Fig. 62. Rhynchosaur skulls: A, B, *Stenometopon*, from above and from the side. After Boulenger. One fourth natural size. C, *Hyperodapedon*, from the side. After Huxley. D, the same, from above. After Burckhardt. E, from below. After Boulenger. One fourth natural size.

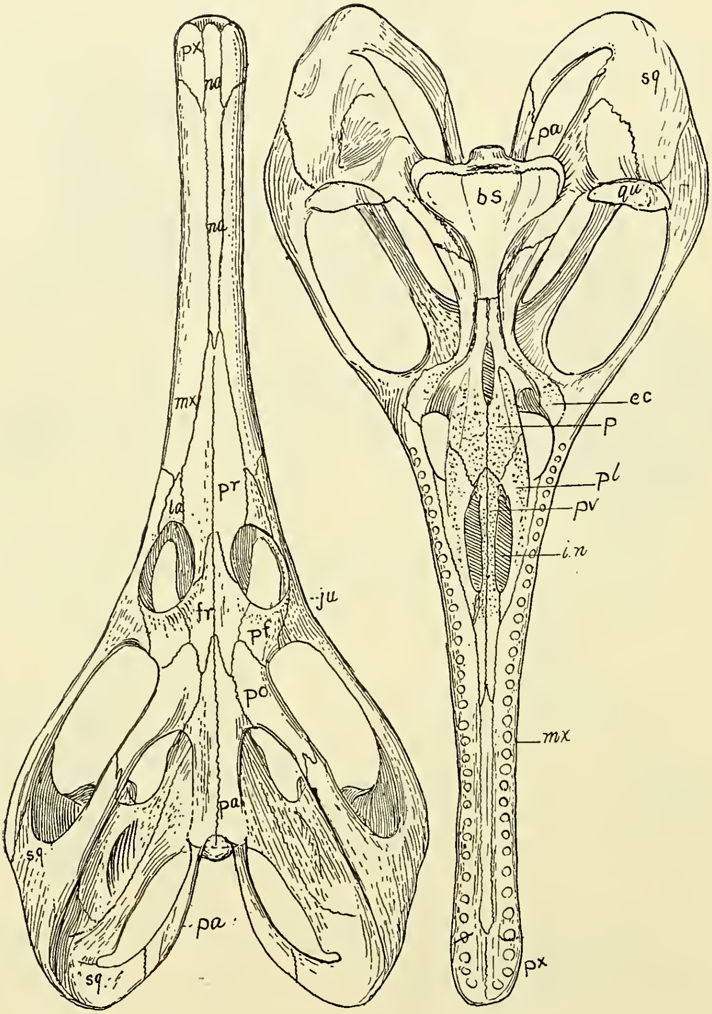

Fig. 63. Choristoderan skull: *Champsosaurus*, from above and from below. After Brown. One half natural size.

THE SKULL OF THE PSEUDOSUCHIA

(Fig. 65 A–E)

The skull of the typical Pseudosuchia is very much like that of the Pelycosimia (Fig. 64), in structure. All the bones of the skull roof are present except the dermosupraoccipital, tabular, and supratemporal; the lacrimal is small; there is no parietal foramen; and the palate bones have the primitive relations. Other forms, however, referred to this group provisionally, have both the dermosupraoccipital and tabular (*Youngina*, Fig. 64 C), and teeth on the prevomers and pterygoids (*Proterosuchus*). The upper and lateral temporal openings, a large antorbital vacuity and one in the mandible, are like those of the Parasuchia. The antorbital foramen is large, as are also the orbits. The supratemporal foramen is large and never posterior in position.

THE SKULL OF THE PELYCOSIMIA

(Fig. 64)

The skull of the Pelycosimia differs from that of the Phytosauria chiefly in the position of the external and internal nostrils near the extremity of the face, and at a considerable distance in front both of the orbits and antorbital openings. The face is short in front of the nostrils. There is also no respiratory channel back of the internal nostrils, so characteristic of the phytosaurs. The skull is markedly carnivorous in type.

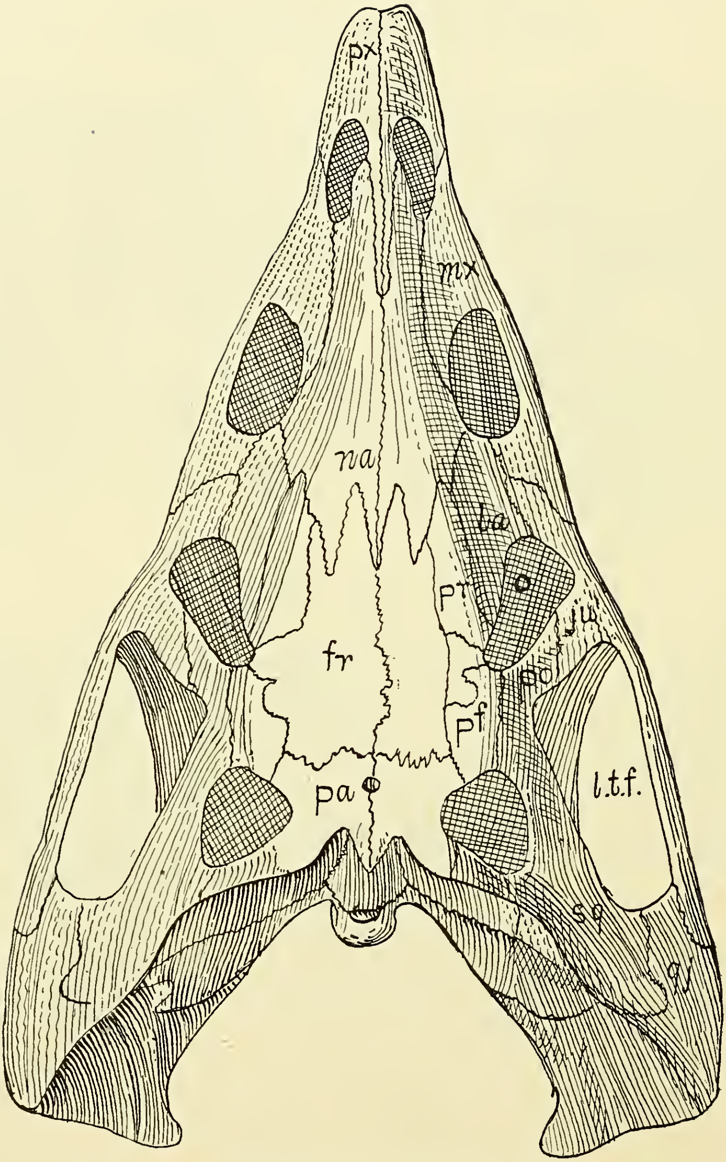

Fig. 64. Pelycosimian skull: *Erythrosuchus*, from above. After von Huene. One sixth natural size.

The Skull of the Phytosauria

(Figs. 65, 66, 67)

The skull of the Phytosauria is nearly uniform in general structure, characterized especially by the elongated face and posterior location of the external nostrils. No bones are fused in the midline, and none, save the primitive dermosupraoccipital, tabulars, and supratemporals are missing. The paroccipitals, as usual, are firmly fused with the exoccipitals. There is no parietal foramen. The supratemporal openings are more or less depressed below the level of the parietals but retain their primitive boundaries. The well-developed quadratojugals enter into the formation of the lateral temporal openings posteriorly. There is a primitive quadrate foramen between the quadratojugal and the quadrate. The stapes is slender. There is a large antorbital foramen bounded by the maxilla, nasal, lacrimal, and jugal.

The greatly elongated face is composed chiefly of the premaxillae, which extend back to the anterior ends of the nares, with the septomaxillae intervening, in the middle. The nostrils are surrounded by the large nasals and are elevated to or above the superior plane of the skull.

The bones of the palate retain their primitive relations, and there are small posterior palatine vacuities, larger in the more primitive forms. The pterygoids meet broadly in the median line, forming the roof of a deep respiratory channel between the heavy, underarching palatines, in some almost forming an incipient secondary palate, in the phytosaurs, as in the crocodiles, doubtless caused by the large flat tongue. The interpterygoidal opening and parasphenoid are small.

The elongate prearticular of the mandible is fused with the articular. As usual in slender-jawed reptiles with a long symphysis, the splenial participates in it, an acquired character. The condition of the coronoid is not yet definitely determined, but it is doubtless present, though small. A large foramen, so generally characteristic of the Archosauria, is constant in the outer wall of the mandible between the surangular, angular, and dentary.

The teeth are numerous, set in deep sockets and confined, as in other archosaurians, to the premaxillae, maxillae, and dentaries,

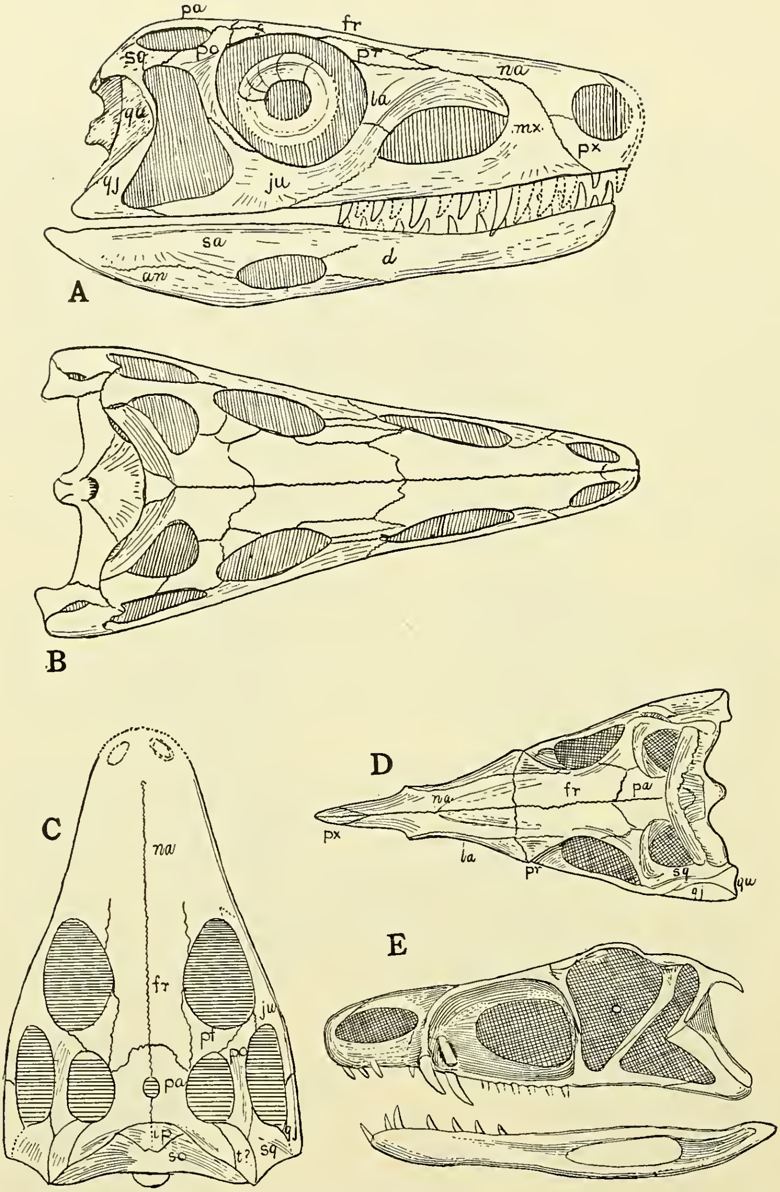

Fig. 65. Pseudosuchian skulls: A, B, *Euparkeria*, from the side and from above. After Broom. Five sixths natural size. C, *Youngina*, from above. After Broom. Three halves natural size. D, E, *Ornithosuchus*, from above and from the side. After Boulenger. One half natural size.

either cylindrical throughout or partly or chiefly flattened and denticulated. The first two or three teeth on each side, especially above, are cylindrical and much elongated. The dentulous portion of the premaxillae is long, with twenty or more teeth on each side.

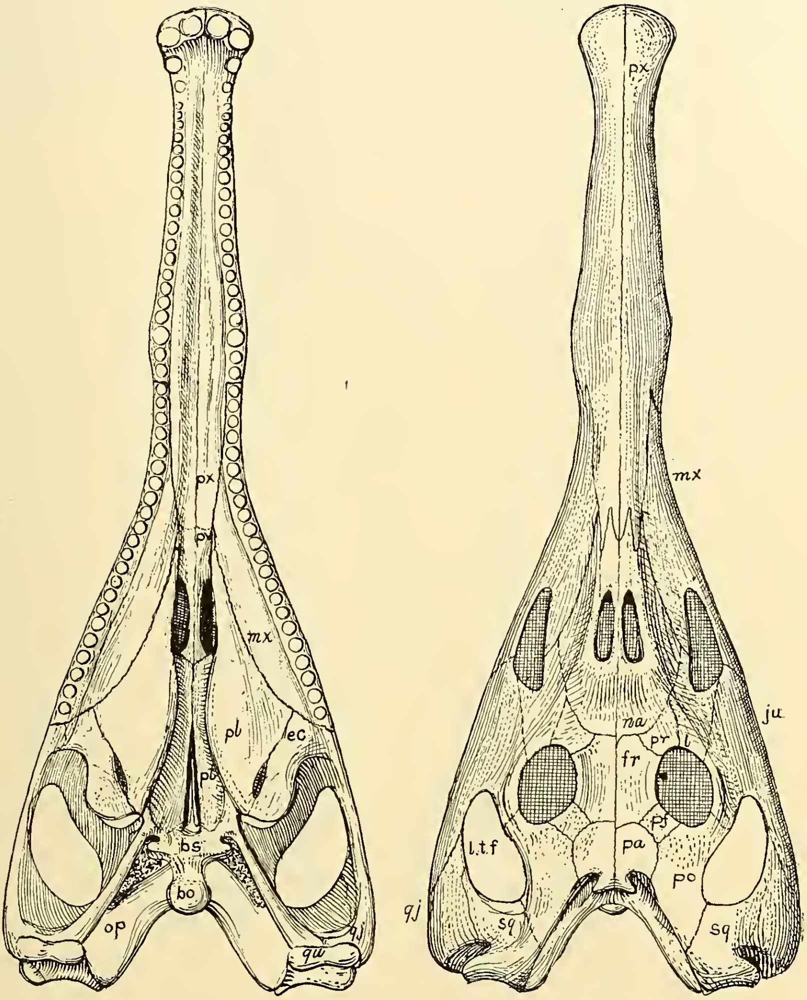

FIG. 66. Phytosaur skull: *Machaeroprosopus*, from above and from below.

The chief differences in the skull structure of the various members of the order are found in the relative position of the external nares,

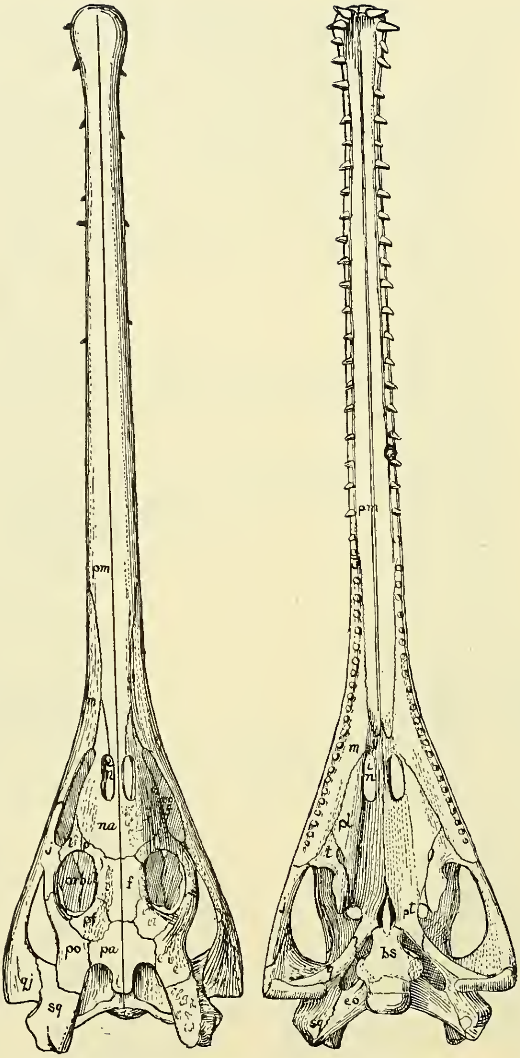

FIG. 67. Phytosaur skull: *Mystriosuchus*. *pm*, premaxilla; *m*, maxilla; *na*, nasal; *f*, frontal; *p*, prefrontal; *l*, lacrimal; *pf*, postfrontal; *po*, postorbital; *pa*, parietal; *sq*, squamosal; *qj*, quadratojugal; *pl*, palatine; *t*, transverse; *in*, internal nares; *en*, external nares; *pt*, pterygoid; *bs*, basisphenoid; *eo*, exoccipital. After McGregor.

the extent of the elevated facial carina in front of the nares, and the shape of the teeth, more slender and cylindrical in those with slender jaws, more flattened and compressed in those with a compressed and elevated face, doubtless because of the more dominant fish-eating habits of the former, the more general carnivorous habits of the latter.

The Skull of the Crocodilia

(Figs. 68, 69)

The skull of the Crocodilia invariably lacks the postfrontals, supratemporals, epipterygoids, tabulars, septomaxillae, and parietal foramen, and the paroccipital is fused with the exoccipital. The parietals and frontals are fused in the midline. The supraoccipital is a triangular bone, excluded from the foramen magnum. The quadratojugals take part in the formation of the lateral temporal opening, narrow bones between the quadrates and jugals extending forward to meet the postorbitals. The quadrates are firmly wedged in between the quadratojugals, postorbitals, parietals, exoparoccipitals, postoptics, squamosals, proötics, basisphenoid, and pterygoids, an extensive connection. The supratemporal openings are large in the early forms, small in the later ones, and almost [or entirely] obsolete in some. The lateral temporal opening is separated in the teleosaurs from the orbits by an unmodified postorbital bar immediately below the skin. In the broader-faced amphicoelian and in all the procoelian types it is a cylindrical bar with a considerable space between it and the skin. The postoptics (Fig. 69 D, *as*) are fully ossified, extending from the basisphenoid to the frontals. There is no ossified interorbital septum. An antorbital vacuity is often present in the teleosaurs, but only rarely has been found in the early procoelian types. The nasals may or may not separate the external nares, connecting with the premaxillae; they are divided by a cartilaginous septum in life. The nares are always at the extremity of the face, no matter how long and slender it may be. There is a eustachian canal connecting with the otic sinuses, in the median line between the basioccipital and basisphenoid.

The most important modifications of the crocodilian skull are found in the palate, distinguishing these reptiles from all others. The maxillae meet broadly in the middle line, excluding the prevomers

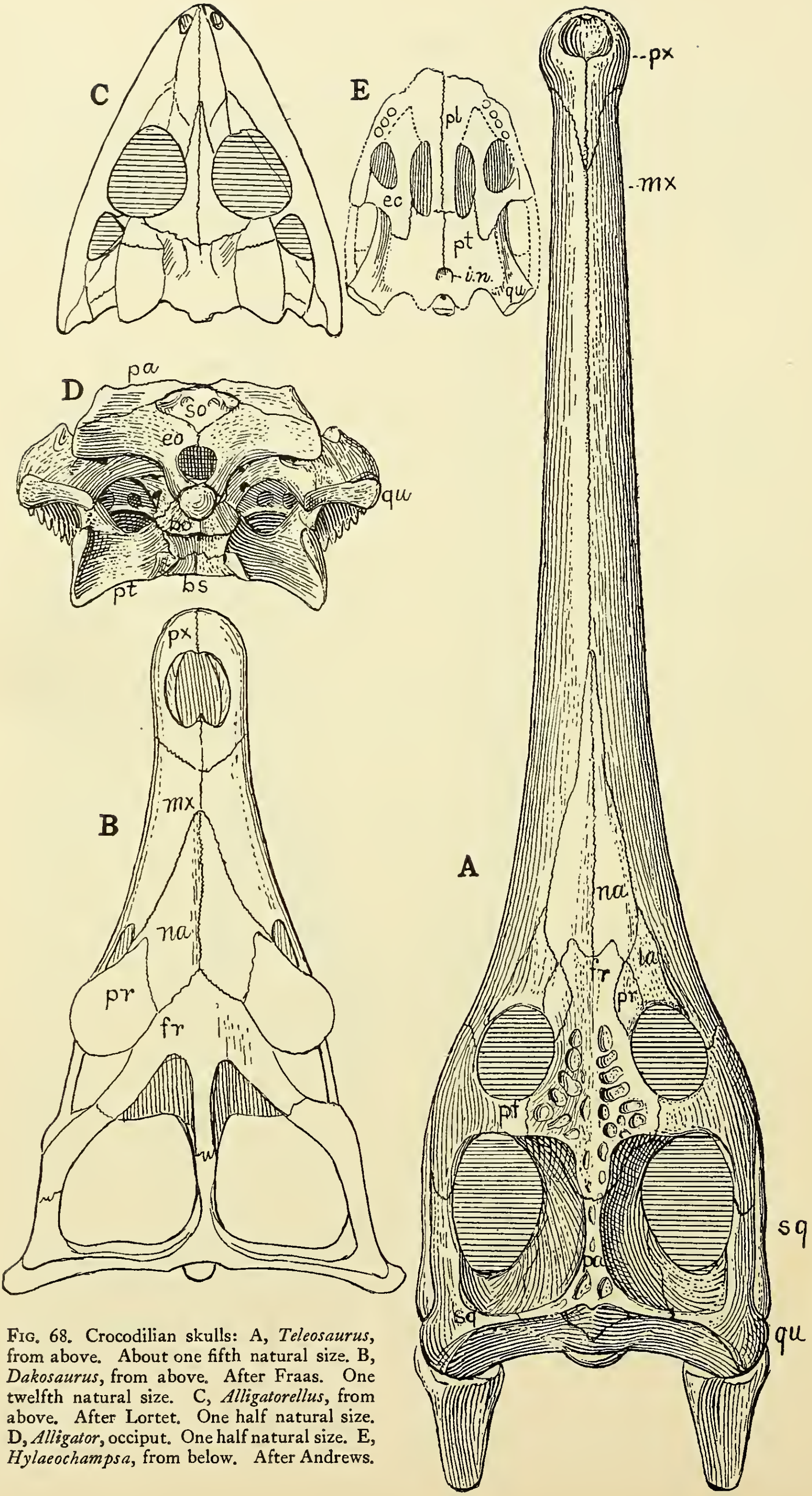

Fig. 68. Crocodilian skulls: A, *Teleosaurus*, from above. About one fifth natural size. B, *Dakosaurus*, from above. After Fraas. One twelfth natural size. C, *Alligatorellus*, from above. After Lortet. One half natural size. D, *Alligator*, occiput. One half natural size. E, *Hylaeochampsa*, from below. After Andrews.

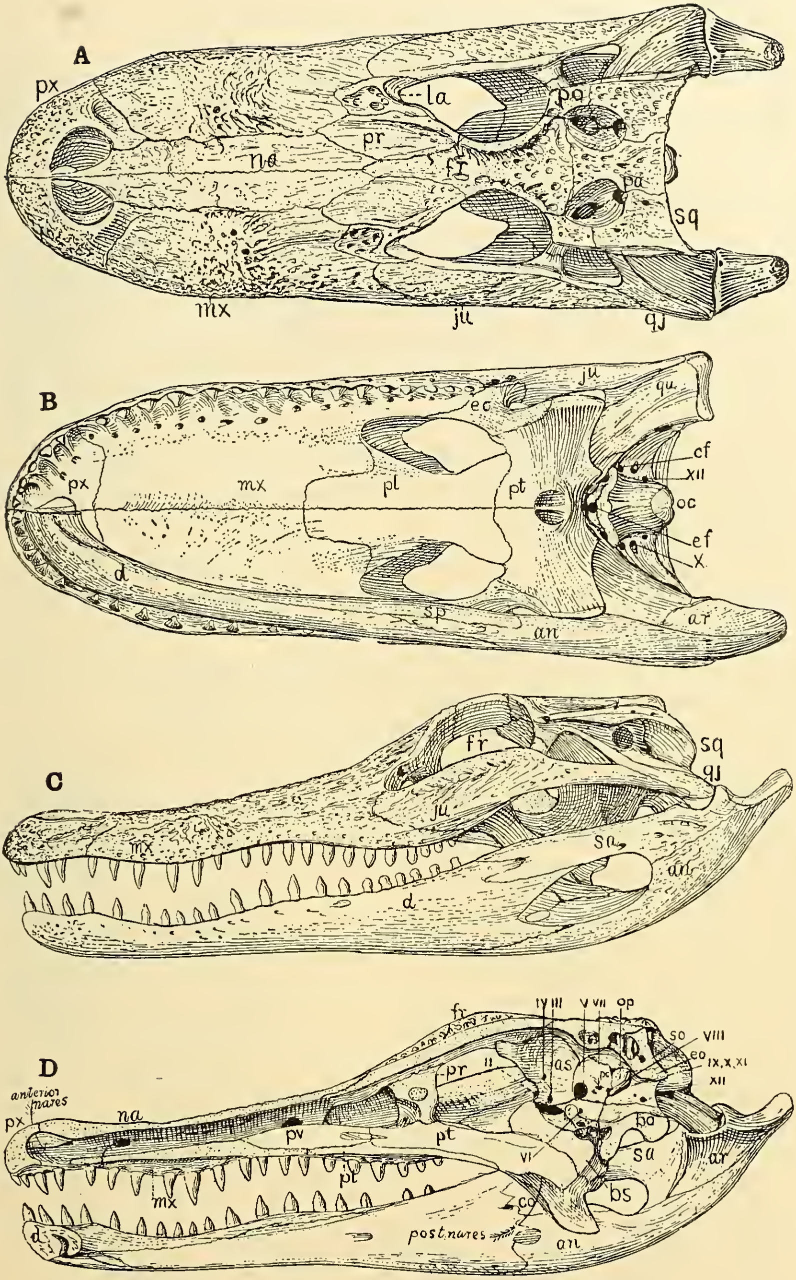

Fig. 69. Alligator skull: one half natural size.

from the palatal surface, except rarely just back of the premaxillae in the caimans, or in front of the pterygoids in the tomistomids. The palatines also meet in the middle line in all, sending up processes for articulation with the postorbital, and forming the floor of the respiratory canals. The prevomers form a pair of tubes above the maxillae and palatines, articulating posteriorly with a suprapalatal prolongation of the pterygoids; they are separate as usual, and do not often appear on the palatal surface. The pterygoids also meet in the middle line, in all procoelian forms completely surrounding the internal nares, which may or may not be divided by a median partition, meeting below the nasal tubes in front of them. In the early teleosaurs these openings were at the posterior border of the palatines. In the goniophilids the openings are surrounded by both palatines and pterygoids.

The pterygoids articulate posteriorly and externally with the postoptics by a narrow pillar, possibly representing the epipterygoids. There are large posterior palatine vacuities at the sides of the palatines, and, in *Hylaeochampsa*, an additional opening in the palate between the ectopterygoid and maxilla.

In the mandible (Fig. 69 D) the splenials meet in a median symphysis in slender jaws. The prearticular is apparently wholly absent, or fused with the angular. There is a large mandibular foramen between the angular, surangular, and dentary on the outer side, absent in the Thalattosuchia.

THE SKULL OF THE DINOSAURS (SAURISCHIA, ORNITHISCHIA)

(Fig. 70)

[No manuscript. Skull characters noted, pages 17, 28, 32, 214, 291–296.]

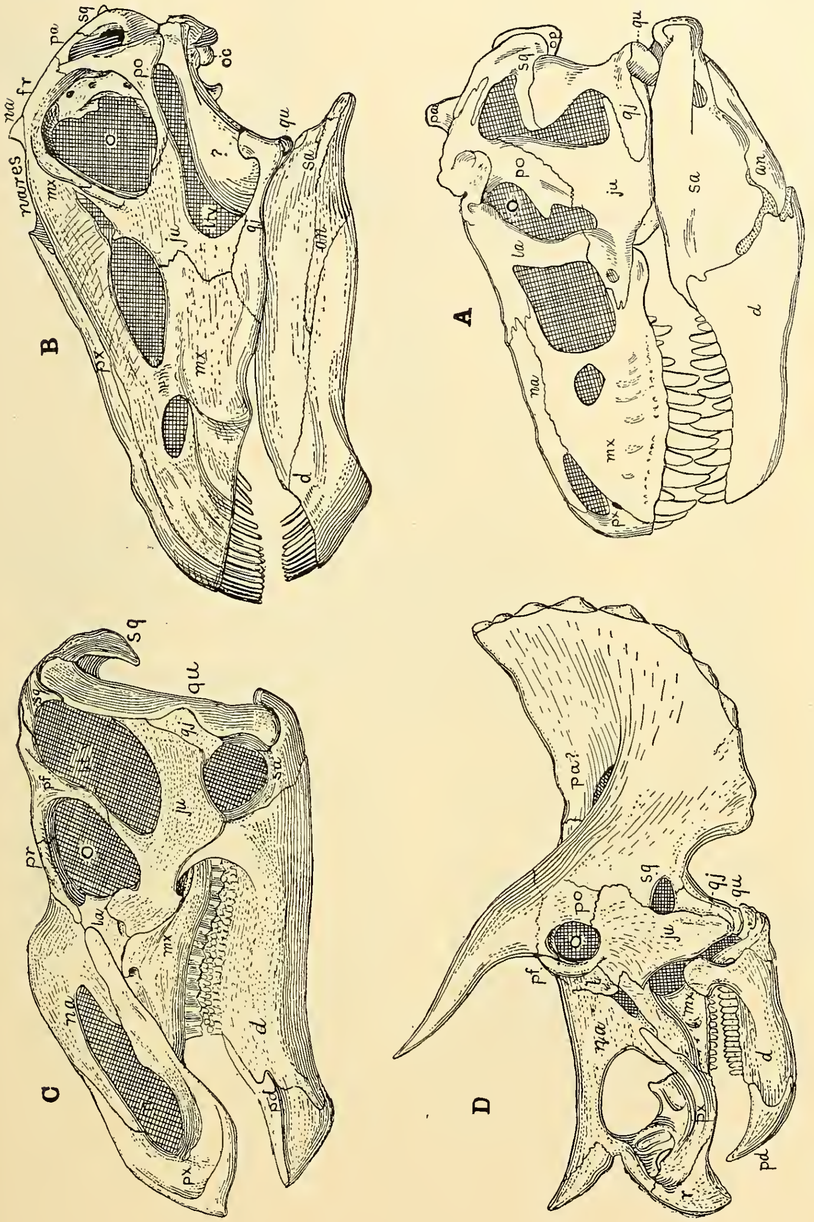

FIG. 70. Dinosaur skulls: A, *Tyrannosaurus*. After Osborn. One eighteenth natural size. B, *Diplodocus*. After Holland. One sixth natural size. C, *Kritosaurus*. After Lambe. One twelfth natural size. D, *Triceratops*. After Marsh. One twelfth natural size.

THE SKULL OF THE PTEROSAURIA

(Figs. 71, 72)

[No manuscript. Skull characters noted, pages 11, 14, 17, 19, 21, 28, 214, 296–298.]

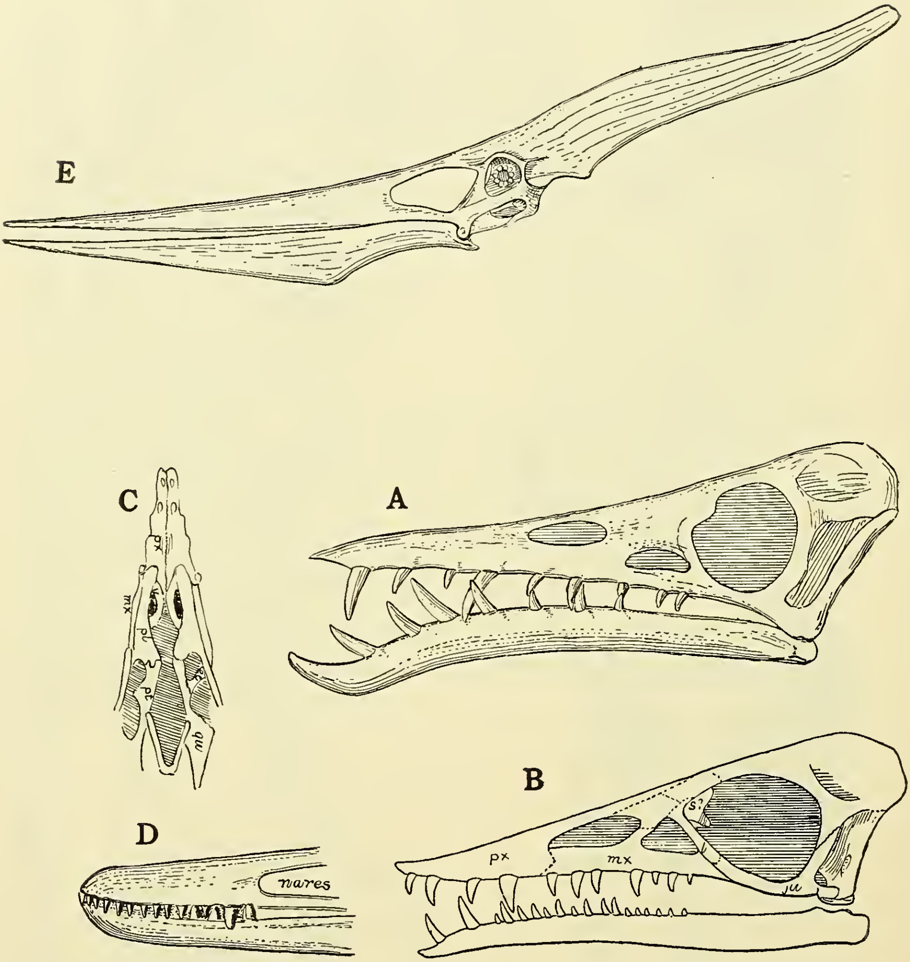

FIG. 71. Pterosaur skulls: A, *Rhamphorhynchus*, from the side. B, *Campylognathus*, from the side. After Plieninger. One half natural size. C, *Rhamphorhynchus*, front part of palate. After von Huene. One half natural size. D, *Ornithodesmus*, end of beak. After Hooley. One fourth natural size. E, *Pteranodon*. About one fourteenth natural size

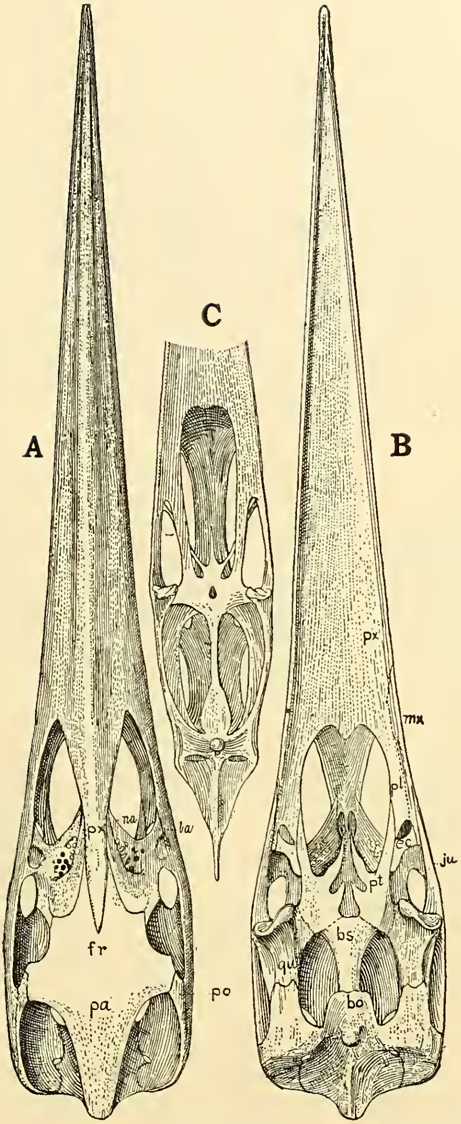

Fig. 72. Pterosaur skulls: A, *Nyctosaurus*, from above; B, the same from below. About five eighths natural size. C, *Pteranodon*, from below, after Eaton. About one fourth natural size.

CHAPTER II

THE VERTEBRAE

The spinal column or backbone of reptiles, as of all other air-breathing vertebrates, is made up of a variable number of separate segments called *vertebrae.* A vertebra (Fig. 73 B) is composed of a body, or *centrum*, and an arch, or *neurapophysis*, each ossifying separately and uniting at variable times, the neurocentral sutures more persistent than in most mammals, young or aquatic reptiles always (Fig. 87 B, C), adult land reptiles often showing them.[1]

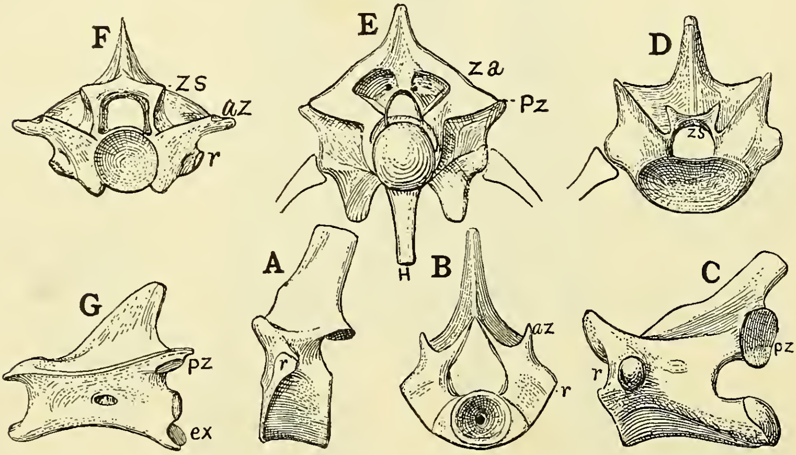

Fig. 73. Anterior dorsal and cervical vertebrae: A, B, *Sphenodon* (Rhynchocephalia), anterior dorsal from the side and front; C, D, *Iguana* (Lacertilia), anterior dorsal from the side and front; E, F, Ophidia, anterior dorsal from behind and in front; G, *Pteranodon* (Pterosauria), cervical from the side, after Eaton.

Projections from the vertebrae, called processes or apophyses, serve for the attachment of muscles or ligaments, for articulation with adjacent vertebrae, or for the support of ribs, and are often characteristically different in different reptiles. Two pairs of processes springing from the arch, one in front and one behind, are

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[1] [For the modern embryological viewpoint of the composition of reptilian vertebrae see Schauinsland, in Hertwig's *Handbuch der Entwickelungsgeschichte der Wirbeltieren*, etc., 1906. — Ed.]

known as *zygapophyses*. The pair in front, the *prezygapophyses* (*az*), always has the flat or concave articular surface directed upward, that is, toward the dorsal side, or upward and inward; while that of the posterior pair, the *postzygapophyses* (*pz*), is turned downward, that is, toward the ventral side, or downward and outward. The zygapophyses may be obsolete or even absent in the posterior part of the column of aquatic reptiles.

The vertebrae of all snakes, some lizards, and some mosasaurs, have additional articulations, or rather, extensions of the zygapophysial articulations about their inner ends, known as *zygosphenes* (Fig. 73 D, F) and *zygantra* (Fig. 73 E). The zygosphene is a wedge-shaped process at the anterior end of the arch, above and between the zygapophyses, which fits into a corresponding cavity, the zygantrum, at the posterior end of the next preceding vertebra. Zygosphenes and zygantra strengthen the articulations, though restricting vertical flexure. They occur, as is seen, only in reptiles with a long, flexible vertebral column,[1] and are absent in those mosasaurs in which the column is less elongate and flexuous. Zygosphenes are also known to occur in certain aquatic Stegocephalia with long, slender vertebral columns.

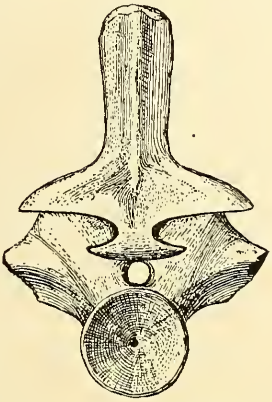

Fig. 74. Dorsal vertebra: *Diadectes* (Cotylosauria) from behind, showing diapophyses, postzygapophyses, and hyposphene.

In certain other reptiles this arrangement is reversed, in that the wedge-shaped median process, called *hyposphene* (Fig. 74) is below and between the inner ends of the postzygapophyses, fitting into a cavity, the *hypantrum*, at the front end of the next succeeding vertebra. Hyposphenes and hypantra are especially characteristic of certain cotylosaurs, placodonts, and dinosaurs, where they were first recognized and described.

The later pterodactyls have another pair of articulating processes, called *exapophyses* (Fig. 73 G), at each end of the cervical vertebrae on the ventral side, their articulating surfaces facing in opposite directions to those of the zygapophyses above them. They strengthen the articulations, but limit torsion, and are substitutes

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[1] [Exceptions to this rule occur in recent lizards. — Ed.]

for the peculiar saddle-shaped articulations of the cervical vertebrae of birds.

On the dorsal side of the arch, in the middle, is the spine or *neurapophysis*, of extremely variable size and length, sometimes rudimentary, sometimes very long. As a rule, the spines are longest and stoutest at the beginning of the dorsal series, for the attachment of muscles and ligaments controlling the neck and head. The spines are always short in legless or slender crawling reptiles (Fig. 73 D–F) and are never long or slender in aquatic reptiles, in front at least. The spines of most sauropod dinosaurs in front of the sacrum are broadly divided, V-shaped, doubtless for the lodgment of stout muscles and ligaments used in controlling the long neck.

A longer or shorter process on the sides of the arch for the support in part or wholly of the ribs is known as a *diapophysis* (Fig. 73 B, 75). A like process or facet on the side of the centrum anteriorly for articulation of the head of the rib is called a *parapophysis* (Fig. 73 F). Either is commonly called a transverse process, and the same term is often applied to a like process on the sides of the caudal vertebrae, of which probably the anterior ones, at least, in all cases are merely coössified ribs.

A process, paired or single, on the under side of the vertebrae, is properly called a *hypapophysis* (Figs. 73 E, 75 A). Hypapophyses are characteristic of snakes, often as far back as the tail; in some instances they are developed to serve as a sort of masticatory apparatus for the crushing of eggs in the stomach.[1] They also often occur on the cervical vertebrae of lizards, crocodiles, and turtles. Paired hypapophyses (*lymphapophyses*) are characteristic of the caudal vertebrae of snakes, where they replace the absent chevrons.[2]

When the ends of the centra are concave, as they are in all early reptiles, nearly all fishes, and most amphibians, the vertebrae are known as *amphicoelous* (Fig. 74). If the cavities are deeply concave, communicating with each other through the centrum, the vertebrae are called *notochordal*; that is, the notochord was continuous in life. And this was the primitive condition found in the Cotylosauria (Fig.

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[1] [The eggs are cut, not crushed, and in the oesophagus, not the stomach (Fitzsimons). — Ed.]

[2] [The distinctions between lymphapophyses and hypapophyses break down in the embryology of modern lizards. — Ed.]

74) and Triassic Ichthyosauria and continuous to the present time in the living gecko lizards. More usually, since middle Permian times the cavities are shallow, bowl- or saucer-like, or almost flat (*platycoelous*) or even quite flat (*amphiplatyan*).

Until after the middle Jurassic times the vertebrae of all known reptiles were amphicoelous. A ball-and-socket joint appears at that time, so far as we yet know, with the concavity in front, the ball or convexity behind. This kind of vertebra, called *procoelous*, gradually became the prevailing one, all reptiles since early Eocene times, except the geckos among lizards, the turtles, and *Sphenodon*, possessing them. Procoelous vertebrae appeared among the Crocodilia in early Cretaceous times (*Hylaeochampsa*), amphicoelian types, however, persisting until early Eocene (*Dyrosaurus*). The vertebrae of all known snakes (Fig. 73 E, F), dating from Lower Cretaceous, are procoelous, as are also the presacral vertebrae of the Pterosauria, dating possibly from early Jurassic times. The caudal vertebrae of some turtles are procoelous. Procoelous vertebrae, however, are not restricted to reptiles, some modern frogs having them. They doubtless arose in terrrestrial crawling reptiles with a flexuous column, and it was doubtless from such ancestors that the aigialosaurs and mosasaurs, aquatic reptiles, inherited them. Possibly the pterodactyls acquired the ball-and-socket articulations after the attainment of flight.

The presacral vertebrae of the sauropod, as also the cervical vertebrae of many theropod and orthopod dinosaurs, have the convexity of the centrum at the front end, just the reverse of procoelous. Such vertebrae have been called *opisthocoelous*, and are doubtfully known in other reptiles, save the cervicals and caudals of certain turtles. They do occur, however, in the cervical region of certain Triassic Stegocephalia, and in some modern fishes and many modern salamanders.

Most remarkable are the cervical vertebrae of the Chelonia. The earliest that we know had amphicoelous vertebrae throughout the column, but most others have an extraordinary combination of all types, amphicoelous, procoelous, opisthocoelous, plano-concave, plano-convex, and even biconvex, otherwise known in only the first caudal vertebra of the procoelian crocodiles. *Platypeltis* (=*Amyda*) *spinifera*, a living river-turtle, has opisthocoelous cervical vertebrae, and certain pleurodiral turtles have saddle-shaped articulations. In no other order of reptiles are the variations so great as in this.

The *pleurocoelous* (Fig. 75) presacral vertebrae of the sauropod dinosaurs are peculiar in having large cavities in the centra, separated by a median partition, with an oval or round orifice at each side. Not only is the centrum thus lightened in these dinosaurs, but the arch is curiously strengthened by plates and buttresses. Certain other South African reptiles (*Tamboeria*) also have pleurocoelous vertebrae. It is supposed that this hollowness and lightness of the cervical and dorsal vertebrae, correlated with the otherwise solid or cancellous skeleton, served to keep the body erect in water, their natural habitat in wading or swimming.

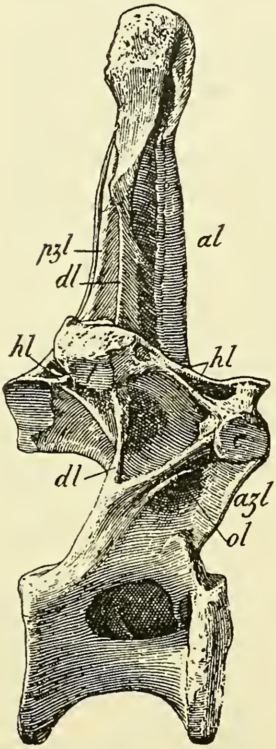

Fig. 75. Dorsal vertebra of *Diplodocus* (Saurischia). After Hatcher. One tenth natural size.

Except in the snakes and legless lizards, where but two regions are recognized, the caudal and precaudal, the spinal column of reptiles is divisible into cervical, dorsal, sacral, and caudal regions, and sometimes lumbar also, as in mammals. The cervical region is that in front of the shoulder-girdle, the dorsal that between the shoulder and hip girdles, the sacral that which supports the hip girdle, and the caudal that of the tail.

We may hardly venture to guess as to the primitive number of vertebrae in reptiles. We are quite sure that there has been an increase in number in some, a decrease in others. The land temnospondylous amphibians that we know have but one real cervical vertebra, the so-called atlas, twenty-two to twenty-five dorsals, one or two sacrals, and a short or moderately long tail. *Trimerorhachis*, an aquatic Lower Permian temnospondyl, has thirty-one precaudal vertebrae and no differentiated sacrals. The earliest reptile that we know, *Eosauravus*, subaquatic in habit, had at least twenty-four or twenty-five precaudals, two sacrals, and a long tail. In no embolomerous amphibian is the number of vertebrae known.

The numbers of presacral and sacral vertebrae in reptiles may be tabulated as follows:

	Presacral	Sacral
Cotylosauria	23–26	1–3
Chelonia	18	2–3
Theromorpha	23–27	2–3
Therapsida	25–28	2–7
Nothosauria	40–42	2
Plesiosauria	40–105	3–4
Proganosauria	29–34	2
Ichthyosauria	40–65	0
Sauranodon (Saphaeosaurus)	22–23	2
Kionocrania (Lacertilia)	22–74	0–2
Rhiptoglossa	16	2
Dolichosauria	29	2
Mosasauria	29–42	0
Rhynchocephalia	25	2
Rhynchosauria	23–24	2
Choristodera	23–26	2
Pseudosuchia	23–26	2
Phytosauria	26	2
Eusuchia	23–24	2
Thalattosuchia	25	2
Theropoda	23	2–5
Sauropoda	26	4–5
Stegosauria	27	3–4
Trachodontia	30–34	8–9
Iguanodontia	24–28	4–5
Ceratopsia	24	7

The earliest reptiles had functional ribs and a sacrum, and we may omit the very variable tail in our comparisons. The majority of terrestrial reptiles, it is seen, have between twenty-three and twenty-six presacral vertebrae. In all probability the earliest reptiles were lowland and crawling in habit, and it is legitimately presumable that they had not less than twenty-three nor more than twenty-six vertebrae in front of the sacrum, a single sacral, and not more than sixty caudals, the largest number found in any early reptile, or altogether between eighty and ninety vertebrae in the whole column, as against thirty-five in modern turtles and four hundred and fifty in some modern snakes. The smallest number of presacral vertebrae known in any reptile — sixteen — is recorded for *Brooksia*, a recent chameleon lizard.

Intercentra. The earliest reptiles probably all have a small or vestigial, more or less wedge-shaped bone intercalated between the adjacent ventral margins of the centra throughout the column, to which Professor Cope in 1878 gave the name *intercentrum* (Fig. 76 E). Intercentra had previously long been known as "intervertebral" or "subvertebral wedge-shaped bones," but their significance was ill understood. With the more complete ossification of the vertebral centra they began to disappear in the dorsal region, in early or middle Permian times, but have remained to modern times in the gecko lizards and in *Sphenodon.* They have persisted in nearly all reptiles in the tail as the *chevrons,* and more or less in the neck, having been entirely lost as simple intercentra only in the crocodiles and a few other reptiles. The intercentrum of the first vertebra has remained functional in all Amniota as the basal piece or "body" of the atlas.

Intercentra are characteristic of deeply amphicoelous or notochordal dorsal vertebrae, that is, in the more primitive vertebrae, and never occur in procoelian, amphicoelian, or opisthocoelian reptiles. They occur in many procoelous lizards throughout the neck, often in their normal places between the centra but frequently shifted forward on the preceding centrum, either loosely attached or coössified with an exogenous outgrowth, forming with it a functional hypapophysis. Where they occur between the centra they may be elongated into false hypapophyses. A similar condition is known in some Chelonia on the first two to four vertebrae, where they are usually paired. Double intercentra have also been observed in the anterior vertebrae of *Procolophon,* a cotylosaur, and in the young of certain plesiosaurs. In the Ichthyosauria, though the centra are deeply biconcave, only two to four intercentra have been observed. They have also been found in the anterior vertebrae of some plesiosaurs.

It is now universally believed that the undivided or *holospondylous* vertebrae of reptiles were evolved from divided or *temnospondylous* vertebrae of the Stegocephalia. It was Cope who first recognized the identity of the parts and his views are now generally accepted, though not by all.

Temnospondylous vertebrae are of two kinds, called by Cope *embolomerous* (Fig. 76 A–C) and *rhachitomous* (Fig. 76 D). The former are known in only a few amphibians, from the Mississippian, Pennsylvanian, and Lower Permian, but best in *Cricotus* (Fig. 76 A–C) from Illinois and Texas. Rhachitomous vertebrae are much more widely known in numerous forms from the Pennsylvanian and Permian of various parts of the world.

An embolomerous vertebra is composed of two subequal, notochordal disks, the anterior one the intercentrum, or *hypocentrum*, bearing the exogenous chevron in the tail; the posterior one the *pleurocentrum;* and the arch or *neurocentrum*, resting upon both the intercentrum and pleurocentrum, but chiefly the latter. The articular surface for the head or *capitulum* of the ribs is chiefly on the intercentrum; the surface for the articulation of the *tubercle* of the rib, on either the arch or diapophysis.

A rhachitomous vertebra (Fig. 76 D) differs in that the intercentrum or hypocentrum is more or less wedge-shaped, with its base on the ventral line, its apex not reaching the dorsal side; while the pleurocentra behind are paired, with the basal side above and their apices reaching the ventral line only narrowly or not at all. The neurocentrum, as in the embolomerous forms, is borne by all three bones, but chiefly by the pleurocentra. The head of the ribs articulates with the intercentrum, the tubercle with the diapophysis of the neurocentrum.

The earliest known amphibian vertebrae are embolomerous; rhachitomous and holospondylous vertebrae appearing later, so far as our present knowledge goes. And this is one of the reasons why it would seem that the embolomerous type is the more primitive, giving origin directly to the reptilian holospondylous type, as was first suggested by Cope; that the rhachitomous type was derived from it by the loss of the upper part of the intercentrum and the lower part of the pleurocentrum and the division of the latter into two lateral parts. This reversion of the pleurocentrum to a more primitive ontogenetic condition is the chief objection to this theory, nevertheless it is the more probable. We have seen that the more primitive phylogenetic condition of the intercentra persists longest in the neck and tail. In the caudal vertebrae of *Eryops* (Fig. 76 D), and probably other rhachitomous amphibians, there is an intermediate condition between the embolomerous and rhachitomous types, in which the single pleurocentrum is typically embolomerous, that is, disk-like and perforated for the notochord; while the intercentrum bearing its exogenous chevron is typically rhachitomous, in that it is wedge-shaped. And this very probably represents the real intermediate condition between the embolomerous and holospondylous vertebrae. Evidence that reptilian vertebrae arose in this way is also seen in the dorsal vertebrae of a young *Seymouria*, the most amphibian-like, otherwise, of all known reptiles (Fig. 76 E). The intercentrum is here remarkably large for a reptile, nearly half as long as the notochordal centrum or pleurocentrum. And it is also almost the condition found in the first vertebra of primitive reptiles, the atlas (Fig. 79), as will be shown in the discussion of that bone. Additional evidence is furnished by the fact that while truly embolomerous vertebrae occur in fishes, in the modern *Amia*, for instance, real rhachitomous vertebrae

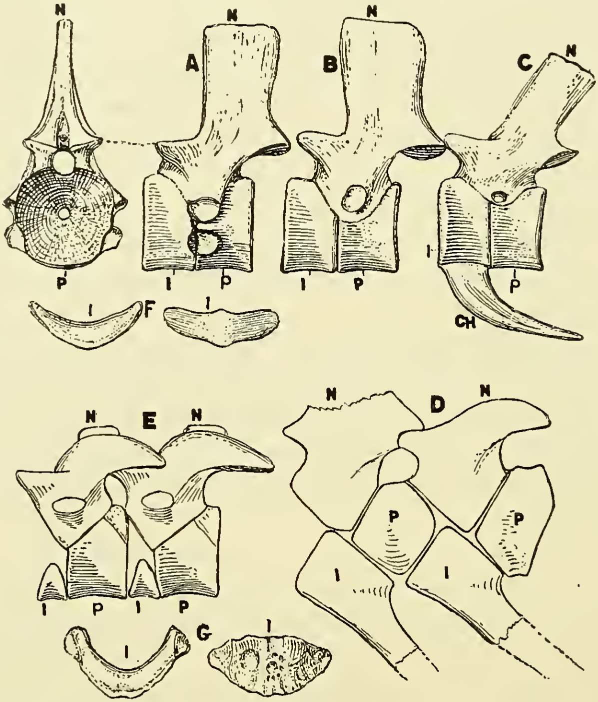

Fig. 76. Vertebrae: A, B, C, *Cricotus* (Temnospondyli), dorsal, basal caudal, and median caudal, from the side and front. D, *Eryops* (Temnospondyli), caudal, from the side. E, *Seymouria* (Cotylosauria), median dorsal, from the side. F, *Dimetrodon* (Pelycosauria), dorsal intercentrum from behind and below. G, *Trimerorhachis* (Temnospondyli), intercentrum from side and below.

are known only among amphibians. Certain ancient fishes (*Eurycormus*), it is true, with dorsal embolomerous vertebrae, have in the tail pseudo-rhachitomous vertebrae, composed of two half-disks, the one with its base below, the intercentrum, the other with it above, the undivided pleurocentrum.

The evolution, then, of the holospondylous reptilian vertebra from the temnospondylous amphibian vertebra seems clear: by the simple increase in size of the notochordal centrum and the progressive decrease of the intercentrum to a wedge-shaped, subvertebral bone, and its final loss everywhere in the column save in the atlas and chevrons of the tail; and thus the term hypocentrum becomes purely a synonym of the earlier term intercentrum. The retrogression of the disk-like pleurocentrum into the paired pleurocentra of the Rhachitomi, is paralleled by the separation of the primitively single intercentrum into pairs, observed in *Procolophon*, many turtles, and some plesiosaurs.

CERVICAL VERTEBRAE

(Figs. 77–81)

The number of vertebrae in the neck or cervical region of reptiles is not always easily determinable. In those reptiles having a sternum, the first rib attached to it definitely determines the beginning of the thorax. The distinction is almost as definite in those in which there is a change in the articulation of the rib from the centrum to the arch, as in the Sauropterygia and Archaeosauria. But the early reptiles had no sternum, and free ribs were continuous from the atlas to the sacrum without change in their mode of articulation. In such, the changes in their shapes, with other modifications, may indicate approximately the beginning of the dorsal series. Better evidence, however, is found in the position of the pectoral girdle as found in the rocks.

The number is very variable, more so than that of the dorsal vertebrae. The Cotylosauria, like the Temnospondyli, have but one or two vertebrae which may properly be called cervical, since the pectoral girdle is almost invariably found lying immediately back of the skull, the front end of the interclavicle, indeed, between the angle of the jaws. Primitive reptiles, then, like their immediate ancestors, the Stegocephalia, had practically no neck, and but little motion of the head in a lateral direction.

The Theromorpha have a longer neck, with at least six and probably seven vertebrae (Fig. 77), as shown by the lengths of the ribs, by the diapophyses, and mored efinitely by the position of the scapula and clavicles as observed in various specimens. These numbers, six or seven, are those given for the Therapsida, as this order is imperfectly known, and seven is the number that has remained so persistently in their descendants, the mammals. Modern chameleons have but five; true lizards, the Chelonia and Rhynchocephalia, eight; the monitor lizards, Crocodilia, Theropoda, Iguanodontia, and Ceratopsia, nine; the Pterosauria and Phytosauria, eight or nine; the Pseudosuchia, eight to ten; the Trachodontia and Sauropoda, as many as fifteen. It must be remembered, however, that in some cases these numbers are only approximately correct, dependent upon the interpretation of what constitutes a cervical vertebra by different observers.

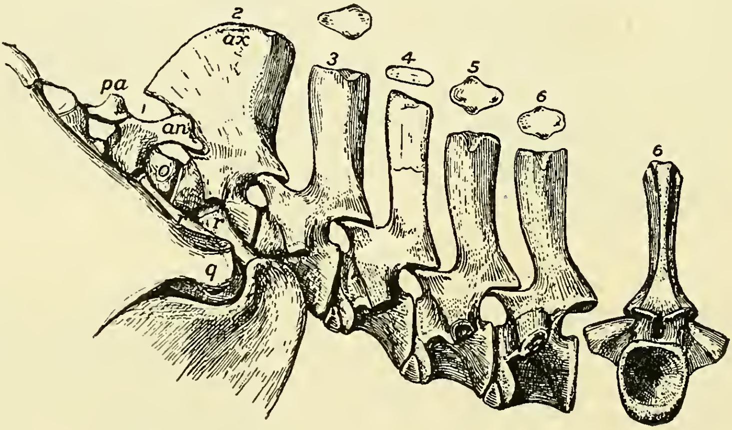

Fig. 77. Notochordal cervical vertebrae, with intercentra, of *Ophiacodon*, a primitive theromorph: *pa*, proatlas; *an*, arch of atlas; *o*, odontoid; *ax*, axis.

On the other hand, among strictly amphibious or aquatic reptiles there has been an increase or decrease in the number, the latter in the tail-propelling aquatic types. The ancient proganosaurs have ten or eleven; the dolichosaur lizards, thirteen; the nothosaurs, sixteen to twenty-one or twenty-two; the plesiosaurs, from thirteen to as many as seventy-six; probably also the increase in number among the trachodont and sauropod dinosaurs may be attributed to water habits. The marine crocodile, with a fin-like tail, lost two, like the mosasaurs and aigialosaurs, having seven; *Pleurosaurus* probably had but five; and the ichthyosaurs, the most specialized of all aquatic reptiles, had practically no neck.

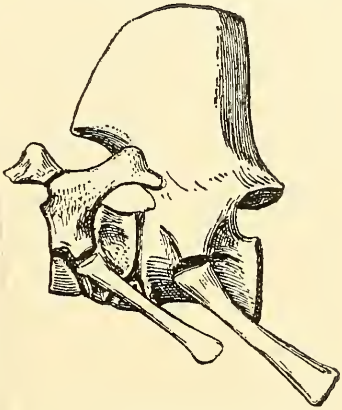

Fig. 78. *Ophiacodon.* Proatlas, axis, and ribs.

The first two or three of the cervical vertebrae are markedly differentiated in all reptiles, as in the higher animals. The first of these, the *proatlas*, is inconstant and vestigial, and has not been included in the numbers above given. The second, the first of our usual nomenclature, is the *atlas*. The third, more or less closely united with the atlas, is the *axis*, or *epistropheus*. The following cervical vertebrae, when present, are differentiated more or less from the dorsal series by their less erect or shorter spines, transverse processes, or the slenderness and mode of rib articulation. The cervicals of the later pterodactyls have additional articulations on their ventral sides, as has been described above (p. 91).

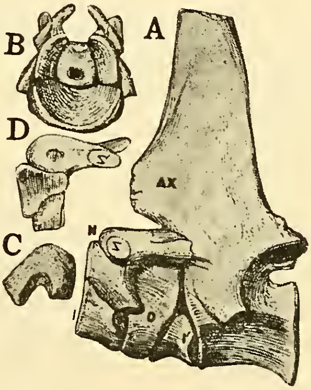

Fig. 79. Theromorph vertebrae: A, *Dimetrodon*, atlas and axis; B, the same atlas, from the front; C, the same proatlas, from the side; D, *Sphenacodon*, neurocentrum of atlas, inner side. *i*, intercentrum; *o*, pleurocentrum (odontoid); *n*, neurocentrum (arch).

Proatlas. The proatlas (Figs. 79 C, 80 D, L) is a small, more or less vestigial neural arch between the arch of the atlas and the occiput, usually paired. It is believed to be the arch of a vertebra formerly intercalated between the atlas and the skull; by some, homologous with the so-called atlas of the Amphibia; by Baur, as the representative of a vertebra fused with the occiput in the reptiles; by others, as merely the separated spine of the atlas; by others, as the arch of a vertebra whose centrum is represented by the anterior end of the odontoid. Another theory, which has less to commend it, is that of Jaekel, namely, that the centrum of the proatlas is the so-called intercentrum of the atlas, necessitating the view that the axial intercentrum is merely an accessory or provisional bone developed below the odontoid to fill out what would otherwise be an unoccupied space!

Positive evidence of the proatlas has been discovered in several genera of the Cotylosauria, but no complete specimen has yet been discovered; it is doubtless present throughout the order. It is present in many if not all forms of the Theromorpha and Therapsida. In *Ophiacodon* (Fig. 78) and *Dimetrodon* (Fig. 79) of the former group, it is a small bone on each side, articulating in front by a facet on the exoccipital, behind with an anterior zygapophysis on the arch of the atlas, both surfaces looking more or less downward. These articular surfaces appear to be present in all known genera. In the Crocodilia, occurring as far back as Jurassic times, it is a single bone in the adult, roof-shaped, arising from paired cartilages. In *Iguanodon* (Fig. 80 L), of the predentate dinosaurs, as also in several genera of the Sauropoda, and the Triassic *Plateosaurus* of the Theropoda, it is paired, as in the modern *Sphenodon* (Fig. 80 D), also articulating with the atlas. A roof-shaped, unpaired proatlas has been described in *Rhamphorhynchus*, a Jurassic pterosaur. It has also been reported in the chameleon lizards and the mammals *Erinaceus* and *Macacus*. As an abnormal element it was also found by Baur in a trionychoid turtle (*Platypeltis spinifer*, Fig. 32), partially fused with the occiput, and articulating with the arch of the atlas in the primitive way, from which he concluded that the real body of this vertebra had become permanently fused with the basioccipital. Probably it will be eventually discovered in many other extinct reptiles.

Atlas (Figs. 78, 79, 80). There is no vertebra in the known amphibians which can be homologized with the atlas of reptiles. By some the so-called atlas of the amphibians is thought to be represented by the proatlas; or it may have entirely disappeared. In the earliest reptiles (Fig. 79), the atlas is temnospondylous in structure, that is, composed of a paired arch resting in part upon a large, wedge-shaped intercentrum, in part upon a single large, embolomerous, notochordal pleurocentrum, all of them loosely connected with the axis, the arch of the atlas or neurocentrum articulating in the usual way by zygapophyses.

In its highest development, in the mammals, the arch and inter-

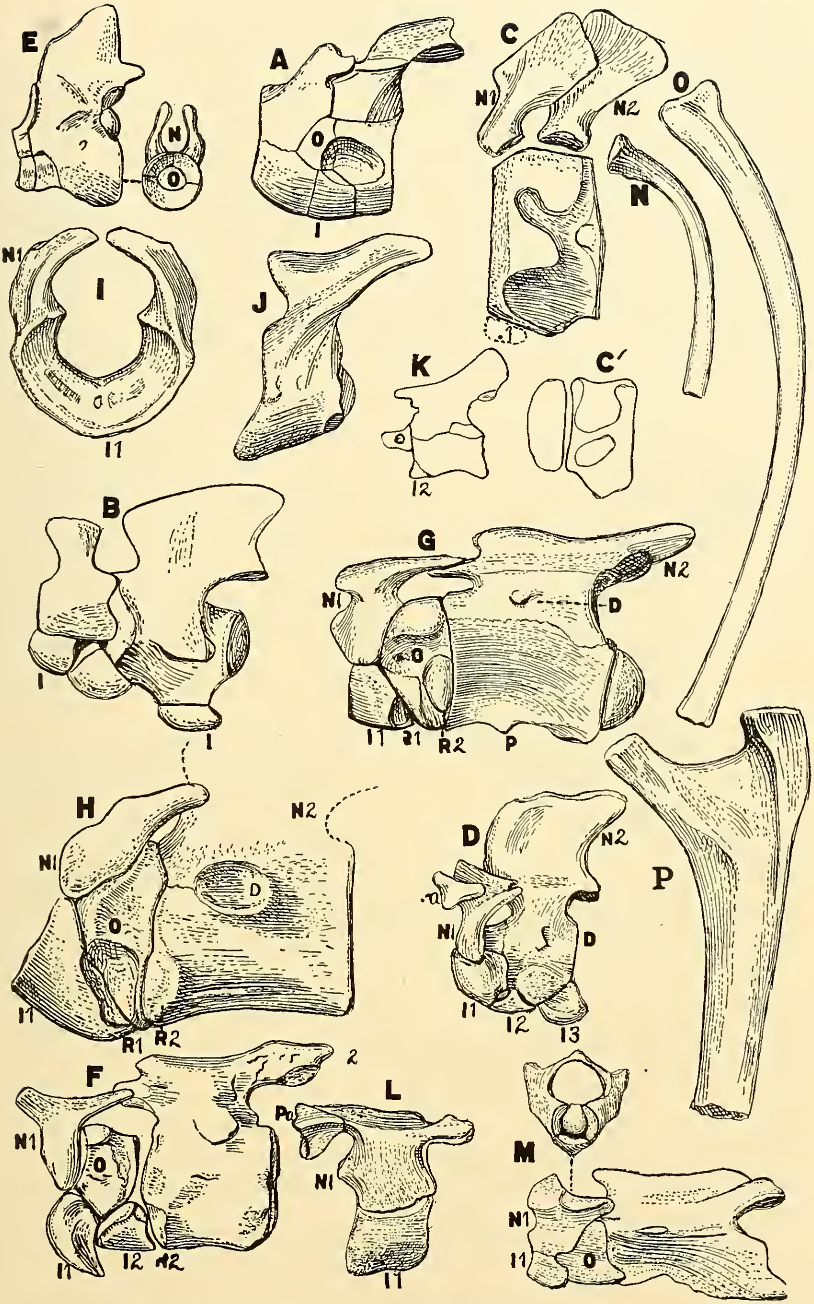

Fig. 80. Atlas, axis, and ribs: A, *Trinacromerum* (Plesiosauria); B, *Platecarpus* (Mosasauria); C, *Baptanodon* (Ichthyosauria), after Gilmore; C′, *Cymbospondylus* (Ichthyosauria), after Merriam; D, *Sphenodon* (Rhynchocephalia); E, *Nyctosaurus* (Pterosauria); F, *Champsosaurus* (Choristodera), after Brown; G, *Gavialis* (Crocodilia); H, *Enaliosuchus* (Crocodilia), after Jaekel; I, J, *Diplodocus* (Dinosauria), after Marsh; K, *Camptosaurus* (Dinosauria), after Gilmore; L, *Iguanodon* (Dinosauria), after Dollo; M, *Chrysemys* (Chelonia); N, *Iguana* (Lacertilia); O, *Trinacromerum* (Plesiosauria); P, *Apatosaurus* (Dinosauria), after Riggs.

centrum are fused into a ring, which revolves about its pleurocentrum, the odontoid, a small, tooth-shaped, or spout-shaped bone firmly fused with the axis in front and usually described as a part of it. Long ago, however, the odontoid was recognized by Cuvier as really the body of the axis. In no reptile did the atlas attain the specialization of the mammals, even approximately, but it most nearly approached it in the Theriodonts. In very few do the two bones of the arch fuse with the intercentrum into a complete arch ring, or does the pleurocentrum unite with the axis as a real odontoid. In few is there any degree of rotation about it, not more than between the axis and the following vertebra. This lack of torsion, in most reptiles at least, was compensated for by the ball-and-socket joint between the single condyle and the atlas, lost in mammals.

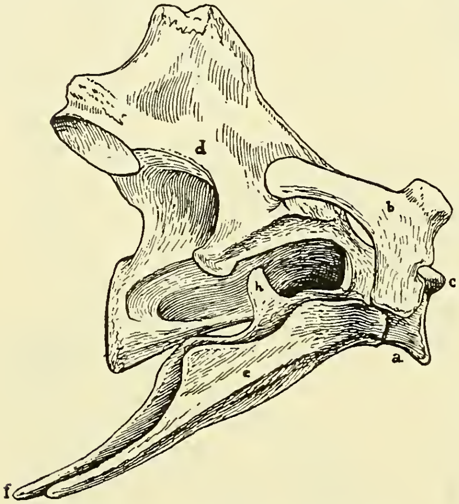

Fig. 81. Atlas and axis of *Diplodocus* (Saurischia). After Holland. One fourth natural size.

In the primitive *Ophiacodon* (Fig. 78) and *Dimetrodon* (Fig. 79) the condylar cup is formed by the intercentrum and arch, completed in the middle by the front end of the odontoid, that is, the pleurocentrum or true centrum, which has no independent motion whatever, and is not united with the axis. The arch bears a rib upon its diapophysis, and the large odontoid is perforated for the notochord, as in the embryonic cartilage of mammals. The pleurocentrum or centrum, large and notochordal primitively, reaching the ventral side of the vertebra, grew progressively smaller till it finally disappeared wholly from side view in the Pterosauria (Fig. 80 E), most Dinosauria, and the Squamata (Figs. 80 B, L). In the Rhynchocephalia (Fig. 80 D), Choristodera (Fig. 80 F), and Phytosauria it is yet largely visible from the side, but the first and second intercentra have become contiguous below it. In the Crocodilia (Fig. 80 G) and Chelonia (Fig. 80 M) the pleurocentrum still retains its primitively large size, reaching the ventral side, doubtless because of the loss, fusion, or great decrease in the size of the axial intercentrum. In the marine crocodiles (Fig. 80 H) the pleurocentrum is more reduced. Among the Chelonia the atlas may fuse into an independent vertebra, articulating with the axis. At other times the odontoid is more or less united with the axis, with no motion between it and the ring of the atlas. The axial intercentrum may be paired or single, fused with the odontoid or apparently absent. When paired they are more or less elongated, forming pseudo-hypapophyses, serving for the attachment of neck muscles.

In the Plesiosauria (Fig. 80 A) the odontoid is to a greater or less extent visible from the side, but is much reduced. In both the plesiosaurs and pterodactyls the atlas and axis are fused, indistinguishably so in the adult; both are slender-necked animals with small or vestigial cervical ribs. In the short-necked Ichthyosauria the atlas and axis show a progressive fusion from the earlier forms (Fig. 80 C), in which a complete disk represents the atlas, to those in which the bodies of atlas and axis are imperfectly or indistinguishably fused (Fig. 80 C).

Axis (Figs. 78–81). The axis differs from the following vertebrae in its broader and stouter spine, its usually more elongated centrum, and in its relations with the atlas. Its prezygapophyses are small and turned outward at the base of the spine. In the Cotylosauria and Theromorpha the front end of its centrum is deeply concave, the persistent notochord continuous through the notochordal odontoid. In procoelian, opisthocoelian, and platycoelian vertebrae the front end is flattened for sutural or ligamentous union with the odontoid. Its centrum is usually longer and usually bears a rib, though in the modern cocodiles (Fig. 80 G) and the dinosaurs (Fig. 81) its rib has migrated forward.

The axial intercentrum is nearly always present, primitively larger than the following intercentra, and is intercalated between the bodies of the atlas and axis in the usual way. Among the crocodiles (Fig. 80 G, H), anomodonts, and some lizards it has disappeared or is represented by the merest vestige. It is small in the dinosaurs and chelonians.

DORSAL VERTEBRAE

(Fig. 82)

The smallest number of dorsal vertebrae known in reptiles is that of the Chelonia, invariably ten. In the chameleon lizards there are as few as eleven; in the pterodactyls about twelve. In the latter order three or more of the anterior ones may be more or less immovably united for the support of the pectoral arch, forming the *notarium*. In the Chelonia they are fused throughout in the carapace. The largest number of dorsal vertebrae in reptiles having a sacrum, forty-one or forty-two, is found in *Pleurosaurus*, a slender, aquatic Jurassic reptile. About thirty is the usual number in the plesiosaurs. In terrestrial reptiles the number never exceeds twenty-two or twenty-three and is usually about eighteen. In reptiles lack-

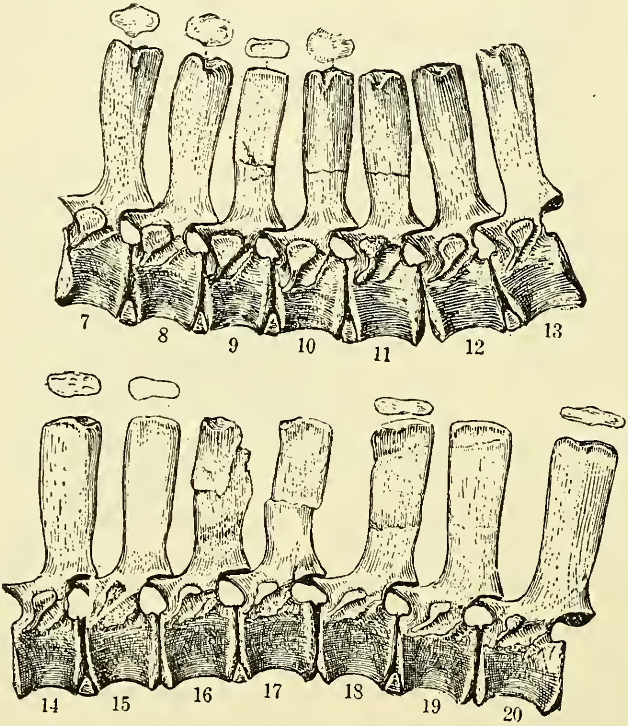

FIG. 82. *Ophiacodon mirus* Marsh (Theromorpha). Seventh to twentieth vertebrae, from the side. One half natural size.

ing a sacrum the number between the girdles may be much greater, thirty-five in the mosasaurs, and as many as seventy-four in some terrestrial, legless lizards.

As has been said, there is not often the same distinction between thoracic and lumbar vertebrae that there is in mammals. There are, however, even in the Cotylosauria, examples (Fig. 164) of true lumbar vertebrae, that is, vertebrae in front of the sacrum not bearing ribs of any kind.

Sacral Vertebrae

(Fig. 83)

The sacrum of land vertebrates is composed of from one to four or five vertebrae, either fused together or separate, bearing short, stout ribs for the support of the pelvis. Rarely among the amphibians are there more than one; certain temnospondyls and modern urodeles[1] are known to have two. It is quite certain, however, that reptiles began their career with but a single rib-bearing sacral vertebra, inasmuch as *Seymouria* of the Cotylosauria is known to have no more (Fig. 1). A second vertebra (Fig. 84), however, was soon added from the basal caudal series by the enlargement of the ribs to come in contact with the ilium on each side. And this num-

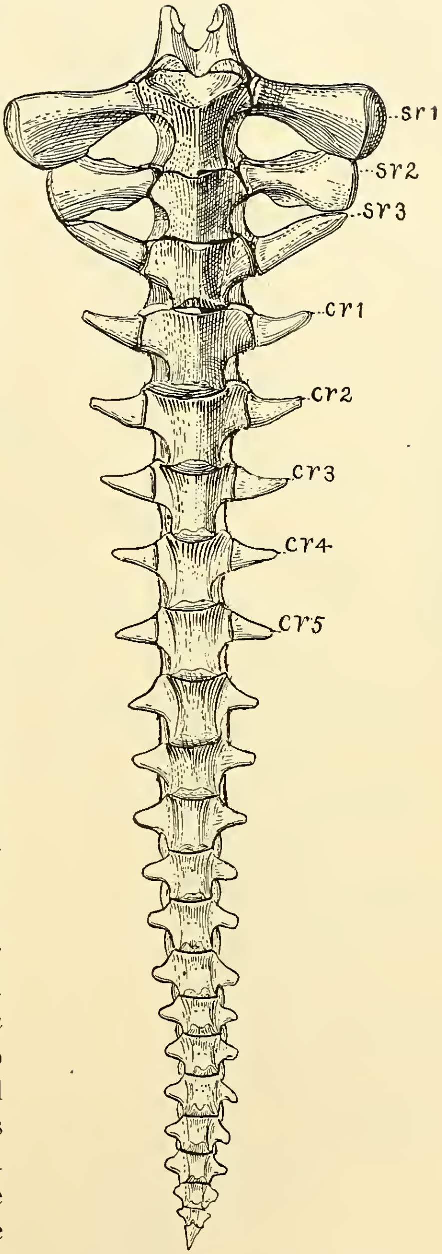

Fig. 83. Sacrum and caudal vertebrae of *Macrochelys* (Chelonia), seen from below.

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[1] [Also some frogs. — Ed.]

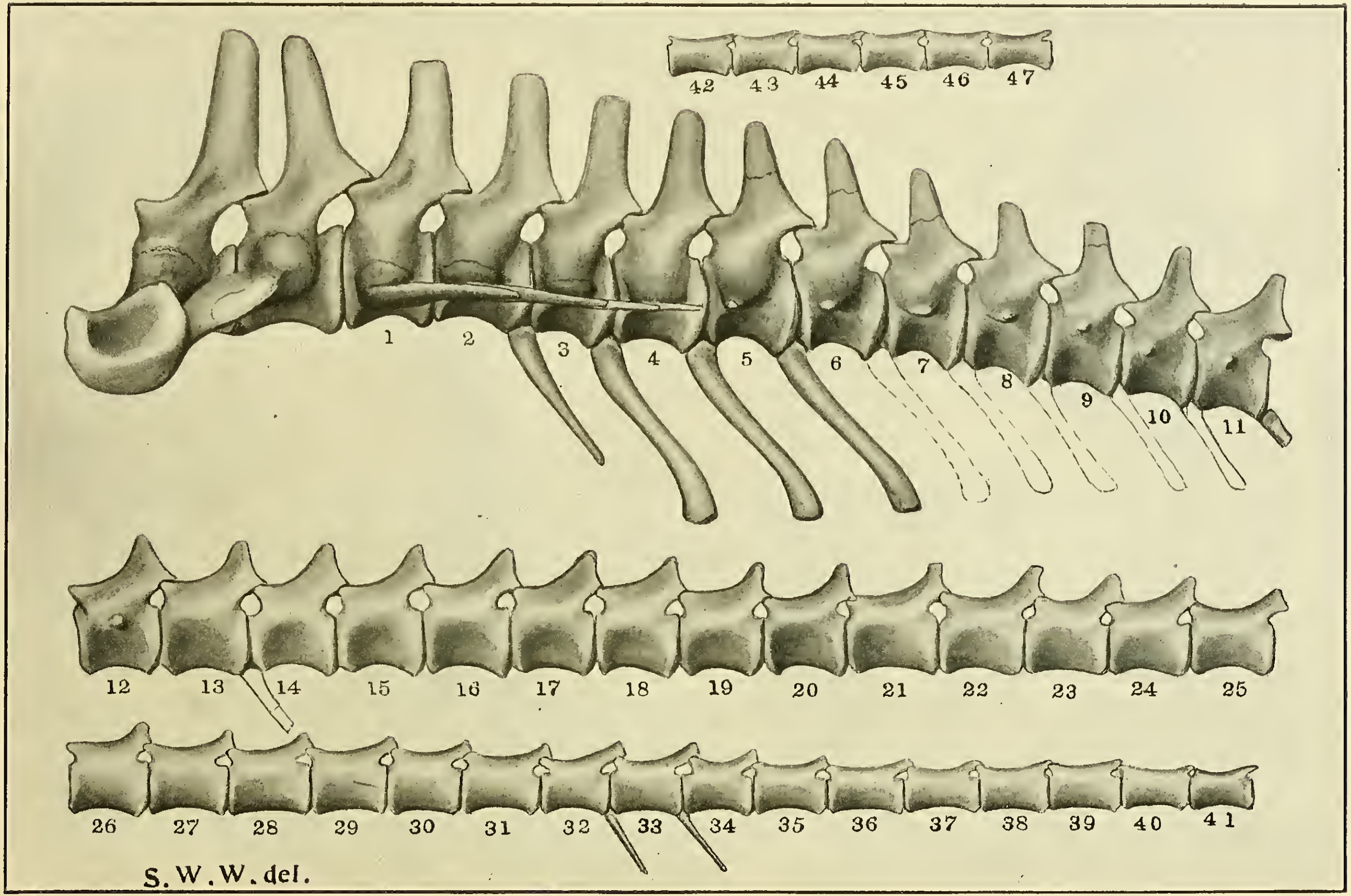

FIG. 84. Sacrum and tail vertebrae of *Varanosaurus* (Theromorpha).

ber, two, has remained persistent in most reptiles and even most mammals to the present time. A third vertebra, from the caudal series, was early united in many Theromorpha and the latest Cotylosauria. Still another, and possibly two, were joined in the Dinocephalia and Anomodontia. The Plesiosauria, purely aquatic animals with propelling legs, have three or four sacrals. From one to three additional vertebrae have been fused with the sacrum in front in the Pterosauria (Fig. 118 D), and some Dinosauria, but they are not true sacral vertebrae.

Not only may the sacral vertebrae be closely fused, but their arches and spines may become almost indistinguishably united. Usually, however, the zygapophyses remain visible and are sometimes functional. In *Iguana*, even the zygosphene and zygantrum are present between the two sacrals. The sacrum is lost, not only in the snakes and legless lizards, but also in the mosasaurs and late ichthyosaurs, where hind legs have lost locomotive functions.

CAUDAL VERTEBRAE

(Figs. 76, 83–85)

The tail of the earliest known reptile, from the Coal Measures of Ohio (Fig. 84), was long and slender. The Cotylosauria had, for the most part, only a moderately long tail, with not more than sixty vertebrae. The length of the tail, however, depends so much upon habits that it may be extremely variable even in members of the same order. Stumpy-tailed lizards (*Trachysaurus*), for instance, have practically no tail, while other skinks have a very long and slender one. Invariably it is long in tail-propelling, swimming reptiles; such reptiles move sinuously through the water, preventing much use of the legs as propelling organs. Those with propelling legs, on the other hand, have a broader and flatter body and short tail, of use only as a steering organ. However, sauropod dinosaurs, though supposed to be exclusively water animals, have a very long and slender tail, more or less whiplash-like at the end. As a rule, swift-moving, crawling reptiles have a long and slender tail, while short-tailed reptiles are invariably slow in their movements upon land.

The spines of the caudal vertebrae in land reptiles are seldom long; certain chameleon lizards and the basilisc lizard are exceptions; the vertebrae distally are more slender and the zygapophyses weak. One of the first indications of swimming habits, at least in those reptiles with long tails, is the widening and elongation of the caudal spines throughout, [less] at first [anteriorly] and then more distally until a terminal fin is developed with the end of the column in the lower lobe (Fig. 85).

The basal caudal vertebrae, from one to six in number, those without chevrons but with ribs, are called *pygals*. They have the ordinary intercentra in those reptiles in which they [intercentra] are persistent throughout; sometimes with rudimentary chevron-like processes.

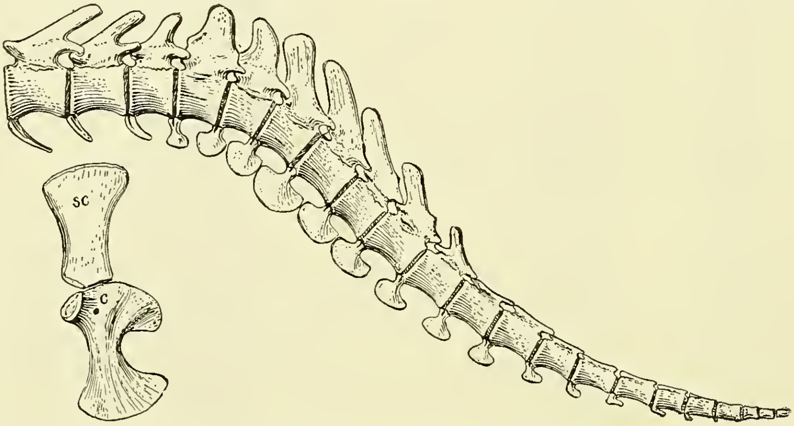

FIG. 85. Tail, scapula (*sc*), and coracoid (*cor*) of *Geosaurus* (Thalattosuchia). After Fraas.

The cloaca in the living animal occupies the space below them. The number is more or less reduced in modern reptiles; the Crocodilia have but one, most lizards, two.

There is an unossified vertical septum through each caudal centrum in many lizards, the Proganosauria *Saphaeosaurus* and *Sphenodon*, along which it readily breaks, causing the easy loss of the distal part. This septum was once supposed to represent the division between the primitive component parts of the centrum. It is now thought to be an acquired character, not occurring in the early embryo.

Chevrons, or *haemapophyses* (Fig. 84) for the protection of the vessels on the under side of the tail, really outgrowths from the intercentra (Fig. 76 D), occur below and between the caudal centra in most reptiles. Usually single and Y-shaped — whence the name chevron — they may be paired in the Plesiosauria and Ichthyosauria. The medial ones of the Sauropoda have two Y-shaped, broadly divergent branches united at their base. More or less vestigial in the turtles, they are absent in snakes, replaced by a pair of vertical hypapophysial-like processes (*lymphapophyses*).

Chevrons articulate as a rule intercentrally, but sometimes exclusively to the distal part of the preceding centrum with which they may be coössified, as in some mosasaurs and lizards, especially those in which the cervical intercentra have migrated forward to articulate or be coössified with the median hypapophysis. Chevrons primitively, as in the temnospondyl amphibians, have their branches united above in an intercentrum-like bone, a condition found in the proximal chevrons of *Sphenodon*. In later reptiles, for the most part, the two branches articulate separately. At the tip of the tail they are vestigial or absent.

CHAPTER III

THE RIBS AND STERNUM[1]

The ribs of reptiles, like those of the amphibians, primitively articulate with all vertebrae, at least as far back as the middle of the tail. The first to become fixed or closely united with the vertebrae, after the sacral, were the caudal, next the lumbar, and last of all the cervical. The dorsal ribs are free, except in the Chelonia, some Pterosauria, and some armoured dinosaurs.

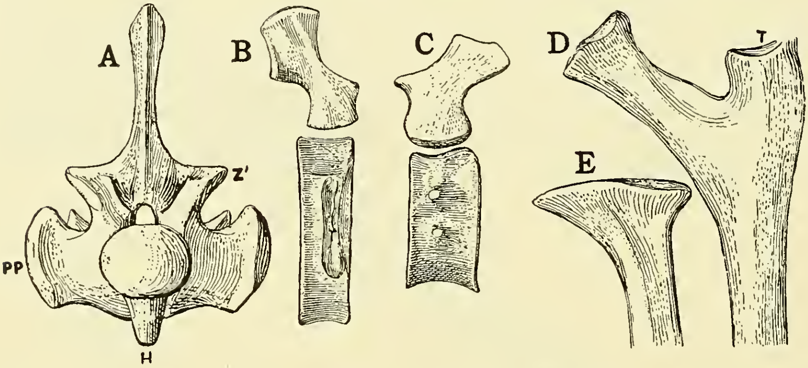

Fig. 86. Vertebrae and ribs: A, *Clidastes* (Mosasauria), posterior cervical vertebra, from behind; B, *Cymbospondylus* (Ichthyosauria), anterior dorsal vertebra, from the side, after Merriam; C, *Ichthyosaurus* (Ichthyosauria), middle dorsal vertebra, from the side (after Broili); D, *Dimetrodon* (Theromorpha), anterior dorsal rib; E, *Diadectes* (Cotylosauria), anterior dorsal rib.

The ribs of the Temnospondyli (Fig. 86) articulate with intercentrum and arch, usually without differentiation of the articular surfaces. And this was the original mode among reptiles. With the diminution in size of the intercentrum, the head, or *capitulum*, joins the adjacent ends of two centra across the intervertebral cartilage, the articular surface, however, continuous to the *tubercle*, which articulates with the end of the diapophysis. This continuous articulation from the intercentral space to the arch was the almost invari-

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[1] [For the morphology and variation of the ribs, in connection with the segmentation of the vertebrate body, see Bütschli, 1921, *Vorlesungen über Vergleich Anat.;* Kingsley, *Compar.-Anat. Cert.* — Ed.]

able rule among the Cotylosauria (Fig. 86 E) and occurs occasionally in the Theromorpha and even in the recent *Sphenodon.* Such ribs, though usually called single-headed, are not really so since both capitulum and tuberculum are present, though connected. A better name for them is *holocephalous.* Soon, however, the articular surfaces become restricted to the head and tubercle, that is, there is an emargination of the articular surface between them, the so-called neck, and the rib is truly double-headed, or *dichocephalous* (Fig. 86 D). Strictly speaking, single-headed ribs are those which have lost either the head or the tubercle.

This early mode of articulation of double-headed ribs, the head across the intervertebral cartilage, the tubercle to the diapophysis of the arch, has continued through those reptiles [see above] and through the mammals. And this is essentially the mode of rib articulation in the Diaptosauria.

In many reptiles, however, perhaps in part because of the closer articulation of the vertebrae, the head has migrated backward to articulate with a facet or process on the anterior end of the centrum, the parapophysis, and there it has remained in the cervical vertebrae of most reptiles, and in the dorsal vertebrae of the Squamata and their allies. In the dorsal region there have been many modifications. In those reptiles which are here classed under the Parapsida, that is, the Ichthyosauria, Proganosauria, *Pleurosaurus*, and Squamata (Figs. 80 N, 73 C–F), the tubercular part of the articulation has been largely or wholly lost, and the single-headed ribs remained attached more or less wholly to the centrum. In the later Ichthyosauria and later Plesiosauria, it is true, the ribs are often dichocephalous (Fig. 86 C), both articulations uniting with the centrum. There is, however, in such forms no real tubercle. The ribs of *Araeoscelis*, a Lower Permian reptile, are single-headed and central in the cervical region, imperfectly double-headed in the dorsal region. So also, the ribs are described as single-headed in *Pleurosaurus*, *Protorosaurus*, the Proganosauria, and Thalattosauria (Fig. 87), probably all with a single, typical, upper temporal opening. The dorsal ribs (Figs. 80 O, 89) of the

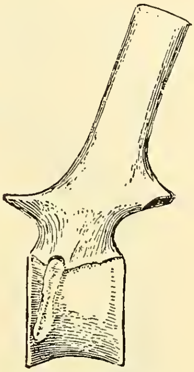
FIG. 87. Dorsal vertebra of *Thalattosaurus.* (After Merriam.)

Sauropterygia articulate with the diapophysis (*d*) exclusively by a single head, the cervical ribs (Fig. 89 *r*) exclusively with the centrum, usually also by a single head.

The dorsal ribs of the Archosauria, that is, the Pseudosuchia, Parasuchia (Fig. 88), Crocodilia (Fig. 90), Dinosauria (Fig. 80 P), and Pterosauria, are double-headed, the anterior ones at least, but both articulations are with the arch or diapophysis. And this mode of articulation would seem to exclude their immediate ancestral relationship to the birds, in which the head of the ribs articulates with the centrum throughout.

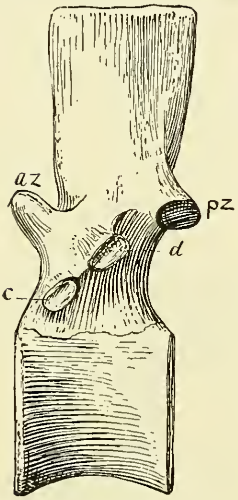

Fig. 88. Dorsal vertebra of phytosaur: *az*, anterior zygapophysis; *pz*, posterior zygapophysis; *d*, *c*, articulations of rib.

Atlantal ribs, present in all early reptiles, have been lost in modern ones, except the Crocodilia, where they are attached exclusively to the intercentrum, in the ancient *Metriorhynchus* to both arch and intercentrum. In the Dinosauria, some of them at least, the first intercentrum bears a small rib (Fig. 81).

Axial ribs are more often present, but are lost in not a few reptiles, particularly the Pterosauria (Fig. 80 E) and Chelonia (Fig. 80 M). In early crocodiles the axial rib articulated with diapophysis and parapophysis; in later crocodiles the diapophysial articulation is lost, though a vestige often remains, and the single-headed rib has migrated forward on the odontoid.

The dorsal ribs of the Eunotosauria and all Chelonia[1] have expanded to meet or fuse with each other, forming more or less of a carapace (Fig. 91). Peculiarly expanded and overlapping ribs in the posterior dorsal series occur in some of the Theriodontia. In *Cynognathus* the thirteenth to the seventeenth ribs shorten rapidly and project widely with a remarkable expansion near the proximal end, which overlaps the succeeding rib in a concavity on its anterior border. In the lumbar series (Fig. 92) they lose the free portion of the shaft, ending in wide,

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[1] [This leaves out of account the costal plates which enter into the formation of the carapace. See Gadow, "Reptiles and Amphibia," *Cambridge Nat. Hist.;* Procter, 1923, *Proc. Zoöl. Soc.* — Ed.]

interlocking ends. Such ribs gave great strength to the lumbar region, and are perhaps analogous to the greatly expanded transverse processes of the crocodiles.

The first four to six ribs of the Cotylosauria, and rarely also of the Theromorpha, are progressively flattened and dilated, sometimes, as in *Diadectes* and *Limnoscelis* (Fig. 95), remarkably so, for the direct support of the short and broad scapula. Not only are these ribs so remarkably dilated in *Diadectes*, but, continuing the expansion backward, there are three flat dermal plates overlying the following ribs.

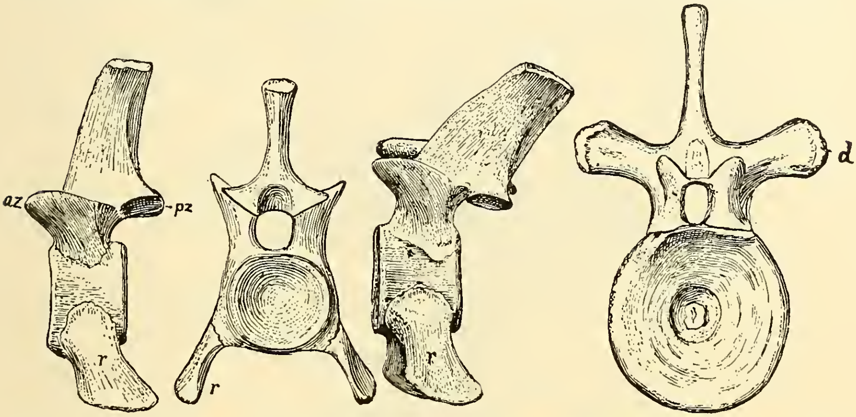

Fig. 89. Plesiosaur vertebrae: *Polycotylus*. Cervical vertebrae from the side and behind, and dorsal vertebrae from in front: *az*, anterior zygapophysis; *pz*, posterior zygapophysis; *r*, *r*, *r*, cervical ribs; *d*, articulation of dorsal rib.

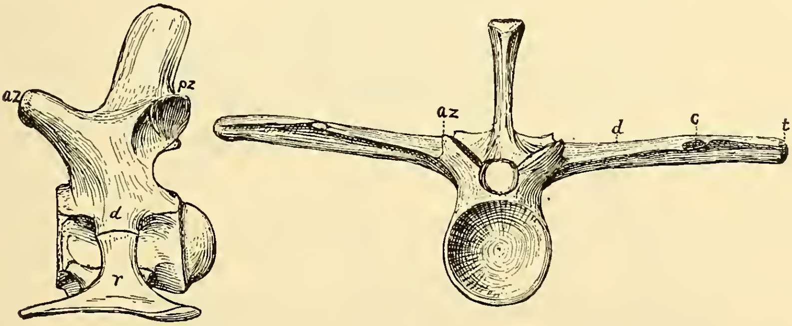

Fig. 90. Vertebrae of gavial from the side (cervical), and from in front (dorsal): *az*, anterior zygapophysis; *pz*, posterior zygapophysis; *d*, diapophysis; *r*, cervical rib; *c*, articulation for head; *t*, for tubercle of dorsal rib.

The cervical ribs of the Crocodilia (Fig. 90) and Dinosauria are short and more or less "hatchet-shaped," either fused or more or less closely united to arch and centrum. The free cervical ribs of lizards and mosasaurs begin upon the axis. Only vestiges of ribs remain in the pterodactyls and turtles; they are nearly always fused. Three or four of the single-headed ribs of the Sauropterygia articulating with both centrum and arch are known as *pectoral* ribs.

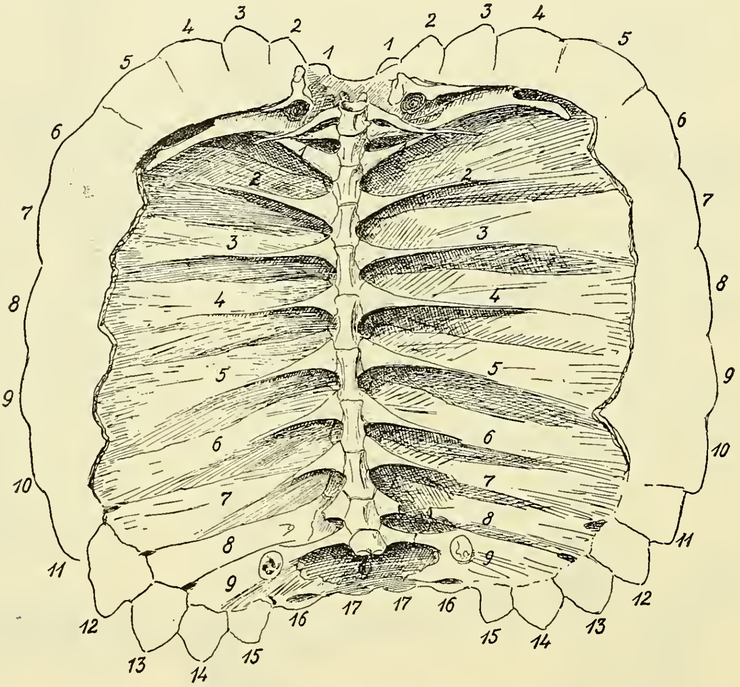

FIG. 91. Inner side of carapace of *Stegochelys* (Chelonia). After Jaekel. About one sixth natural size.

In certain early cotylosaurs (Figs. 128, 164), four or five vertebrae in front of the sacrum bear no ribs of any kind; in others, *Seymouria* (Fig. 1) for instance, free ribs continue to the sacrum. Many other reptiles have a variable number of the presacral ribs coössified with the centrum, or centrum and arch, so-called transverse processes.

Sacral ribs. True sacral ribs often retain their primitive attachments (Fig. 93), the capitular part articulating more or less intercentrally with the preceding vertebra, the tubercular part with the

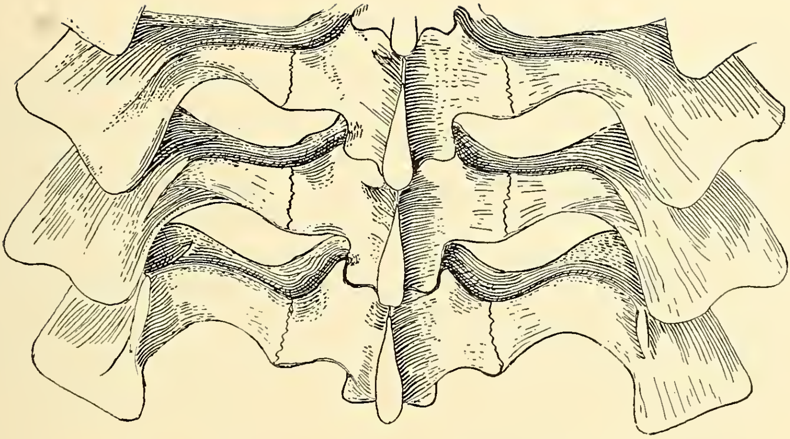

Fig. 92. Vertebrae: *Cynognathus* (Cynodontia), posterior dorsal vertebrae, from above. After Seeley. One half natural size.

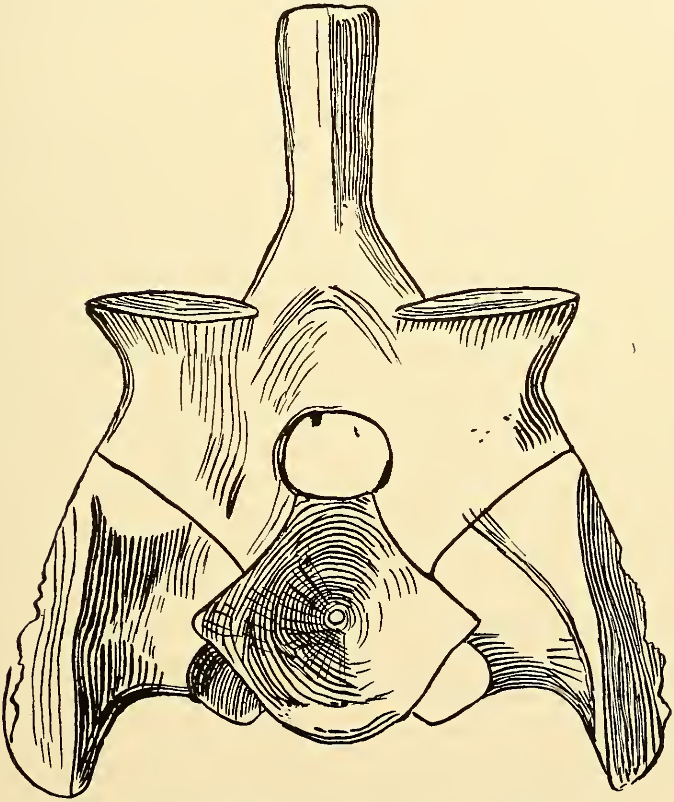

Fig. 93. *Nothodon lentus* Marsh (Cotylosauria). Sacral vertebra, from in front. Natural size.

arch. Real sacral ribs have been in all cases added from behind, since the caudal ribs have retained more or less in all animals their original attachments, while the lumbar or posterior dorsal ribs have often undergone changes. It is improbable that there has ever been any "migration" of the sacral vertebrae; that is, the first true sacral vertebrae of all animals[1] are identical with the single sacral vertebra of *Seymouria*. Additional sacral ribs have been due to the gradual elongation of the basal caudal ribs and their articulation with the ilium, as shown in the tail of the alligator snapper turtle. The second and third pairs were added very early in the history of reptiles.

Remarkably, in the Lacertilia evidences of sacral ribs have not been found, the ilia being supported by transverse processes, outgrowths of the centra (Moodie).

Not only are the two sacral ribs of the Crocodilia (Fig. 121) primitive in their attachments, but the centra also have retained their primitively amphicoelous structure.

On the other hand, additional vertebrae have joined the sacrum in front, as many as three in some reptiles, but in such cases the ribs have not reverted to their primitive attachments if modified, though they may extend to the ilium. In the Ceratopsia three lumbar vertebrae have been fused with the sacrum, and their diapophyses with the ilium. Indeed in some instances (*Monoclonius* for instance) a vestigial free rib may remain on the first, so-called sacral vertebra. In the later pterodactyls there are several such *sacro-lumbar* vertebrae, and also in the Anomodontia (Fig. 119 C), groups that have been accredited with from seven to ten sacral vertebrae. In all these the ilium is greatly prolonged in front of the acetabulum. The projections from the vertebrae have often been called indiscriminately transverse processes, but that term is true only of the sacro-lumbars.

Whether or not the dinosaurs acquired the third or the fourth sacral vertebrae after their divergence from their immediate ancestral stock is perhaps a question. But two are accredited to *Hallopus*, a primitive type. There can be no question, however, but that the dinosaurs, both the Saurischia and the Ornithischia, descended from reptiles with but two sacral vertebrae, since the allied Crocodilia

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[1] [But few contemporary morphologists would endorse this view. It certainly does not apply to the Amphibia and is very doubtful for the Chelonia. — Ed.]

and Pseudosuchia have but that number, and since doubtless the Diapsida began with but two.

Many temnospondylous amphibians have on the hind border of the dorsal ribs an angular *uncinate process*, like that so characteristic of birds. Such ossifications have never been observed among the older reptiles. They occur in the Jurassic *Homoeosaurus* and the modern *Sphenodon* of the Rhynchocephalia; imperfectly ossified processes also occur in the Crocodilia. In many other reptiles they doubtless remained unossified, and in much probability will yet be found in other reptiles as fused processes or separate ossifications.

VENTRAL OR ABDOMINAL RIBS

Many, perhaps most, of the Stegocephalia, especially the Branchiosauria, had on the under side of the body an armature of bony rods, or plates, of various forms, called by Baur *gastralia*, by Gegenbaur the *parasternum*, and ordinarily known as *ventral* or *abdominal* ribs. They are arranged in a V-shaped pattern with the apex in front, and may sheath the whole under side of the body, extending on the limbs. In some cases, exterior to these a distinct armor of dermal plates has been observed. Among the temnospondylous amphibians they occur more rarely. In *Cricotus*, an ambolomerous type, they sheath closely the under side of the abdomen, each composed of an unpaired median piece, and numerous lateral ones. Among the Rhachitomi they have been observed in *Archegosaurus* in the shape of slender rods. They are unknown in the Stereospondyli.

Ossified parasternal ribs, in greater or lesser numbers and complexity, occur in some members of every chief group of reptiles, though far from constantly in each group. Among the Cotylosauria they are known in three families, the Sauravidae, Captorhinidae, and Procolophonidae; they are certainly absent in some, if not many, of the known genera of the order. They have been observed in only a few of the Theromorpha, and are certainly absent in some of the families. They are known in *Galechirus* of the Dromasauria; among the Proganosauria; *Protorosaurus*, *Kadaliosaurus*, *Pleurosaurus*, and *Saphaeosaurus* of the subclass here called the Parapsida; in *Aigialosaurus* and some recent lizards; in the Choristodera, *Homoeosaurus*, *Hyperadapedon*, and *Sphenodon* of the Rhynchocephalia; in the Pseudosuchia (*Scleromochlus*), Phytosauria, Pterosauria, Crocodilia, and Theropoda, of the Archosauria; in the Sauropterygia, Ichthyosauria, and Chelonia. They are thus, it is seen, characteristic of the Reptilia as a whole, though frequently absent in forms related to those which possess them. No explanation has yet been given of their inconstancy.

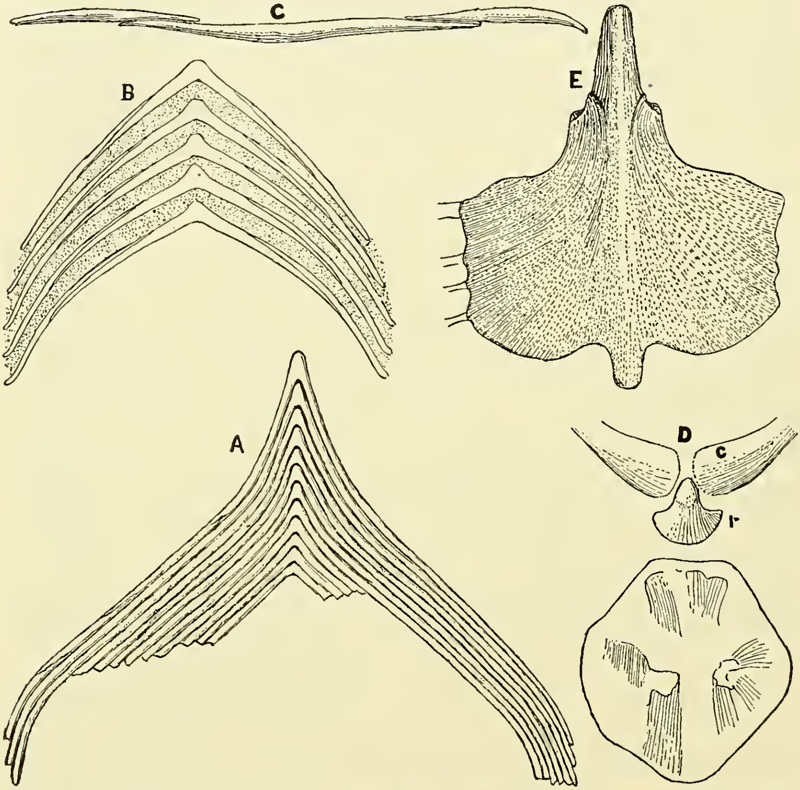

Fig. 94. Sternum and parasternum: A, *Theropleura* (Theromorpha). About one half natural size. B, *Sphenodon* (Rhynchocephalia). Three halves natural size. C, *Champsosaurus* (Choristodera). One half natural size. D, *Lystrosaurus* (Anomodontia). One half natural size. E, *Nyctosaurus* (Pterosauria). Nearly one half natural size.

The most primitive parasternals known among reptiles are those of the Cotylosauria and Theromorpha (Fig. 94 A), slender, bony rods composed of several pieces on each side, meeting in a median, unpaired, V-shaped piece. They sheath closely the whole under side of the abdomen from the coracoids to the pelvis, twelve to fifteen times as numerous as the overlying vertebrae, and more than two hundred in number. Anteriorly they are covered or underlaid by the distal end of the interclavicle. In the modern *Sphenodon* (Fig. 94 B) there are about twenty-four such rods, each composed of a median, unpaired piece and a lateral splint, every alternate one of the first eleven attached to the end of a dorsal rib. In the Phytosauria they are similar, nineteen or twenty in number. The Choristodera (Fig. 94 C), Plesiosauria, and Ichthyosauria, aquatic reptiles, have larger and stouter parasternals, consisting of a straight or slightly curved median piece, and three or four lateral splints on each side. The Crocodilia (Fig. 121 C) have seven or eight pairs, each composed of two slender rods on each side (not joined in the middle). In earlier members of the order there was a larger number, and some of them, at least, were composed of the usual V-shaped median piece and a lateral splint on each side. The last pair is enclosed in a dense sheath of fascia continuous with the ends of the so-called pubes.

Among the modern lizards abdominal ribs are often present, especially in the chameleons, each composed of one broadly V-shaped piece, either connected with the dorsal ribs or free, sometimes paired and usually cartilaginous. Only in a few forms have they been observed as slender ossifications. Clearly endoskeletal in origin, they have been supposed to be not true parasternals, and have been called distinctively *abdominal* ribs. That they are not continuations of the dorsal ribs seems evident from the fact that they are sometimes much more numerous than the overlying vertebrae. These lacertilian ribs are located, it is said, in the rectus abdominis muscles. The parasternals of *Sphenodon* are in the superficial part of the rectus and external oblique muscles, and are united by a dense sheath of fascia.

The later pterodactyls have five or six flattened parasternals, the anterior ones broadly V-shaped, the posterior ones paired. In the earlier pterodactyls the unpaired median piece has one or two lateral splints. They have also been observed in various genera of theropod dinosaurs. In the Chelonia they are represented by the posterior three pairs of plastral elements, as usually accepted, but it is possible that these are really dermal elements and [not] true parasternals. The extinct *Saphaeosaurus* (*Sauranodon*) had a full armature of ossified parasternals similar to those of *Sphenodon.*

Parasternal ribs have long been considered to be of dermal origin, skin bones which have sunk into the muscles. The abdominal ribs of the lizards are undoubtedly true endoskeletal bones, and Fürbringer has suggested that in these animals they are new growths, supplanting the dermal parasternals which have long since disappeared, and that they represent the ends of the dorsal ribs, or outgrowths from them.

That they and the sternum to which they are supposed to have given origin are really the ends of true ribs is improbable, since no other tetrapods are known in which the dorsal ribs meet on the under side of the body, or even approach each other. It would seem more reasonable that the abdominal ribs of all reptiles are of parenchymatous or cartilaginous origin, and that the anterior ones fused to form the sternum.[1] The so-called sternum of the modern amphibians (there was no sternum of any kind in the Stegocephalia) is an ossification of the myocomata, not derived from the dorsal ribs, and is thought not to be homologous with the sternum of reptiles.

Sternum

The earliest recorded occurrence of a *sternum* or breastbone in reptiles is in the Anomodontia (Fig. 94 D) where, according to Broom, it is generally present and ossified. It is figured in *Keirognathus* as a small, subquadrilateral bone lying over the posterior extremities of the coracoids and distal end of the interclavicle. Only rarely does it occur as an ossification in other reptiles, the best examples of which are the Pterosauria (Fig. 94 E) where, as a broad, shallow concave bone, it covers the whole under side of the thoracic region with a stout manubrium-like process in front, but without a true keel. On either side of the base of the median anterior protuberance it gives articulation to the elongate coracoid. Its lateral margins have articular facets for four or five, sometimes ossified, sternal ribs. Posteriorly in the middle it is contiguous with the parasternal ribs.

In many reptiles the sternum is wholly absent, even as a cartilaginous element. There was no space, even for a rudimentary one, in the Ichthyosauria and Sauropterygia back of the united coracoids and in front of the parasternals. It has been thought that its absence in these orders is due to its loss; it is more probable that their an-

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[1] [For further support of this view, see C. L. Camp, 1923, *Bulletin*, Amer. Mus. Nat. Hist., vol. XLVIII, pp. 389–393.]

cestors never possessed it. There could have been no sternum, even a small cartilaginous one, among the Cotylosauria and Theromorpha, since in several instances in both these orders the parasternals have been found sheathing the whole abdomen from the coracoids to the pelvis. Probably this was the condition in all the early reptiles; probably also the condition in the early Rhynchocephalia, since *Rhynchosaurus* had parasternal ribs reaching nearly to the coracoids, leaving little or no space for a sternum.

In the modern Lacertilia (Fig. 99) and in *Sphenodon* there is a more or less calcified, thin, rhomboidal plate articulating on each side with the coracoid in front and ending in a single or paired continuation, the *xiphisternum.* It gives articulation on each side to from one to four or five, exceptionally more, sternal ribs, also cartilaginous. Rarely, no ribs articulate with the sternum, and the sternum itself may be represented by a pair of small cartilaginous plates or may be wholly absent. Sometimes it has single or paired perforations. Similar cartilaginous sterna have been found in the Dolichosauria and Mosasauria, and doubtless it was present in most of the extinct members of the order.

In the Chelonia there is no trace of a sternum. In the living Crocodilia the sternum is a small, oval, cartilaginous plate, continued into a pair of cartilaginous xiphisternal rods to which six or eight dorsal ribs are attached by the intervention of cartilaginous sternal ribs. Nothing is known of the sternum in extinct crocodiles or phytosaurs; probably it was present as a cartilage.

The sternum has been found in not a few dinosaurs. Among the Sauropoda it has been recognized in a pair of oval, ossified plates.

CHAPTER IV

THE PECTORAL AND PELVIC GIRDLES

The Pectoral or Shoulder Girdle

(Figs. 95–113)

Those bones which form the framework for the support of the anterior extremities in vertebrate animals are collectively called the *pectoral* or *shoulder* girdle. In our own skeleton, as in that of most mammals, there are but two on each side, the *scapula*, or shoulder-blade, and the *clavicle*, or collar-bone. A third bone, or possibly two, on each side, are represented in most mammals by mere vestiges, which early unite with the scapula to form the *coracoid* process. In

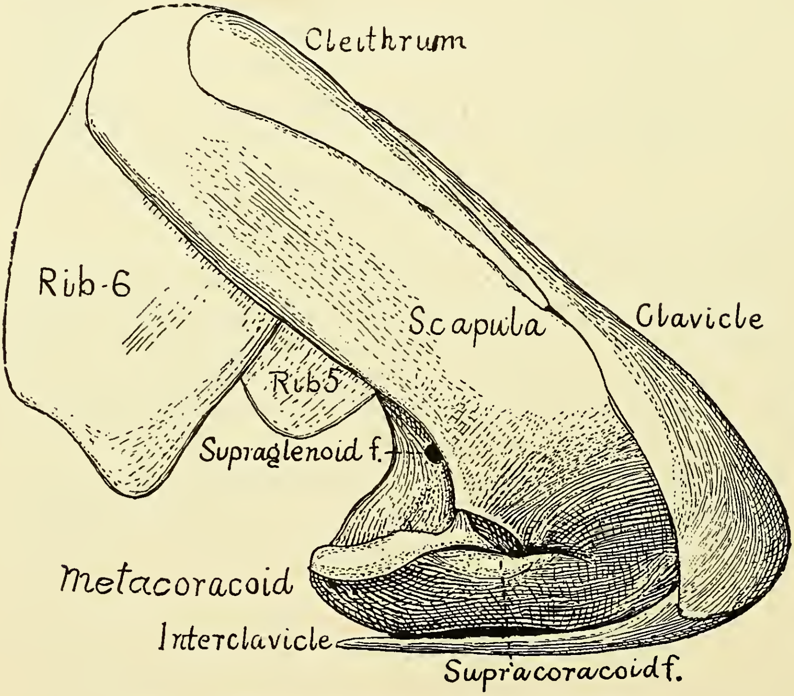

Fig. 95. *Diadectes* (Cotylosauria). Pectoral girdle, right side.

the lowest living mammals, of which *Ornithorhynchus* and *Echidna* are the only examples, there are in addition to the clavicles three well-developed bones on each side, the scapula and two bones articulating with it at its lower end, the anterior of which, originally named *epicoracoid* by Cuvier, is generally known as the *procoracoid;* the posterior one helping to form the articulation for the arm bone, known as the true coracoid. The homologies of these, or rather of

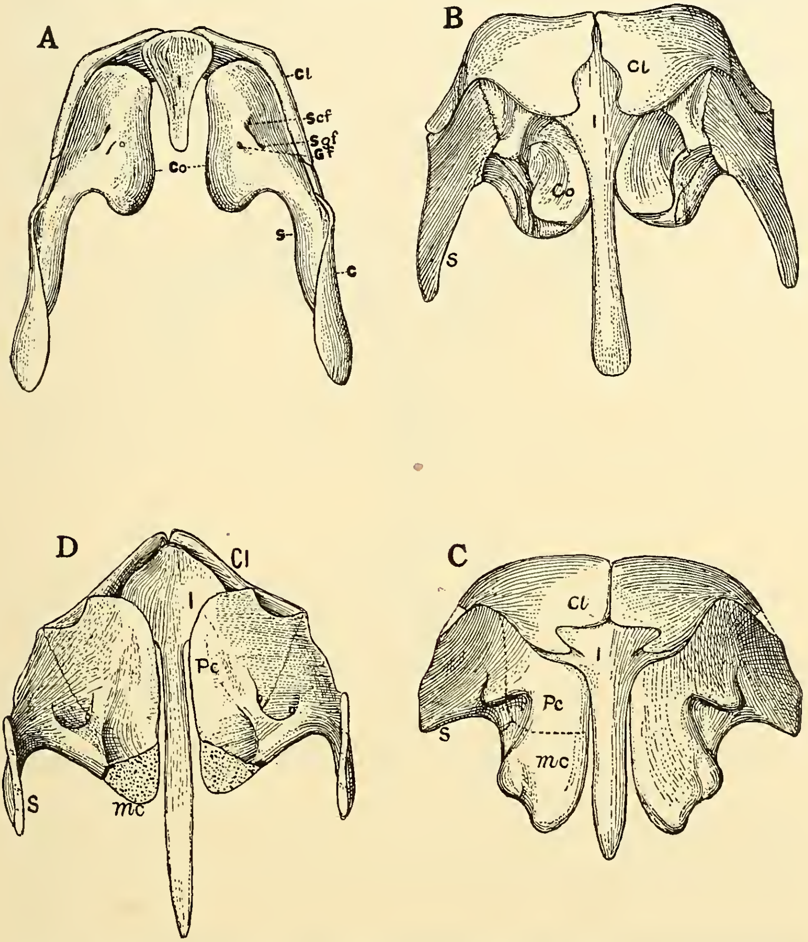

Fig. 96. Pectoral girdles: A, *Cacops* (Temnospondyli), from above. One half natural size. B, *Seymouria* (Cotylosauria), from below. One half natural size. C, *Diadectes* (?), from below. One half natural size. D, *Varanops* (Theromorpha), from above. One half natural size.

the epicoracoid, are yet doubtful, and will be discussed later. There is also a median, unpaired bone in these mammals, the *interclavicle*, unknown in other mammals.

Primitively (Figs. 95, 96), that is, in the oldest known reptiles, the pectoral girdle is composed of eleven separate and distinct bones, at least in early life: the median interclavicle and a clavicle and *cleithrum* on each side, all five of dermal origin, together composing the secondary or *clavicular* girdle; and three bones on each side, the scapula and two coracoids,[1] all of endoskeletal origin, composing the primary or *scapular* girdle.

The cleithrum (Fig. 95), a relic from the fishes, disappeared in Triassic times, after long existence as a mere vestige. The posterior of the two coracoids also disappeared in late Triassic times, in reptiles at least, though a vestige may possibly be present in our own shoulder girdle. The scapula, clavicles, and anterior one of the two coracoids, the so-called procoracoid, are still present in most reptiles; in snakes only are they wholly absent, though much reduced and non-functional in some lizards.

Clavicular Girdle

The clavicular girdle is variable among the temnospondyl amphibians, dependent, as in reptiles and higher vertebrates, upon the habits of the animals. In the aquatic types of all Stegocephalia the clavicles and interclavicles are rugose [on the ventral side], heavy and broad, forming more or less of a pectoral buckler — a peculiar adaptation to their water habits, perhaps in a measure analogous to the plastron of the turtles or the extraordinary development of the coracoids in the plesiosaurs. In such forms also, the cleithrum is reduced. The girdle in the adult land forms, of which *Eryops* (Fig. 108) and *Cacops* (Fig. 96 A) may be taken as types, is almost indistinguishable from that of their contemporary cotylosaurs, except that the cleithrum is larger and the interclavicle less elongate. They are smooth throughout in *Cacops*, the more terrestrial form.

Cleithrum. The cleithrum so generally characteristic of the Stegocephalia (Figs. 96 A, 108) was doubtfully ever functional in reptiles,

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[1] [According to Watson, the coracoid originally was a single piece which never became subdivided in the amphibians, cotylosaurs, or ordinary reptiles, the subdivision occurring only in the Theromorpha, Therapsida, and mammals.— Ed.]

whatever may have been its function in the amphibians; and it was never large. It is known only in certain members of the Cotylosauria, Theromorpha, Dinocephalia, and Anomodontia, best developed perhaps of all in *Diadectes* and its allies of the Cotylosauria (Fig. 95), where its somewhat spatulate upper extremity partly overlies the front, upper border of the scapula, articulating below with the stem of the clavicle. It is vestigial in some forms and seems to be quite wanting in others. Among the Theromorpha it has been observed in *Edaphosaurus* (Fig. 98) as a rod-like bone at the upper front border of the scapula. In the Anomodontia and Dinocephalia (Fig. 107 D) it is a feeble splint, clearly a vestige. There have been several theories as to what has become of it, but none is demonstrable. Its vestigial condition in various cotylosaurs indicates its entire disappearance.

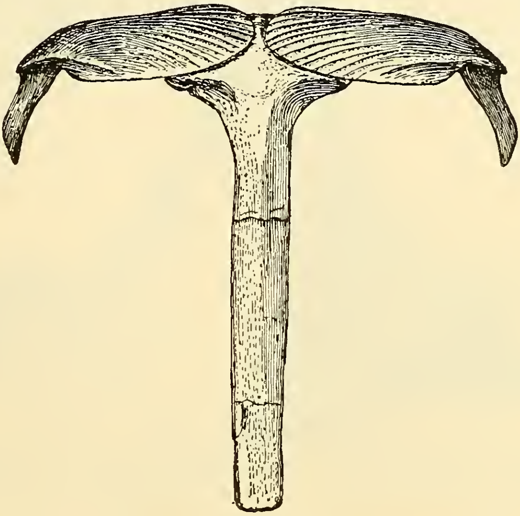

Fig. 97. Clavicles and interclavicle of *Ophiacodon* (Theromorpha).

Clavicles. Clavicles are usually present in reptiles. They are absent in the Crocodilia, serpents, Mosasauria, and some Sauria; more or less vestigial in some lizards; and either absent or vestigial in the Pterosauria and Dinosauria.

In crawling reptiles (Figs. 96 B–99) they are usually curved bones, with a dilated mesial extremity, articulating on the ventral side of the end of the interclavicle; and a more or less slender stem which articulates with the front border of the scapula, or its acromion when present, and also with the lower end of the cleithrum when that bone is present. In modern lizards the clavicles articulate usually with the front border of the cartilaginous suprascapula (Fig. 99). The inner end in some lizards is broad and perforated (Fig. 99 c).

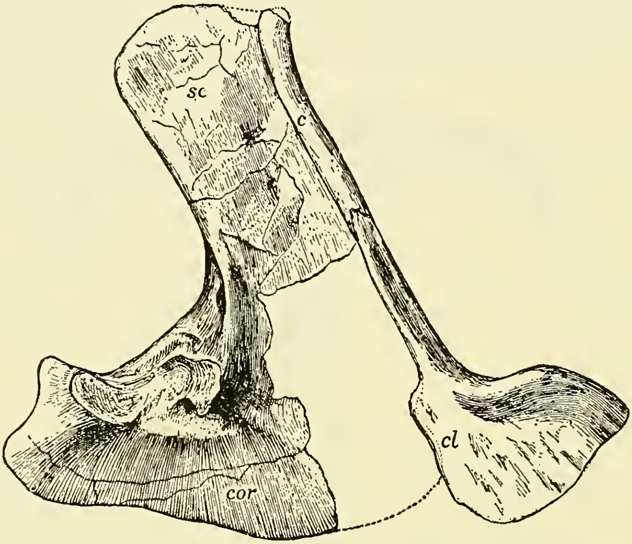

FIG. 98. *Edaphosaurus novomexicanus* (Theromorpha). Pectoral girdle, two fifths natural size: *c*, cleithrum; *cl*, clavicle; *sc*, scapula.

The clavicles of the Chelonia are known as the epiplastra of the plastron (Fig. 100). In the Nothosauria (Fig. 101) they are normal but very stout, firmly united with the scapula and with each other. The clavicles of the Plesiosauria (Fig. 102) are remarkable in some respects. Usually they are a pair of thin, triangular bones, lying upon the *inner* or visceral surface of the proscapular process of the scapula (corresponding to an acromion), of the interclavicle and sometimes also of an anterior process from the coracoid; they may be absent. In the Ichthyosauria (Fig. 103), they are slender, sometimes coössified with each other; nor are they expanded mesially in either the Phytosauria or Choristodera (Fig. 104), and all water reptiles. Doubtful vestiges of the clavicles have been reported in the pterodactyls.

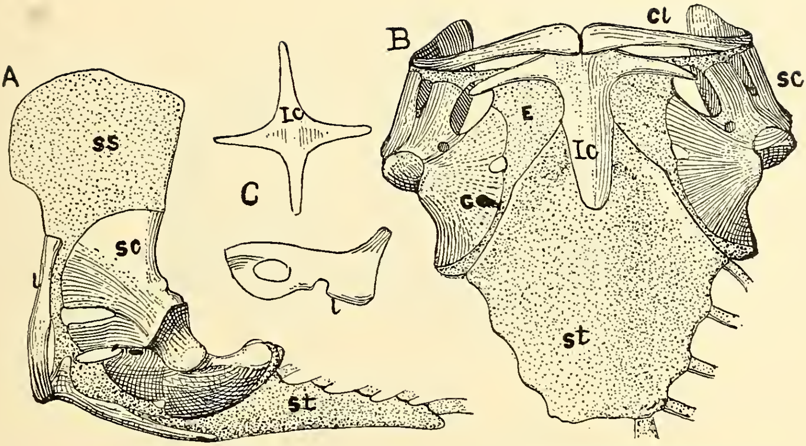

Fig. 99. Pectoral girdles (Lacertilia): A, B, *Iguana;* C, *Zonosaurus* (after Siebenrock). Natural size.

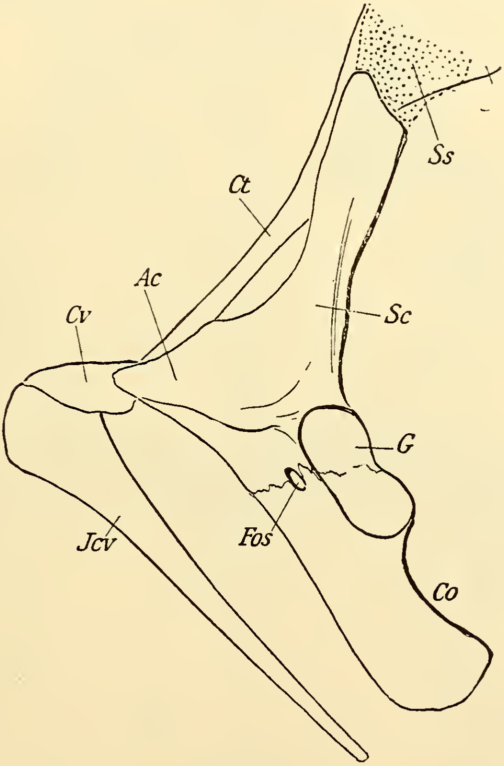

Fig. 100. Primitive chelonian pectoral girdle: *Stegochelys.* After Jaekel.

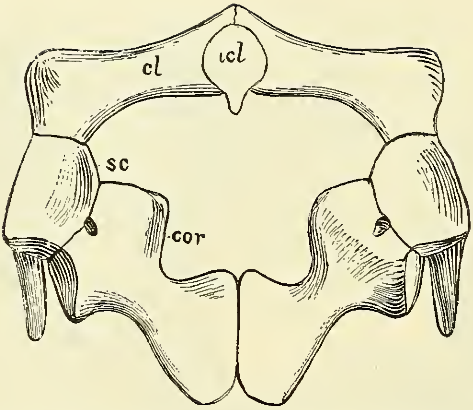

FIG. 101. Pectoral girdle of *Nothosaurus* (Nothosauria), from photograph by E. Fraas: *icl*, interclavicle; *cl*, clavicle; *sc*, scapula; *cor*, coracoid.

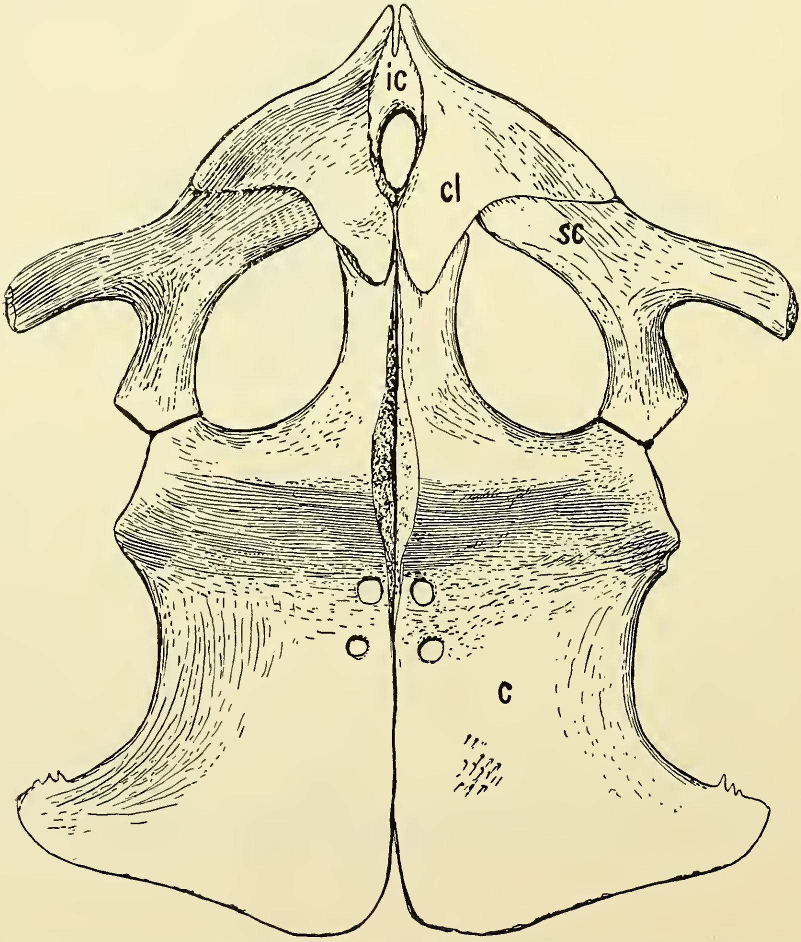

FIG. 102. Pectoral girdle of *Trinacromerum* (Plesiosauria), from above: *ic*, interclavicle; *cl*, clavicle; *sc*, scapula; *c*, coracoid.

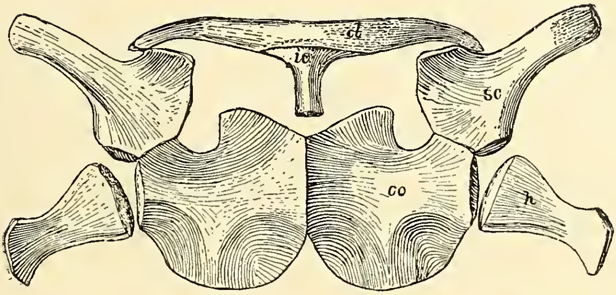

FIG. 103. Pectoral girdle of Ichthyosaur, *Baptanoden* (*Ophthalmosaurus*). After Gilmore.

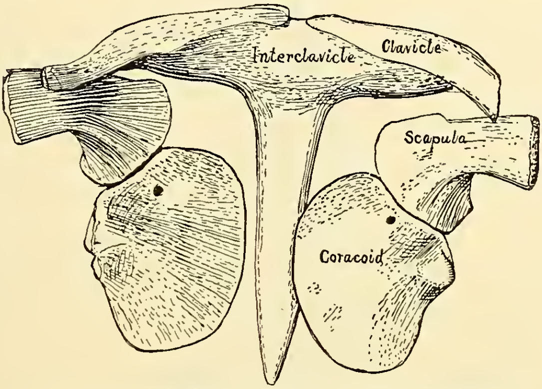

FIG. 104. Pectoral girdle of *Champsosaurus* (Choristodera). After Brown.

Interclavicle. The interclavicle in the earliest-known reptiles (Fig. 96 B, C, D) is an elongate bone with a dilated but not T-shaped anterior extremity. The stem underlies the approximated mesial borders of the coracoids, usually extending beyond them. In a specimen referred to *Pantylus* (Fig. 105), a primitive cotylosaur, the interclavicle is forked in front and somewhat fan-shaped behind, shaped very much like that of the monotremes. In the later cotylosaurs the front end is more dilated, as usual with all later reptiles. In the known forms of the Therapsida (Fig. 107 C) the shape is usually like that of the Theromorpha and Cotylosauria. It is very short and fan-shaped in *Lystrosaurus* of the Anomodontia (Fig. 94 D), where Broom attributes its reduction to water habits.

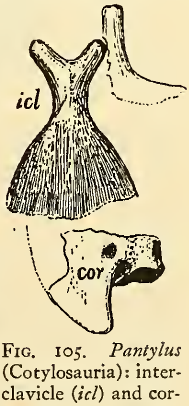

FIG. 105. *Pantylus* (Cotylosauria): interclavicle (*icl*) and coracoid (*cor*). Natural size.

In the Chelonia it is the entoplastron (Fig. 100.) In the Crocodilia (Fig. 121 D) and Mosasauria it is slender and free at the anterior end. The stem is short in the Ichthyosauria (Fig. 103), vestigial in the Nothosauria (Fig. 101). When present in the plesiosaurs it is an oval or triangular bone, in the earlier forms imperforate, in the later ones with a median interclavicular notch or foramen (Fig. 102). The interclavicle is absent in the Pterosauria, Dinosauria, chameleon lizards, and some plesiosaurs.

Scapular Girdle

The scapular girdle, or scapulo-coracoid of the aquatic temnospondyl amphibians of early Permian times, like that of the aquatic reptiles, is broad and short, but that of the terrestrial types is practically indistinguishable from the girdle of the contemporary reptiles. Each side, in both the amphibians and early reptiles, is composed of three bones more or less closely fused: a dorsal one, the *scapula*, and two ventral ones; the anterior one commonly called the *procoracoid;* and a posterior one, often called metacoracoid. The posterior bone was lost in all reptiles by the close of Triassic times.[1]

The three bones of the land Stegocephalia (Figs. 96 A, 108) are so firmly coössified that their sutural distinctions have rarely been observed. Among the Cotylosauria (Fig. 96 B, C) the union was less firm, or became invisible later in life; their sutural divisions have occasionally been observed. Among the Theromorpha, the posterior coracoid, the *metacoracoid*, is often found separated (Fig. 106), or united by a loose suture; in some forms (Fig. 96 D) it remained cartilaginous throughout life, and in all forms it probably did not ossify till growth was far advanced. Among most of the Therapsida the three bones (Fig. 107 A, B, D) fuse in maturity, but not in some, if not all, the Dinocephalia (Fig. 107 D). In the Proganosauria the division between the two bones, if present, has never been observed. In the Eunotosauria of the Upper Permian, the two bones are distinct. In no other reptile has the metacoracoid been certainly observed, though it has been affirmed in the Rhynchocephalia (*Hyperodapedon*), an error.

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[1] [For a different view of the fate of the two coracoids see Watson, 1917, *Journ. Anat.*, vol. LII; Romer, 1922, *Anat. Record*, vol. XXIV, pp. 39–47. — ED.]

It is probable that the three bones early acquired a firm union, both ontogenetically and geologically, and that there was a progressive separation and delayed ossification of the posterior bone in the line leading toward the modern reptiles at least. It is known that in *Ophiacodon* from the Permocarboniferous, ossification of the metacoracoid did not occur till late, and that in *Varanops* (Fig. 96 D) it never ossified. This doubtless explains its absence in all known specimens of *Paleohatteria*, formerly placed among the Rhynchocephalia. Paleontological evidence that it is the posterior bone

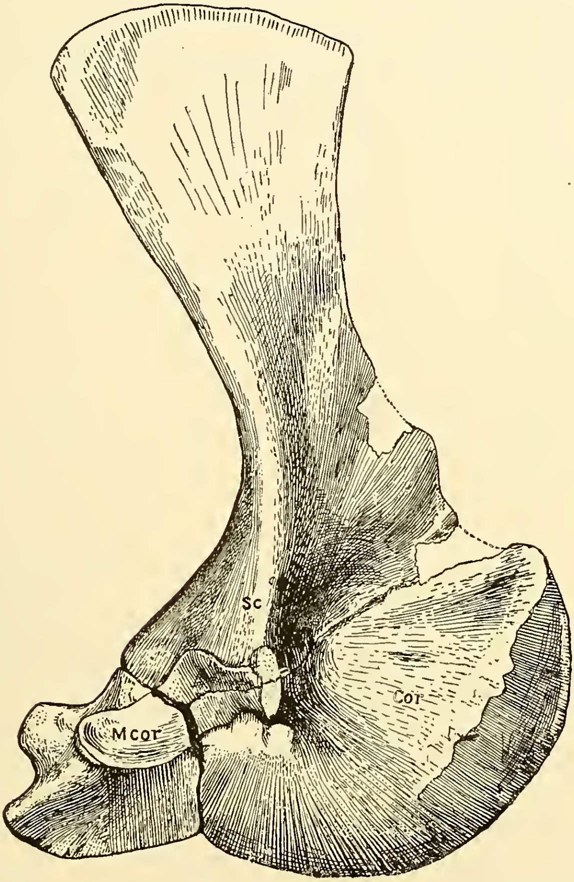


FIG. 106. *Dimetrodon* (Theromorpha): scapula (*sc*), coracoid (*cor*), and metacoracoid (*mcor*).

which has functionally disappeared in all modern reptiles, and not a fusion of the two, now seems complete. The coracoid of lizards, crocodiles, and *Sphenodon* is homologous with the anterior of the two bones, the so-called procoracoid. It was Howes and Lydekker who first reached this conclusion, and who proposed the name metacoracoid for the posterior bone. Whether this conclusion is the right one so far as the monotreme mammals are concerned is still a debatable question. The two coracoids in these mammals seem, and generally are considered to be, homologous with those of the early reptiles. Broom has suggested that in the evolution of the mammals the posterior bone, that is, the metacoracoid, was retained, though lost in the reptiles. Gregory, however, has offered another solution of the problem that would homologize the anterior or "procoracoid" of the reptiles with the posterior bone of the Monotremata. He thinks that three elements are involved in the problem of their evolution:

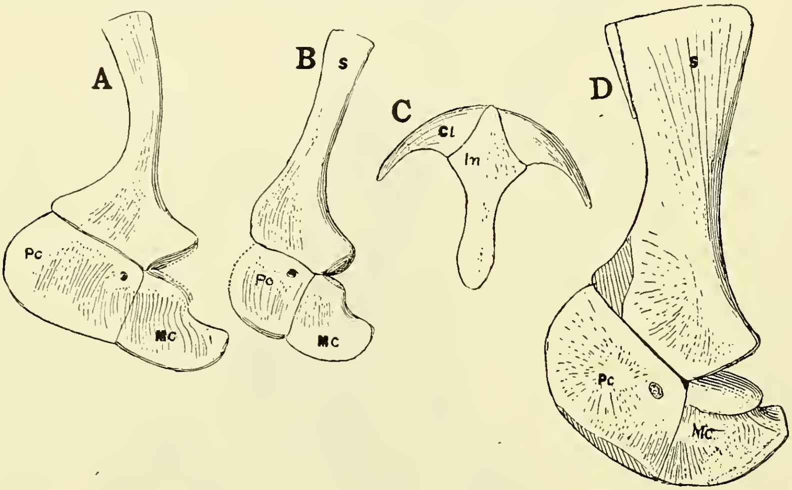


Fig. 107. Pectoral girdles (Therapsida): A, *Galeops* (Dromasauria). Natural size. B, *Galechirus* (Dromasauria). Natural size. C, *Galepus* (Dromasauria). About three fourths natural size. D, *Moschops* (Dinocephalia). One fifth natural size.

"(*a*) The epicoracoid of *Sphenodon*, lizards and monotremes, a sheet of bone lying immediately above the clavicles, and never reaching the glenoid surface.

"(*b*) The true coracoid, or so-called procoracoid, lying behind the clavicles, originally pierced by the coracoid foramen, primitively forming at least the front part of the glenoid, often articulating with the sternum.

"(*c*) The metacoracoid of Permian reptiles, originally forming the back part of the glenoid region, lost in later reptiles (Williston), and in mammals except when preserved as a vestigial element."

It is true that such an element as the epicoracoid has not been found ossified in the early reptiles, but neither have numerous other bones in the mesenchyme of mammals, and its ossification in mammals would be nothing remarkable. A comparison of the epicoracoid of lizards (Fig. 99 B) with that of monotremes will show their identity in relations. And doubtless a similar epicoracoid filled in the interval between the coracoids above the clavicles and interclavicles in the early reptiles (Fig. 96 D). Should it eventually result that Broom's theory is the correct one, that both coracoids have remained in the Monotremata, the posterior one of which presumably represents the chief ossification of the coracoid process of higher mammals, then modern reptiles have no true coracoid, and the bone so called must be known as the procoracoid. The author believes that Gregory's theory is more probable. But, until the real homologies are fully determined, and to save confusion for the present, the terms procoracoid for the anterior bone, metacoracoid for the posterior are adopted in this work.

In all known reptiles possessing a metacoracoid, the suture separating it from the procoracoid enters the glenoid fossa (Fig. 106), except in certain therapsids (Fig. 107), where it joins the scapular suture a little in front of the articular surface. It passes directly inward to terminate in the free border. The scapula-procoracoid suture, in all the Cotylosauria and Theromorpha (Fig. 106) at least, divides nearly equally the glenoid surface in front of the metacoracoid, and is thence directed forward and upward to terminate in the front border.

The supracoracoid foramen, always present in the procoracoid (Figs. 95, 96, 99, 100, 106, 107), though not in the epicoracoid of the monotremes, and usually present in the coracoid of later reptiles (Figs. 112, 113), is absent in the Chelonia (except the Triassic *Stegochelys*), the Pterosauria, Ichthyosauria, Plesiosauria, Rhynchosauria (*Howesia*), many Phytosauria, and the Thalattosauria — chiefly water reptiles, it is seen. It may, in some, be represented by a notch between the scapula and coracoid (Figs. 103, 111), doubtless its original position.

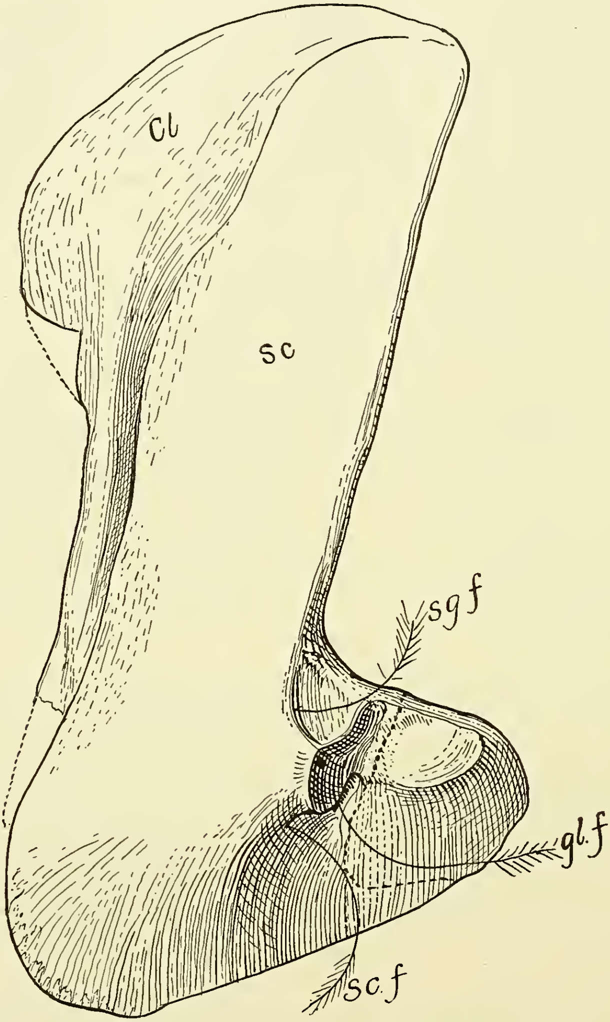


Fig. 108. Pectoral girdle of *Eryops* (Temnospondyli).
Two thirds natural size.

The scapular girdle of the terrestrial temnospondylous (Fig. 108) amphibians has three foramina piercing it: the supracoracoid foramen, already mentioned, entering a little in front of and below the glenoid fossa and opening on the inner side at the lower end of the subscapular fossa; the *glenoid* foramen, entering the glenoid fossa and opening on the inner side in front of the subscapular fossa; and the *supraglenoid* foramen entering the supraglenoid fossa near the hind border and opening at the upper end of the subscapular fossa. The glenoid foramen has not been observed in reptiles. The supraglenoid foramen is present in the Cotylosauria (Fig. 95), Theromorpha (Fig. 96 D), probably the Therapsida, in most modern Lacertilia (Fig. 99), and in *Sphenodon*. It will probably be found in many other forms when searched for. Its external orifice, however, varies much, even in the Theromorpha. In *Ophiacodon* only, so far as has been observed, does it enter the supraglenoid fossa back of the border; more usually, as in many modern reptiles, it is on the outer face of the scapula in front of the border, at a variable distance above the glenoid surface. A small artery traverses it, according to Douthitt.

In the early cotylosaurs and theromorphs (Fig. 106) the glenoid articulation is more or less spiral or "screw-shaped." In most other reptiles it is a simple, oval cavity. In the pterosaurs (Fig. 109) it is saddle-shaped, concave in the dorsoventral, convex in the conjugate, diameter, permitting motion of the arm in two planes only, dorsoventral and antero-posterior.

The double coracoids are never elongated transversely. Turned inward at nearly a right angle from the plane of the scapula, they were approximated along their mesial borders (Fig. 96 D), as shown by many specimens in which they have been found in place. Doubtless *epicoracoid* cartilages occupied the interval in front.

In the single coracoid of later reptiles the glenoid articulation has been completed from behind. In the modern lizards there are emarginations of the mesial border (Fig. 99), the deeper one opposite the supracoracoid foramen; this emargination is very variable in the mosasaurs. It has also been observed in the procoracoid of the theromorphs. The coracoid of the Pterosauria (Fig. 109 A), Chelonia (Fig. 109 B), and Crocodilia (Fig. 112) is elongate. When the sternum is present the coracoid articulates with its anterior lateral border.

The coracoids, presumably the precoracoids only, are extraordinarily developed in the Plesiosauria (Fig. 102), where they sheathe

the whole under side of the pectoral region, meeting in a firm median symphysis; in most plesiosaurs throughout their lengths, but in the Elasmosauridae broadly separated posteriorly by a deep emargination, apparently a specialization (Fig. 110).

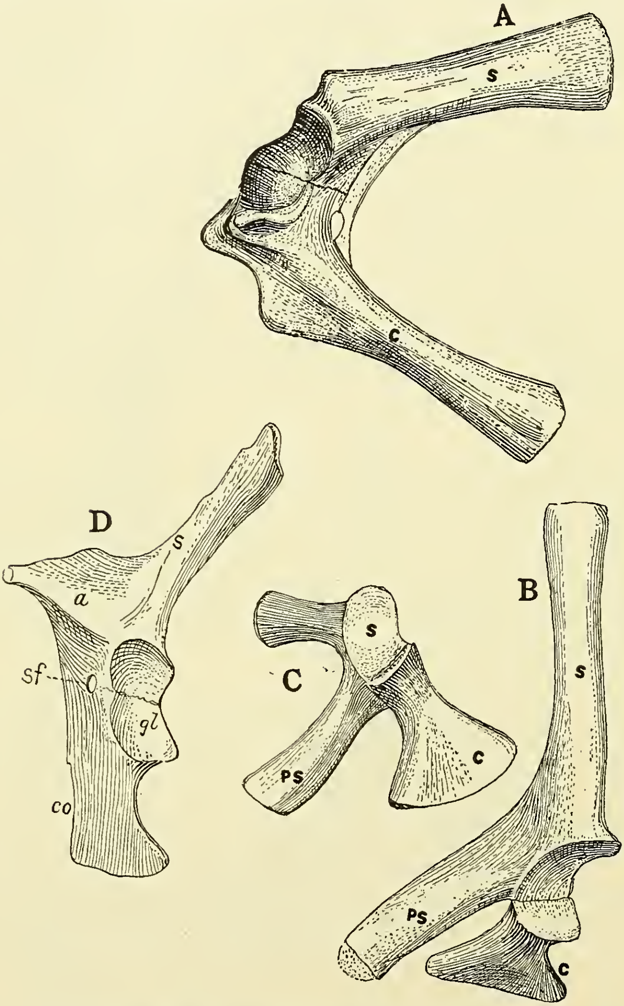


Fig. 109. Pectoral girdles: A, *Nyctosaurus* (Pterosauria). One half natural size. B, C, *Testudo* (Chelonia). One half natural size. D, *Stegochelys* (Chelonia). After Jaekel. One fourth natural size.

In most reptiles the single coracoid is fused with the scapula in adult life, but it is free in the crocodiles, and more or less suturally loose in the early pterosaurs, dinosaurs (Fig. 113), phytosaurs (Fig. 111), and rhynchocephalians.

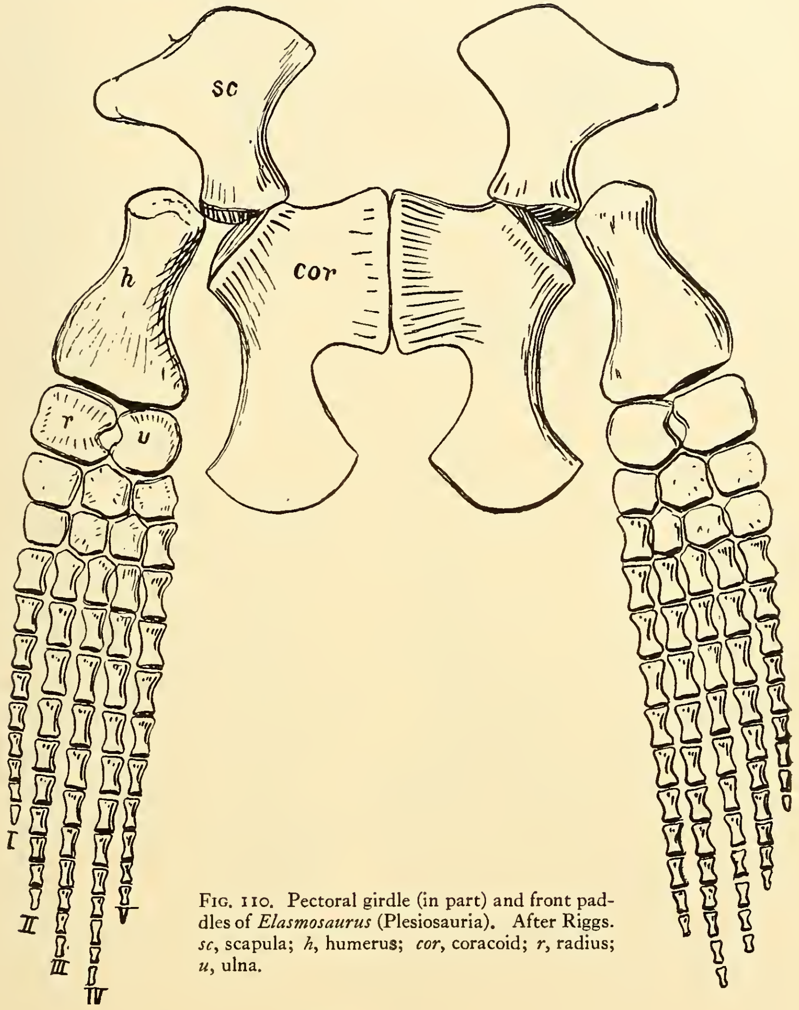


Fig. 110. Pectoral girdle (in part) and front paddles of *Elasmosaurus* (Plesiosauria). After Riggs. *sc*, scapula; *h*, humerus; *cor*, coracoid; *r*, radius; *u*, ulna.

The scapula of the plesiosaurs (Figs. 102, 110) is peculiar in the development of a strong proscapular process projecting downward, forward, and inward, and often meeting its mate in a median symphysis, a character unique among vertebrates. The blade is short and small, of little service for muscular attachment, unlike the scapulae of tail-propelling aquatic reptiles.

Probably the great development of the ventral elements of the pectoral and pelvic girdles in the plesiosaurs implies greatest development of the ventral muscles, used in the antero-posterior and downward movement of the paddles. A clavicular process of the coracoids of the later plesiosaurs (Fig. 102) extends forward to articulate with the proscapular process or with the clavicles. The mode of development of the proscapular process, as shown by Andrews, proves that it is an exogenous process of the scapula, corresponding to the acromion and not to the procoracoid, as it was once thought to do. The scapulae of tail-propelling aquatic reptiles are always short and broad, fan-shaped (Figs. 85, 112). The scapula of the Chelonia is also peculiar (Fig. 109 B, C, D). Enclosed within the thoracic cavity it has two rather slender branches, one extending toward the roof; the other, the proscapular process, springing from near the articular fossa, is directed downward and inward to be attached by ligaments to the interclavicle or entoplastron. Formerly this process was also supposed to be a separate ossification, the procoracoid, fused with the scapula, and on the strength of it a relationship was found with the plesiosaurs. It is now known to be an exogenous process of the scapula. The coracoid is more or less flattened and dilated at its extremity. It is directed inward and backward, and is connected with its mate by ligaments. In *Stegochelys*, a Triassic turtle, the proscapular process is small (Fig. 100).

In *Eunotosaurus*, a Permian genus of South Africa, that has been referred to the Chelonia in a wide sense, the pectoral girdle is of the primitive type, having a moderately long scapula, slender clavicles, and interclavicle, and the two coracoids approximating their mates in the median line.

A distinctly differentiated *acromion* process occurs in reptiles only among the Pariasauridae and especially the therapsids, mammal-like forms from South Africa. A distinct angular process on the front margin of the scapula in the Cotylosauria (Fig. 96 B, C) and Theromorpha (Figs. 96 D, 106), to which the clavicle is attached, however, corresponds to the acromion.

In general, the shorter and stouter are the legs, the shorter and broader are the scapulae. In upright-walking reptiles the scapula is

FIG. 111

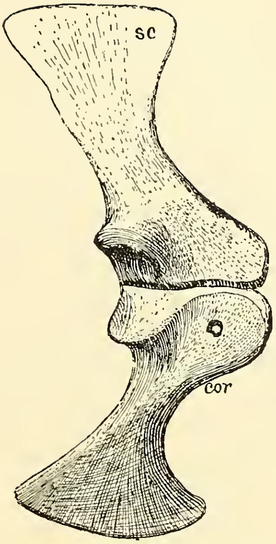


FIG. 112

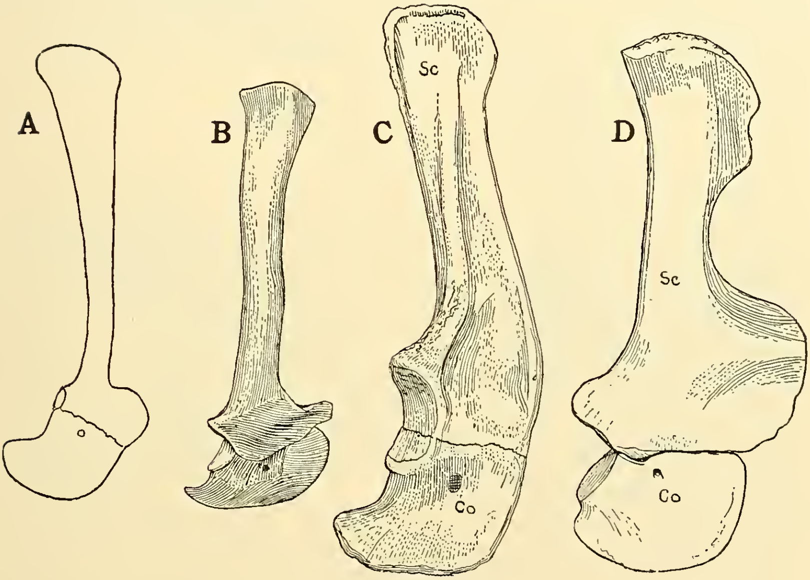


FIG. 113

FIG. 111. Scapula and coracoid of *Rutiodon carolinensis*, an American phytosaur. After McGregor.

FIG. 112. Scapula (*sc*) and coracoid (*cor*) of gavial (Crocodilia).

FIG. 113. Pectoral girdles (Dinosauria): A, *Gorgosaurus* (Saurischia). After Lambe. One sixteenth natural size. B, *Allosaurus* (Saurischia). After Gilmore. About one twelfth natural size. C, *Triceratops* (Ornithischia). After Marsh. One sixteenth natural size. D, *Morosaurus* (Saurischia). After Marsh. One twenty-eighth natural size.

more elongated, in bipedal forms slender. The scapula of the Cotylosauria (Figs. 95, 96, B, C) is relatively short and broad; that of the Theromorpha (Figs. 98, 106) more elongated, but never narrow; that of the therapsid reptiles (Fig. 107) relatively narrow, slender in the Dromasauria. The scapula of the Sauropoda (Fig. 113 D) is relatively long, that of the Predentata (Fig. 113 C) is much more slender, but it is most slender and bird-like of all in the Theropoda (Fig. 113 A, B). The scapula of the Pterosauria (Fig. 109) is always elongated, very slender and bird-like in some of the earlier forms, but stouter and firmly fused with the coracoid in the latest. In the most specialized of all pterodactyls (*Pteranodon*, *Ornithocheirus*) its enlarged distal extremity articulates with the fused spines of the dorsal vertebrae, the only known examples among vertebrates of the articular union of the pectoral girdle with the spinal column.

In the early reptiles the scapula was more nearly erect, or with a slight inclination backward. In the Crocodilia, Pterosauria, and bipedal reptiles, as also birds especially, it is very obliquely placed, the upper end turned backward over the ribs.

The Pelvic or Hip Girdle

(Figs. 114–127)

The *pelvic girdle* or *pelvis*, in reptiles, as in other air-breathing vertebrates, is composed of three bones on each side, more or less firmly coössified in the adult, and collectively known as the *innominate;* the girdle is completed by the sacrum on the dorsal side with which the pelvis is never closely united in reptiles, not even in the Pterosauria. The upper or dorsal bone of the three, that to which the sacral ribs or transverse process of the lumbar vertebra are attached, is the *ilium;* the one on the lower or ventral side in front is the *pubis;* that on the ventral side behind is the *ischium.* On the outer side, where the three bones meet, there is a cup-like depression, sometimes a hole, the *acetabulum,* for the articulation of the thigh bone. In only two groups of reptiles, the Crocodilia and Plesiosauria, is the pubis excluded from union with the ilium. In the snakes and snake-like lizards there are at most only vestiges of the pelvic bones.

The pelvis of the terrestrial temnospondylous amphibians (Fig. 114 A) is almost indistinguishable from that of the contemporary cotylosaur reptiles in early Permian times. The ilium of the rhachitomous forms is not dilated above, as in the reptiles, but even this distinction fails in the more nearly allied embolomerous *Cricotus*, in which the ilium is prolonged backward, quite as in the reptiles. The pubes and ischia meet in a close symphysis without openings of any kind, except the *pubic foramen*, a small hole through the pubis below the margin of the acetabulum, in front of the ischiatic suture, for the passage of the obturator nerve. This "plate-like" structure of the pelvis is characteristic of the Cotylosauria (Figs. 114 B, 115), and more or less of the Theromorpha (Figs. 114 C, 117), Therapsida (Fig. 119), Proganosauria, the Choristodera, and early Rhynchocephalia.

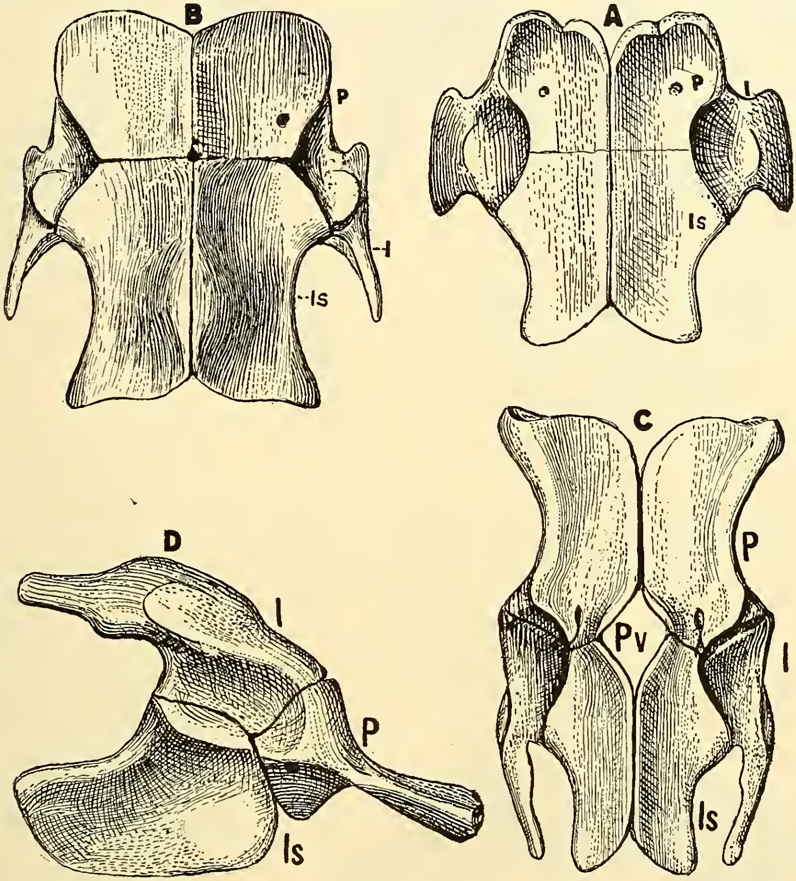


FIG. 114. Pelvic girdles: A, *Cacops* (Temnospondyli), from below. One half natural size. B, *Seymouria* (Cotylosaur), from below. A little more than one half natural size. C, D, *Varanops* (Theromorpha), below and from the side.

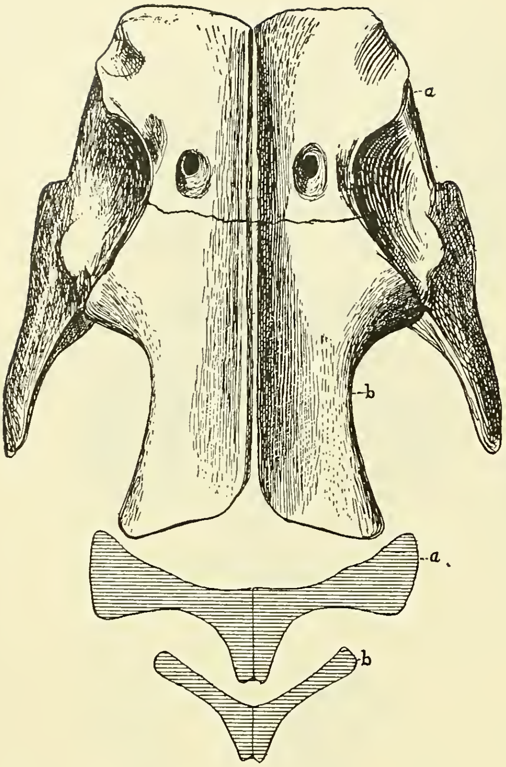


Fig. 115. *Limnoscelis paludis* (Cotylosauria). Pelvis, from below. Two fifths natural size. Cross-section through pubes at *a*; cross-section through ischia at *b*.

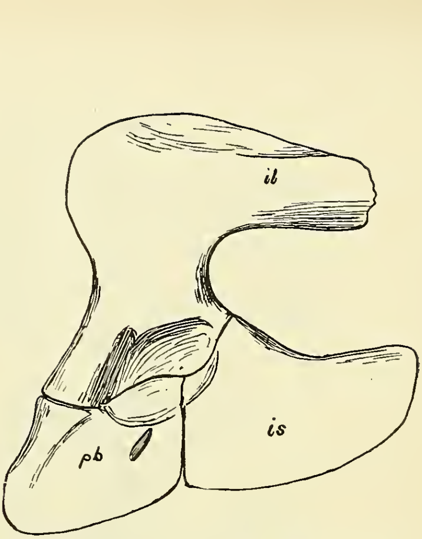
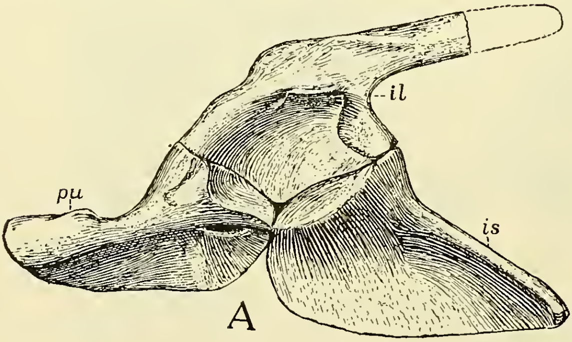


Fig. 116. *Limnoscelis paludis.* Diagram of pelvis, from the side. *il*, ilium; *pb*, pubis; *is*, ischium.



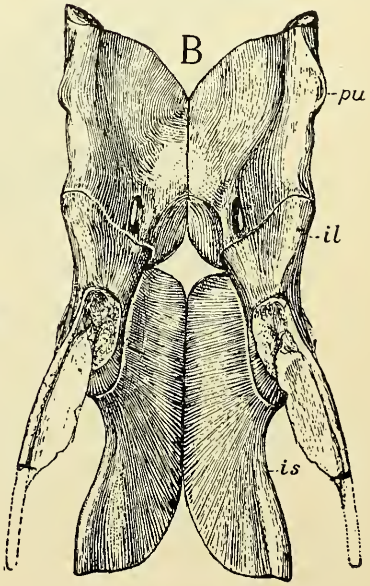


Fig. 117. *Ophiacodon* (Theromorpha). Pelvis. One half natural size. A, from the side; B, from above. *pu*, pubis; *il*, ilium; *is*, ischium.

A small opening soon appeared where the four bones meet below in the Theromorpha (Figs. 114 C, 117), and increased in size, till, in most reptiles, since Triassic times at least, this pubo-ischiatic opening extended on each side nearly to the acetabulum, leaving only a narrow connection between the pubis and ischium (Fig. 118). Later,

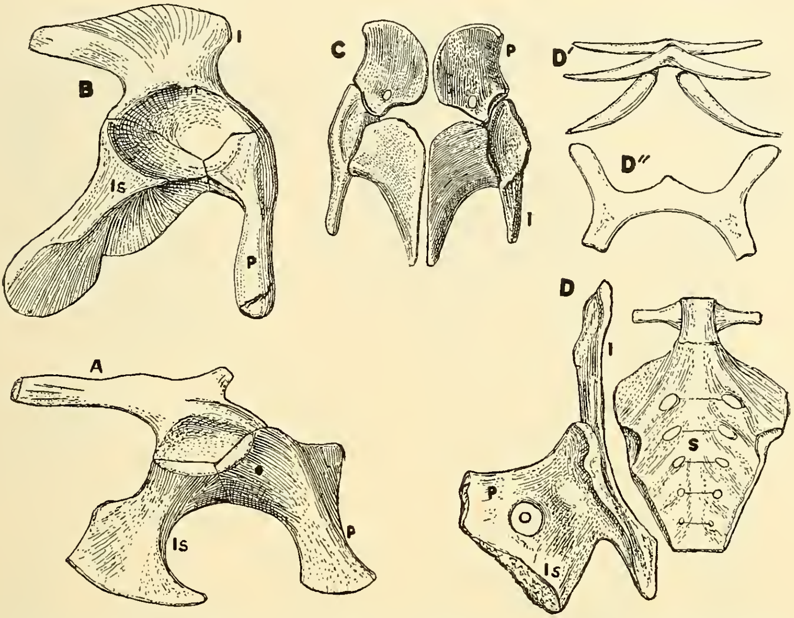


Fig. 118. Pelves and sacrum: A, *Varanus* (Lacertilia), from the right. B, *Erythrosuchus* (Parasuchia), from the right. After Broom. One tenth natural size. C, *Rutiodon* (Phytosauria), from below. After McGregor. One eighth natural size. D, *Nyctosaurus* (Pterosauria), sacrum and right innominate bone from within; D′, anterior parasternal ribs of same; D″, prepubis of the same from below.

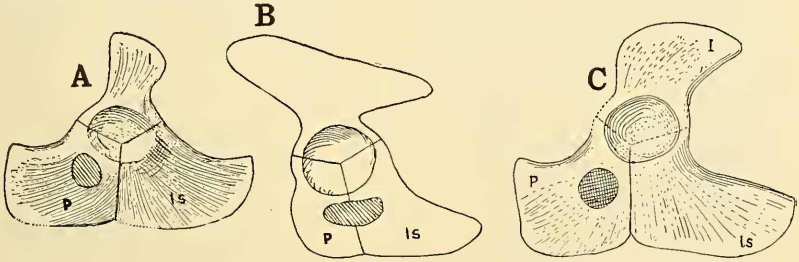


Fig. 119. Pelves (Therapsida): A, *Galechirus* (Dromasauria). After Broom. Nearly natural size. B, *Diademodon* (Cynodontia). After Broom. About one half natural size. C, *Galepus* (Dromasauria). After Broom. Nearly natural size.

the symphysial ends of the pubis and ischium became connected in many by ligaments, or cartilage (Fig. 120), and later in some by bone, producing a false obturator or *thyroid* vacuity on each side. A foramen or vacuity homologous with that in mammals, the so-called

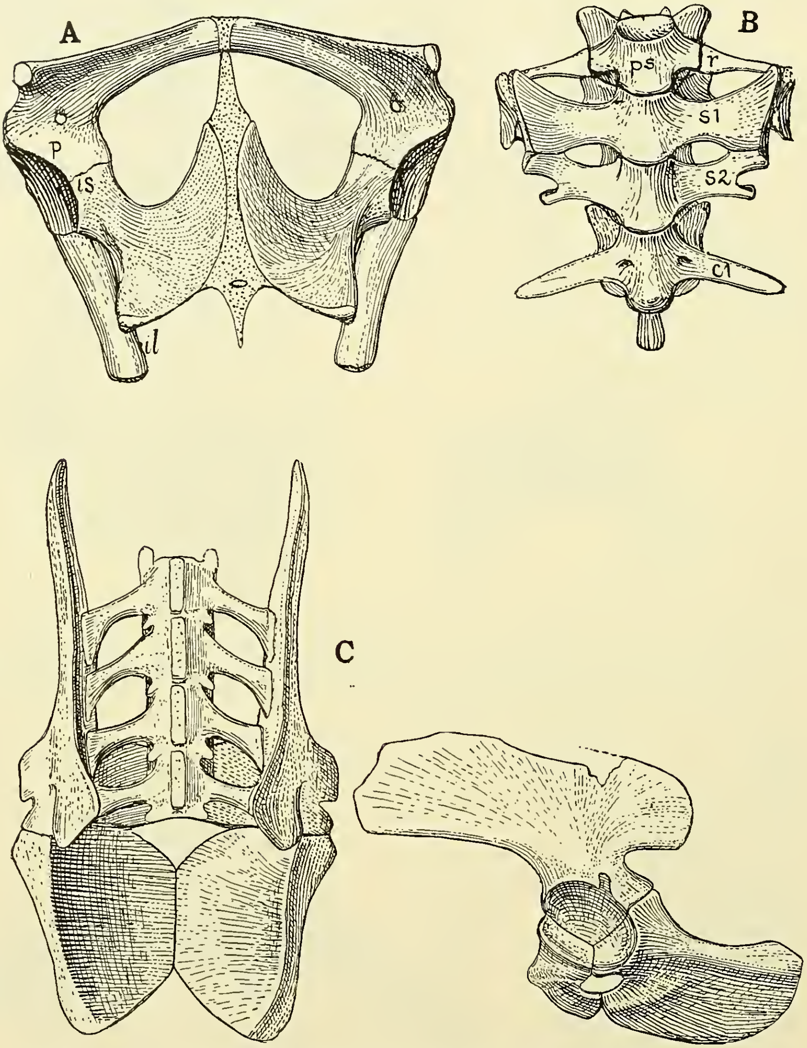


Fig. 120. Pelvis and sacrum. A, *Iguana* (Lacertilia), pelvis from below; B, sacrum from below. About natural size. C, *Dicynodon* (Anomodontia), pelvis, from above and from the side. After Broili. Nearly one half natural size.

obturator foramen, that is between the pubis and ischium with which the real obturator or pubic foramen is merged, occurs in the Theriodontia (Fig. 119), Anomodontia, and later pterodactyls (Fig. 118 D). The formation of a thyroid vacuity in the theriodonts may be due to the gradual increase in size of the pubic or true obturator foramen and its recession backward, as in the Dromasauria, till it finally lies between the two bones, the pelvis still retaining its primitive plate-like character with only a small median pubo-ischiatic vacuity. But this will not explain the thyroid vacuity in *Pteranodon* and *Nyctosaurus* of the Pterosauria (Fig. 118), since it is inconceivable that these reptiles had an unbroken descent from forms without a median vacuity.

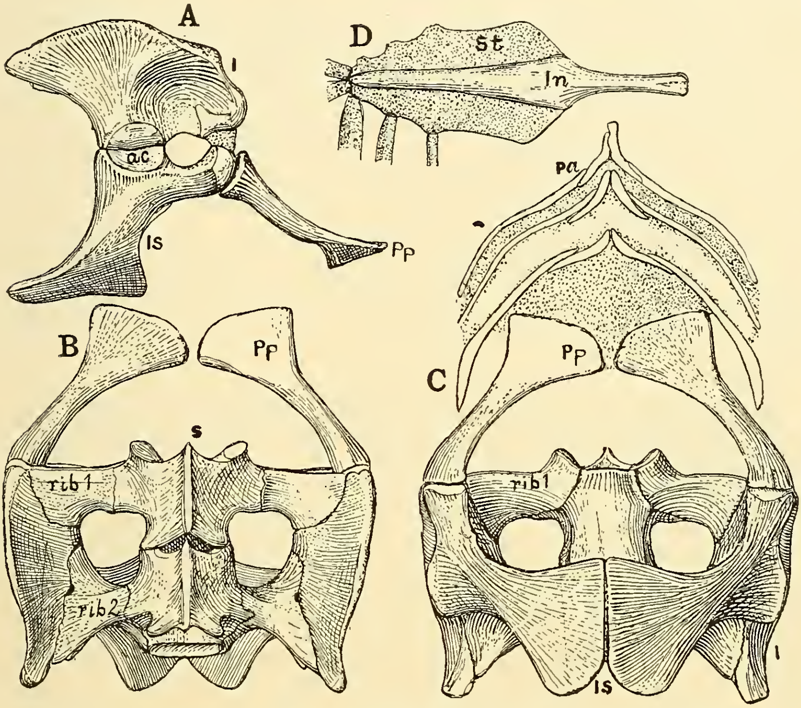


Fig. 121. Pelvic girdle and sternum: *Alligator* (Crocodilia). A, pelvic girdle, from the right; B, the same, from above, showing sacrum; C, the same, from below, with parasternals; D, sternum and interclavicle. One half natural size.

In no reptiles is the pelvis more aberrant than in the Crocodilia (Fig. 121). So characteristic is its structure that it at once distinguishes the order from all others. The ilium is a strong bone firmly united with the two pairs of stout sacral ribs, of which the posterior is the larger. Below, the ilium articulates with the ischium only, to form the acetabulum. In front of the acetabulum it is produced forward to join ligamentously with an anterior process of the ischium, enclosing between them a foramen of considerable size for the passage of the obturator nerve. The ischium is a rather long bone, with a thin, spatulate extremity which joins its mate in a median symphysis. Its anterior process, which may be in part the real pubis, articulates in front with the so-called pubis. This bone is slender, with a thin and dilated anterior extremity which touches, or is closely approximated to, its mate only at its inner anterior corner, and is continuous anteriorly, with a thin but strong plate of fascia joined to the parasternal ribs. With much reason it has long been urged that the anterior projection of the ischium represents the real pubis.[1] In early life it is largely cartilaginous, but becomes fully ossified in the adult. The so-called pubis is probably homologous with the prepubis of the pterodactyls. It has no pubic foramen.

The ilium of the Pterosauria, like that of all bipedal reptiles is produced anteriorly by the sides of the vertebrae, very much so in some forms. The ischium and pubis are closely united into a more or less broad plate, either with a thyroid foramen, as in *Nyctosaurus* (Fig. 118 D) and *Pteranodon*, or with a small pubic foramen below the acetabulum, as in *Rhamphorhynchus*, proving the normal structure of the pelvis, though sutures have not been observed. The prepubes, often called the real pubes, are either paired, as in *Pterodactylus*, or united in a ventral band, as in *Rhamphorhynchus*, *Pteranodon* and *Nyctosaurus* (Fig. 118 D). They articulated with a tuberosity on the front margin of the pubes and in all probability were continued in front with a ligamentous sheath that enclosed the parasternal ribs. The pubes and ischia meet in a symphysis below, though this has been disputed for some.

As remarkable as the pelvis of the crocodiles is that of the Dino-

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[1] [The pubis of the Crocodilia gives attachment to a series of muscles which as a whole are homologous with those that are attached to the true pubis in *Sphenodon* and lizards (Gregory and Camp, *Bulletin*, Amer. Mus. Nat. Hist., 1918; Romer, *ibid.*, 1923, p. 606). If the true pubis of Crocodilia has become vestigial and the prepubis has become the functional pubis, how did the prepubis capture the system of muscle attachments of its predecessor? — Ed.]

sauria, or rather of that division called the Predentata, or order Ornithischia. In the other divisions, the Theropoda (Fig. 122 A) and Sauropoda (Fig. 122 B), the pubes have the normal reptilian structure, though unusually stout and strong, meeting in the middle below in a firm symphysis, much elongated in the Theropoda. The symphysis of the ischia is less strong.

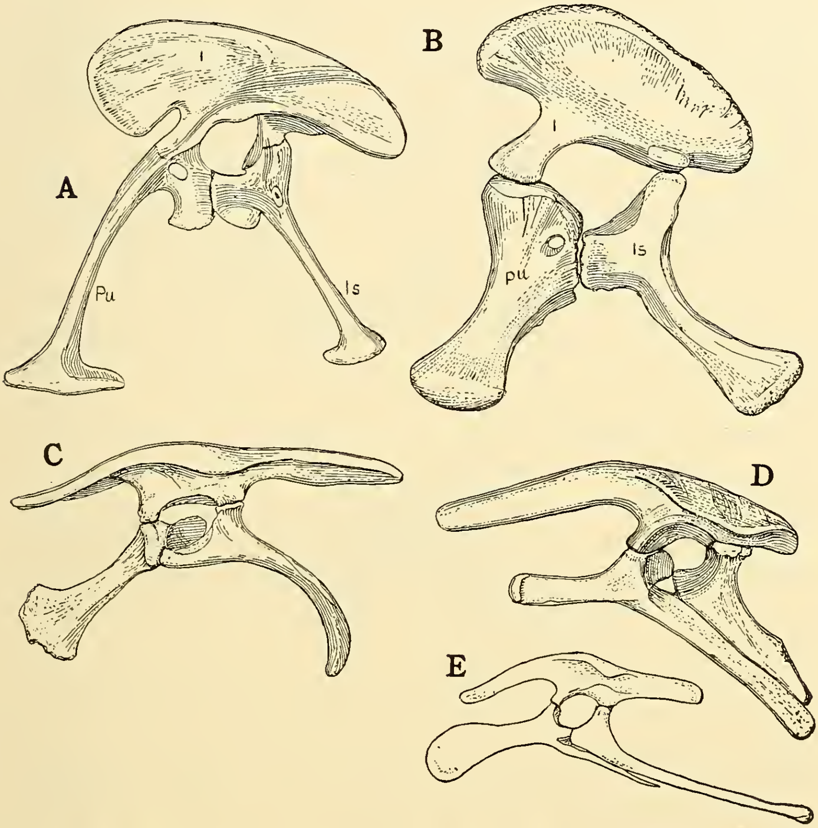

Fig. 122. Pelves (Dinosauria): A, *Ceratosaurus* (Saurischia). After Marsh. One sixteenth natural size. B, *Apatosaurus* (Saurischia). After Marsh. One thirty-second natural size. C, *Triceratops* (Ornithischia). After Marsh. One twenty-fourth natural size. D, *Stegosaurus* (Ornithischia). After Marsh. One twentieth natural size. E, *Trachodon* (Ornithischia). One tenth natural size.

The pubes of the Ornithischia (Fig. 122 C–E) have been the subject of much dispute and speculation. Each is composed of two projections or processes: the anterior one, the so-called *prepubis*, or prepubic process, typically flattened and more or less spatulate distally, is directed forward and downward [upward] and does not join its mate in a median symphysis. At times it may be small or even vestigial (*Ankylosaurus*), but is broad and stout in the quadrupedal Ceratopsia, where apparently it again functions as the normal pubis. The *postpubis*, or postpubic process, typically is long and slender, directed backward immediately below the slender ischium and not meeting its mate in a symphysis; that is, the pelvis is more or less open below, as in birds. The postpubis is vestigial in the heavy quadrupedal Ceratopsia, which have certainly descended from bipedal forms. It is, however, unusually stout in the quadrupedal *Stegosaurus*, possibly as a reinforcement to the ischia in the support of the heavily armored body.

When this peculiarity of the dinosaurian pelvis was first discovered by Hulke and Marsh it was hailed as a direct proof of the dinosaurian ancestry of birds. It may be, however, merely another of the many parallel characters brought about by similar causes. According to one view, the prepubic process is the real pubis, homologous with the pubis of the Saurischia; the postpubic process an outgrowth from it. According to another view, the postpubic process is the real pubis, corresponding to the pubis of birds, the prepubic process homologous with the prepubis of pterodactyls or crocodiles. There has never been, however, any evidence to show that it is derived from a separate center of ossification.

An analogous but not homologous structure is observed in many running birds, the ostriches, *Geococcyx*, etc., where, in addition to the normal, slender, posteriorly directed pubis similar to the postpubic process of the dinosaurs, a more or less prominent pectineal process, arising, however, from the ilium, is directed forward, like that of the dinosaurs. The pubis of birds in its embryonic development turns backward from its normal position. Whence it would appear that the development of the two processes in the dinosaurs has arisen in response to similar causes, and cannot be ascribed to a common heredity, as was once thought. Why the bipedal predentate dinosaurs should have acquired such a remarkable structure of the pelvis, and not the even more bipedal theropods, is not yet entirely clear. It has been ascribed to differences in the posture of the tail in running, but would seem, to the author at least, rather to have been due to differences in procreational methods, the open pelvis of the predentates permitting larger eggs to be extruded, as in the birds. It may be added that the acetabulum of all dinosaurs is perforate, as in the birds.

The pelvis of amphibious or aquatic reptiles is also modified not a little. It lost all connection with the spinal column in the Mosasauria and later Ichthyosauria, but is firmly connected, as usual, in other water animals. The slender ilium of the mosasaurs, like that of the ichthyosaurs, lay loosely in the flesh with its upper end in apposition or ligamentously connected with the end of a transverse process or rib of a single vertebra. The narrow ischia and pubes meet in a symphysis, and there is a pubic foramen.

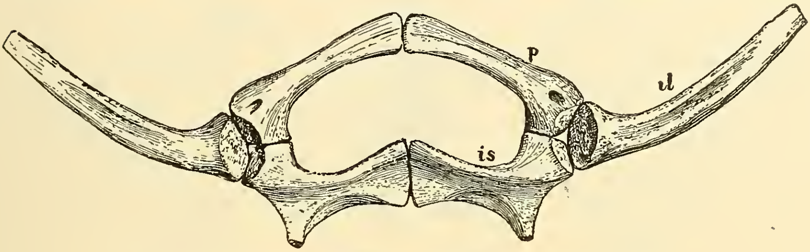

FIG. 123. Pelvis of *Platecarpus* (Mosasauria), from below.

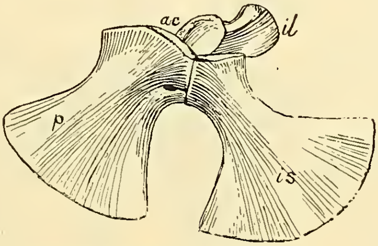

FIG. 124. Pelvis of *Nothosaurus* (Nothosauria). After Andrews.

In the earlier ichthyosaurs the broad ischia and pubes were separated by the broad pubo-ischiatic opening, and the pelvis was connected with a sacrum. In the later forms, however, the pelvis was reduced, the rod-like ilium lay loosely in the flesh, and the pubes and ischia were united without a pubo-ischiatic opening.

In the Nothosauria (Fig. 124) the pelvis, of the usual type, shows only a moderate aquatic adaptation in the broad pubes and ischia.

The ilium is firmly connected with the sacrum, and there is a pubic foramen; the pubo-ischiatic notch is small. In the Plesiosauria (Figs. 125, 126), the slender ilium, connected ligamentously with a sacrum of three or four vertebrae, articulates at its distal extremity with the

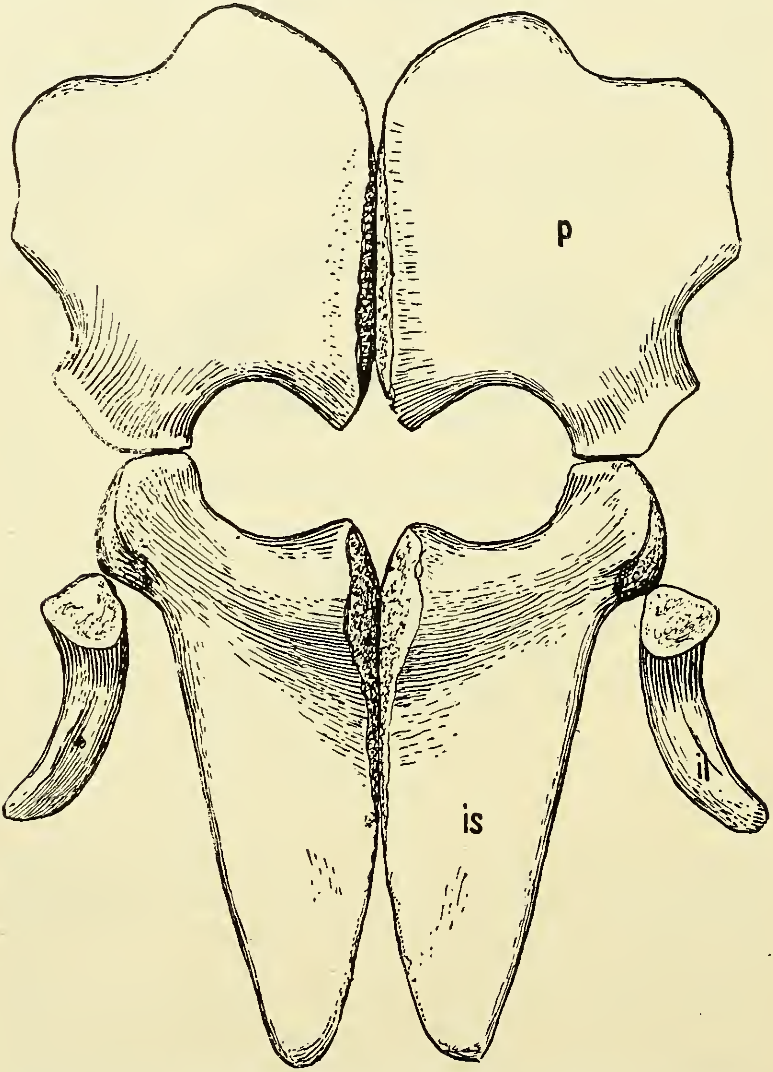

Fig. 125. Pelvic girdle of *Trinacromerum osborni*, an Upper Cretaceous plesiosaur, from above: *p*, pubis; *is*, ischium; *il*, ilium.

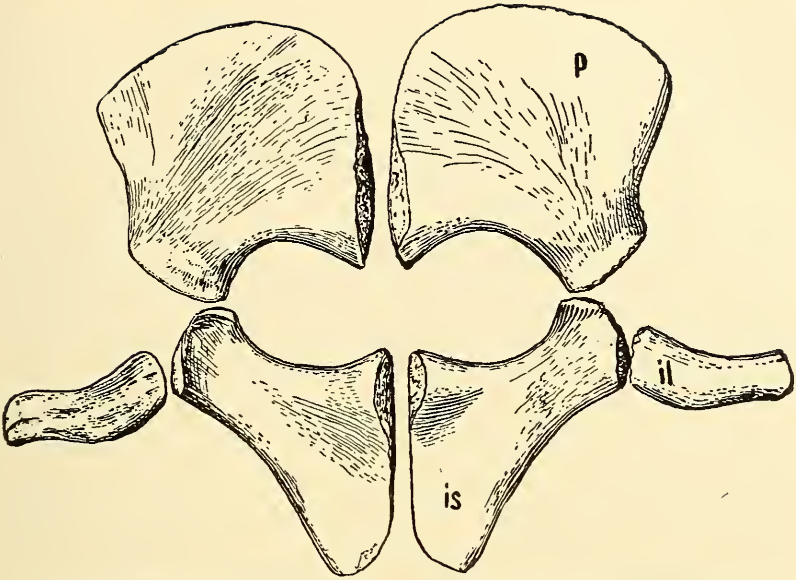

Fig. 126. Pelvic girdle of *Elasmosaurus* (Plesiosauria): *p*, pubis; *is*, ischium; *il*, ilium.

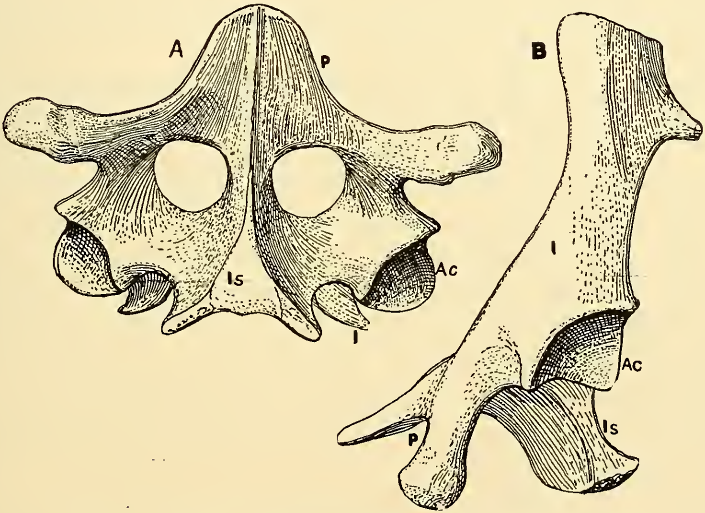

Fig. 127. Pelvis: *Testudo* (Chelonia); A, from below; B, from the side.
One half natural size.

ischium only, and, like that of the Chelonia, is directed upward and backward. The pubes and ischia, like the coracoids, are very broad and flat, secondarily plate-like, meeting in a more or less horizontal symphysis. There is no pubic foramen, and usually the large pubo-ischiatic vacuity is broadly connected across the median line—probably separated by a ligament in life. In some genera, however, *Sthenarosaurus* or *Thaumatosaurus*, for instance, the two bones are secondarily broadly united at their symphyses, producing a false thyroid foramen with which the obturator foramen is confluent, as in mammals. The ischia are triangular or "hatchet-shaped," elongated in the short-necked forms, short in the long-necked.

The pelvis of the Chelonia (Fig. 127), like the pectoral girdle, has been modified by its peculiar relations to the carapace and plastron. There is a large pubo-ischiatic vacuity, often divided in the middle by a cartilaginous septum, but broadly ossified in the land tortoises, as in the plesiosaurian *Sthenarosaurus*. As in the plesiosaurs, there is no separate pubic foramen or notch, rarely absent in reptiles.

The ilium, like that of the plesiosaurs, is elongate and is directed upward and backward to the firm sacrum. The pubis is larger than the ischium and has a stout tuberosity which rests upon the plastron, or, in the Pleurodira, is coössified with it.

Usually in crawling reptiles (Figs. 114–118 A) there is no, or only a small, preacetabular process to the ilium, but always a postacetabular one. In upright-walking animals the preacetabular process is always well developed, sometimes at the entire expense of the postacetabular process. It is unusually long in the Anomodontia (Figs. 120 C, 119), Ceratopsia (Fig. 122 C, E), and Pterosauria (Fig. 118 D), where it is supported by the united or contiguous diapophyses of the lumbar vertebrae, false sacral vertebrae. The ilium is more or less helmet-shaped in the Saurischia (Fig. 122 A, B) as also in some Cotylosauria, Therapsida (*Cynognathus*), and Theromorpha (*Casea*) — all such forms have short toes; possibly it is due to the greater expansion of the gluteal muscles.

The evolution of the reptilian pelvis has been, as we have seen, from the primitive closed and plate-like type, by the progressive development of a vacuity between the ischia and pubes, by the elongation of the anterior process of the ilium, and by its closer union with additional true sacral or lumbar vertebrae.

CHAPTER V

THE LIMBS

Two pairs of limbs are almost always present in reptiles, composed, as in mammals, of four analogous segments: the arm and thigh bones, conveniently called *propodials;* the forearm and leg bones, or *epipodials;* the wrist and ankle bones, or *mesopodials;* the *manus* and *pes*, composed of metacarpals and metatarsals, or *metapodials;* and a variable number of finger and toe bones, known as *phalanges*.

The limbs are best understood and described as though directed outward from the long axis of the body (Fig. 128), the palms of the hands and soles of the feet turned downward or to the ventral side, the epipodials parallel, the thumb or *pollex*, and the big toe or *hallux*, on the anterior or *preaxial* side, the little finger and little toe on the posterior or *postaxial* side. The terms outer and inner are often applied to the anterior extremity, as though directed backward in the axis of the body, the thumb on the outer side. The hind extremities are sometimes described as though parallel with the long axis of the body, with the big toe on the inner side. As the hallux is analogous with the pollex, this nomenclature places them on the opposite sides and should not be used for any vertebrates.

The fore and hind limbs of terrestrial reptiles are of approximately equal length, the hind pair the longer. In aquatic reptiles [*e.g.*, ichthyosaurs, mosasaurs] the front pair are often the larger, and usually the longer; in volant reptiles [pterosaurs] they are much longer than the hind pair. In bipedal reptiles [*e.g.*, later Theropoda] or those usually assuming this posture in locomotion, they are smaller or very much smaller. In climbing and cursorial reptiles the limbs are more or less, sometimes very much, elongated and slender (Fig. 155). The digits of fleet, crawling reptiles are long; those of the more upright-walking kinds (Figs. 145, 141 1), in which the digits of the two sides are brought more nearly parallel to each other, are short. The articular surfaces of the limb joints of aquatic reptiles (Figs. 149, 158) are poorly developed, unextensive, and more or less cartilaginous.

Swimming reptiles with propelling tails [*e.g.*, ichthyosaurs, mosasaurs] have short propodials, sometimes very short; on the other hand, the propodials of limb-propelling water reptiles [*e. g.*, plesiosaurs, proganosaurs] are elongated. The epipodials of ordinary terrestrial reptiles are always somewhat shorter than the propodials. Greater shortening of these bones is indicative of swimming habits, possibly also of burrowing; and in strictly aquatic reptiles they are always very short; indeed the degree of water adaptation may be gauged by the proportional lengths of the epipodials. On the other hand, in springing, leaping, or volant reptiles, they may be considerably longer than the propodials (Fig. 155).

The limbs of some Lacertilia and most Ophidia are wholly absent; some snakes have vestiges of the hind pair, and some lizards only vestiges of either pair or the front pair only. All other known reptiles have four functional limbs.

Primitively (*e. g.*, Figs. 1, 128) reptiles were pentadactylate, with the phalangeal formulae 2, 3, 4, 5, 3 for the front, 2, 3, 4, 5, 4 for the hind pair, the fourth digit the longest and strongest; and most reptiles still retain these characters. The first digit to be lost is the fifth, and only in a few dinosaurs is the first digit wholly lost. In the more upright-walking kinds, those in which the feet of the two sides are brought more nearly parallel in walking, the greater strength of the foot passes more to the preaxial side, and both the fourth and fifth digits may be obsolete or lost, and very rarely the third also. This weakening of the postaxial digits is especially noticeable in the dinosaurs (Figs. 141, 156) and turtles (Fig. 154), in which the posture in locomotion is more like that of mammals. The same character is also observed in the Crocodilia (Figs. 140 A, 157), unlike other crawling reptiles, and tends to confirm Huene's contestation that the ancestors of these reptiles were originally more upright in locomotion than are their descendants.

As a rule the hind limbs of terrestrial reptiles, as of terrestrial mammals, are more specialized than the anterior ones; that is, there are fewer bones, and the ones remaining are more developed than those of the front feet. Among aquatic and volant reptiles, on the other hand, where locomotion is chiefly effected by the fore limbs, these are more specialized. In certain lizards (*Phelsuma*) the first digit has become vestigial, the others are well developed.

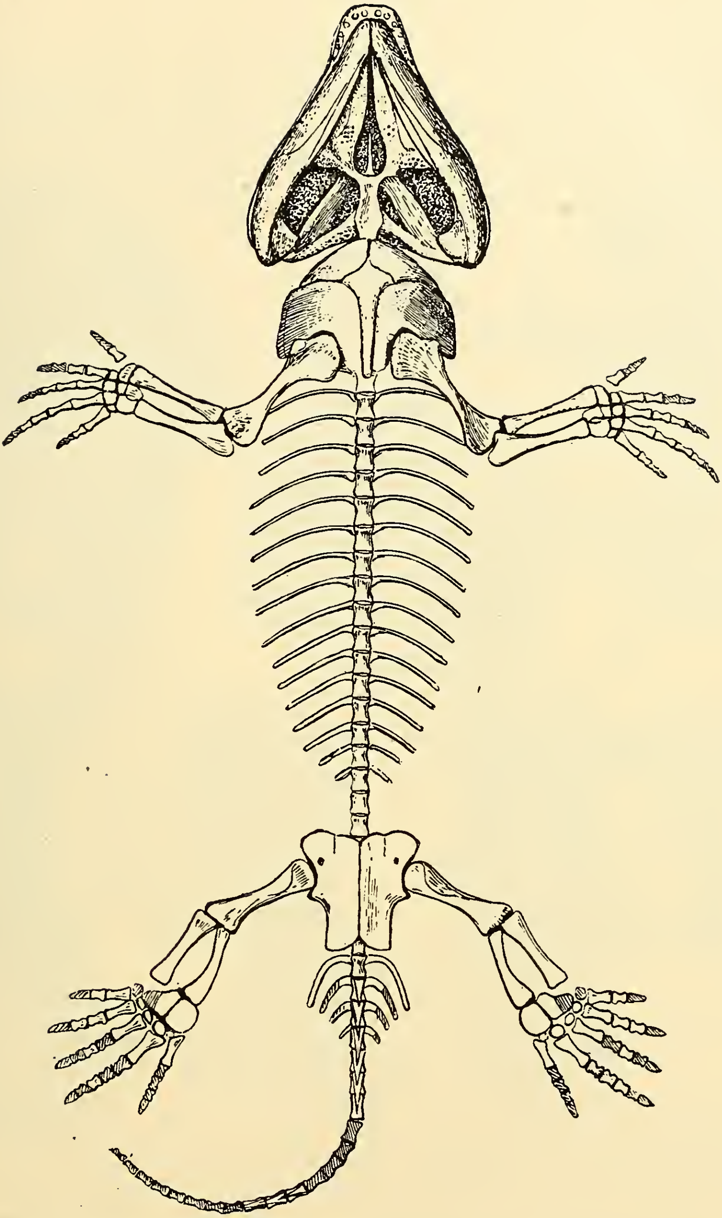

FIG. 128. *Captorhinus* (Cotylosauria): Skeleton, from below. One half natural size.

PROPODIALS

The humerus (Figs. 129–131), or first bone of the anterior extremity, articulates in the glenoid fossa of the scapular girdle, usually by a more or less complete, free, ball-and-socket joint, permitting rotation. In most of the Cotylosauria (Figs. 128, 130, 132) and stouter-limbed Theromorpha (Figs. 129, 131, 134) the articular surface is more or less spiral-like, extending around the head from the ventral postaxial to the dorsal preaxial side, permitting movement in an antero-posterior direction with a concomitant partial rotation as the hand, directed forward obliquely, is brought backward in walking. The bone was not depressible below a horizontal plane without dislocation. The articular surface of the pterodactyl humerus

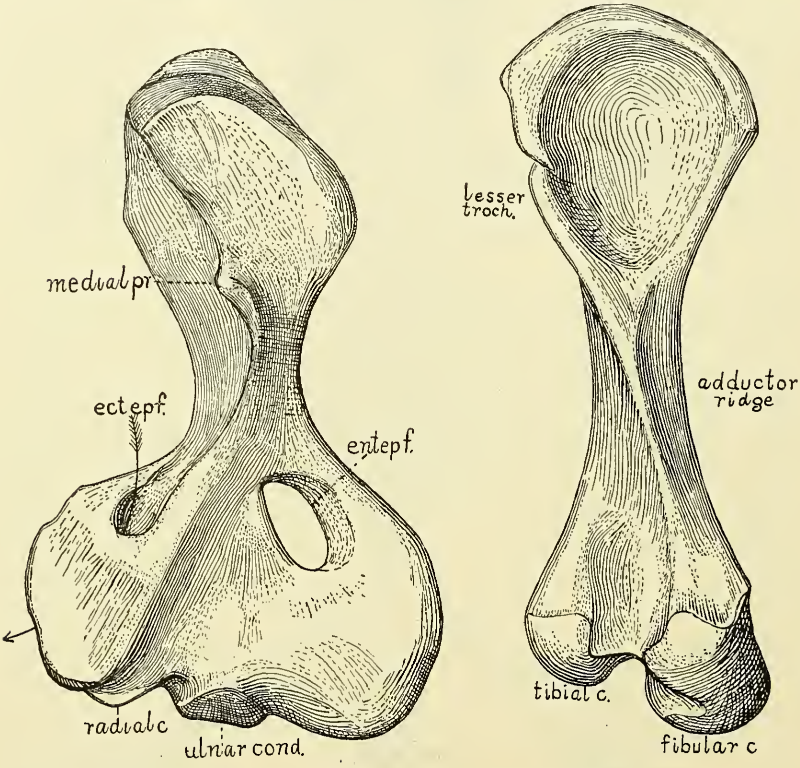

Fig. 129. Theromorph limbs: *Naosaurus*, humerus, dorsal side, femur, ventral side. One half natural size.

(Fig. 141) is saddle-shaped, permitting motion in two planes only — antero-posterior and dorso-ventral.

At the upper or proximal end of the bone, near its articular part, are two more or less prominent processes for the attachment of muscles. That on the preaxial ventral side (Fig. 131), usually situated above the middle third, but often descending nearly to the middle or even below the middle in stout-limbed reptiles, is the

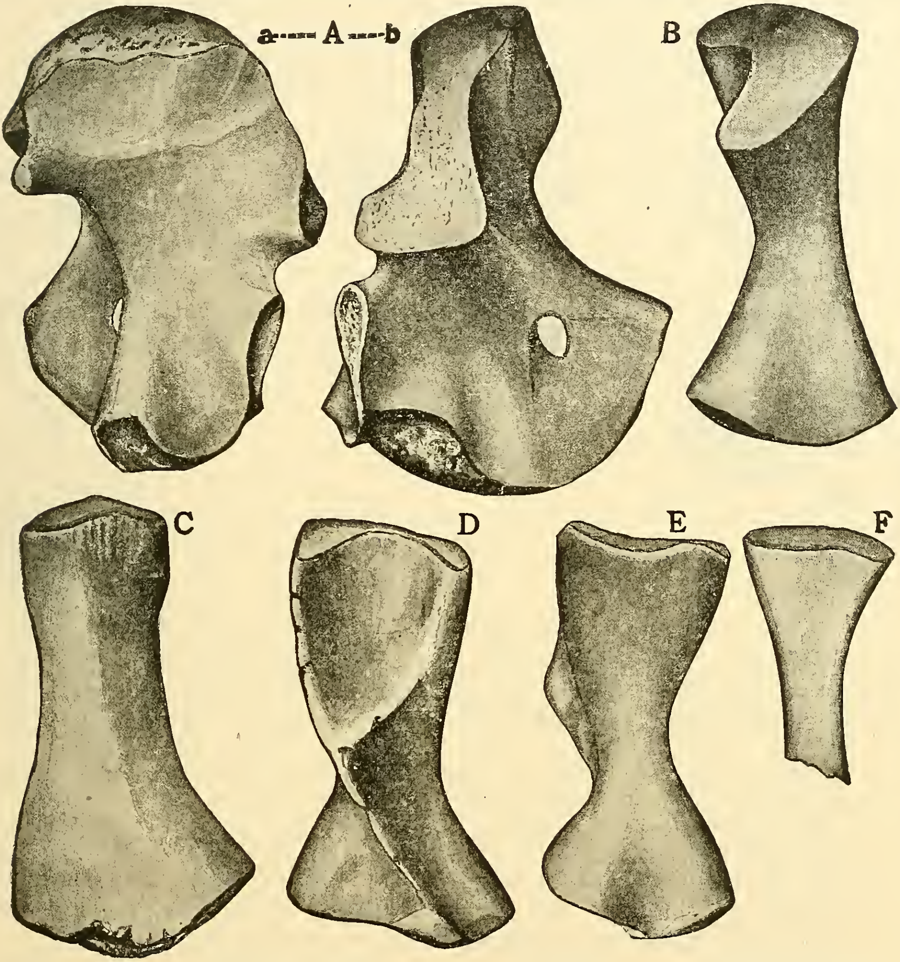

Fig. 130. *Seymouria* (Cotylosauria). Humerus, femur, tibia. A, right humerus, *a* from side, *b* from front; B, left tibia, ventral side; C, radius; D, right femur, from behind; E; left femur, from *Cacops* bone-bed, natural size; F, undetermined.

radial or *lateral* tuberosity or process. On the opposite side, nearer the head, and often not well marked, is the *ulnar* or *medial* tuberosity (Figs. 129, 130). Between the two, on the ventral side, is the *bicipital fossa* (Fig. 131). Immediately below the lateral tuberosity the shaft is usually round or oval in cross-section. Among all reptiles the lateral process is most developed in the pterodactyls (Fig. 141). It is also largely developed in the Cotylosauria (Figs. 128, 130, 133), Theromorpha (Figs. 129, 131, 134), and Anomodontia, sometimes descending below the middle of the bone.

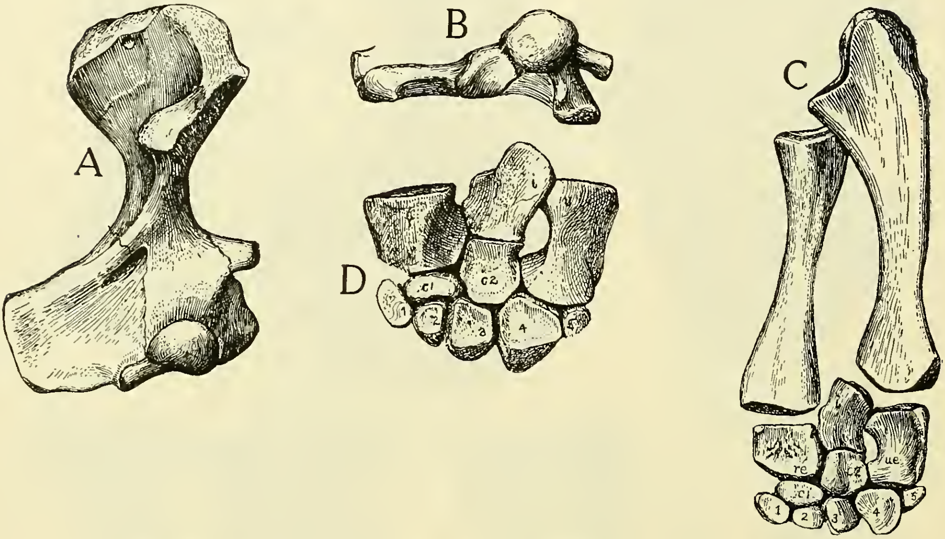

FIG. 131. *Ophiacodon mirus* Marsh (Theromorpha). A, left humerus, ventral side, one half natural size. B, left humerus, distal end, one half natural size. C, left ulna, radius and carpus, ventral side, one half natural size. D, left carpus, dorsal side, three fourths natural size.

The expanded extremities of the humerus are in divergent planes, the angle sometimes slight, at other times approximating or even exceeding a right angle, the bicipital fossa in such cases looking more dorsad than ventrad. The width of the more expanded distal extremity may be less than an eighth of the length of the bone, or may nearly equal it in stout-limbed reptiles like the Cotylosauria (Figs. 130, 133). The distal expansion is always great in the Cotylosauria and Anomodontia, as also in some Theromorpha (Figs. 129, 131). Doubtless in these animals, or some of them at least, the peculiar humerus is to be correlated with the screw-like motion in the glenoid fossa, the horizontal position of the humerus in locomotion, and the more turtle-like mode of progression. The digits in such animals are never long, and the ungual phalanges are short and stout.

At the distal extremity of the humerus (Figs. 131, 133), on the preaxial and more or less ventral side, there is a more or less convex surface, the *radial condyle*, or capitellum, for the articulation of the radius. Contiguous with it on the postaxial side, but more distal and dorsal, is the *ulnar condyle* or trochlea, for articulation of the ulna. In aquatic reptiles (*e. g.*, Fig. 158 C, D) both of these are simple facets at the extremity of the humerus. The projection or process on the radial or preaxial side, above the radial condyle (Figs. 129 A, 131), in the short-limbed cotylosaurs and theromorphs as also the temnospondyl amphibians, sometimes turned more dorsad, is known as the *radial epicondyle*, *ectocondyle*, *ectepicondyle*, or *pre-epicondyle.* In the very stout-limbed cotylosaurs (Figs. 130, 133 *sc.p.*) and theromorphs (Fig. 131), as also the stout-legged temnospondyls (Fig. 136), there is a stout process on the radial side above the epicondyle. It is especially correlated with short digits and doubtless a more turtle-like mode of progression. It may be known as the *supracondylar* process. The distal expansion of the humerus on the ulnar or postaxial side is commonly known as the entocondyle or entepicondyle, misleading terms (Figs. 130, 131, 133 *ent.*).

Piercing the condylar expansions more or less obliquely (Fig. 129 A) are very characteristic foramina in most reptiles. That on the ulnar side, the *entepicondylar* foramen (*entep. f.*), for the passage of the median nerve, occurs in all Cotylosauria, Proganosauria, Theromorpha, and most therapsids, and in not a few mammals. A similar foramen on the radial side, the *ectepicondylar* foramen (Fig. 129 A, *ectep. f.*), for the passage of the radial nerve, is characteristic of most Lacertilia, Chelonia, Choristodera, and Phytosauria. In some of these it is replaced by a groove, and the latter is present in the Mosasauria and young Plesiosauria. Both the ectepicondylar and entepicondylar foramina occur in some Theromorpha and Anomodontia, the Nothosauria, Rhynchocephalia, *Araeoscelis*, *Pleurosaurus*, etc. The Pterosauria, Dinosauria, Crocodilia, Ichthyosauria, and Plesiosauria have no epicondylar foramina.

The humeri of many known temnospondylous amphibians differ but little from those of the Cotylosauria, save in the absence of the entepicondylar foramen. This foramen is reported for *Cochleosaurus,* a rhachitomous temnospondyl, and is known in *Diplocaulus* of the Lepospondyli, but is known in no other amphibian. An ectepicondylar foramen is quite unknown in the class.

Femur. The thigh-bone, or *femur* (*e. g.*, Figs. 129 B, 135), like the humerus, is variable in shape. Its articulation in the acetabulum is by a more or less convex head. The femur of most reptiles is turned outward from the long axis of the body in locomotion, with the articulation at the extremity; or if the bone is directed more or less upward, as well as outward, the convexity is more on the dorsal side, as in the Chelonia. The two femora of a lizard, for instance, cannot be brought parallel with each other in the same direction without dislocation from the socket. There is, consequently, in such reptiles, no real neck, so characteristic of birds and mammals. The dinosaurs (Fig. 132) and pterodactyls (Fig. 155) only, because of the more or less vertical or antero-posterior position of the femora, have the head set off from the shaft of the bone by a more or less well-marked *neck,* most noticeable in the bipedal types of dinosaurs, but also apparent in the quadrupedal. The absence, then, of a neck to the femur is indicative of crawling or aquatic habits. Many of the Therapsida (Fig. 132), though without a differentiated neck, have the proximal preaxial border of the femur more or less curved, with the articulation more on the preaxial side, giving evidence of a more upright, mammal-like mode of progression. *Pariasaurus* of the Cotylosauria has also been restored in a more upright posture, but its femur is quite like that of the earlier cotylosaurs,[1] and like them it probably never was brought below a horizontal position in walking, though, as in *Diadectes,* the mode of locomotion was probably more like that of the turtles, accounting, perhaps, for the reduction of the phalangeal formula in that genus. So also, the propodials of *Lystrosaurus* and doubtless of other Anomodontia were directed horizontally in locomotion.

On the preaxial ventral side, usually on the upper third of the bone, but sometimes, as in the short-limbed Cotylosauria, descend-

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[1] [But Romer (*Bulletin,* Amer. Mus. Nat. Hist., 1922, vol. XLVI, plate XLVI) shows that the pariasaur femur (*Propappus*) differs in significant features from the femora of cotylosaurs, while Amalitzky, Broom, and Romer are agreed that the femur of pariasaurs was directed obliquely downward.—ED.]

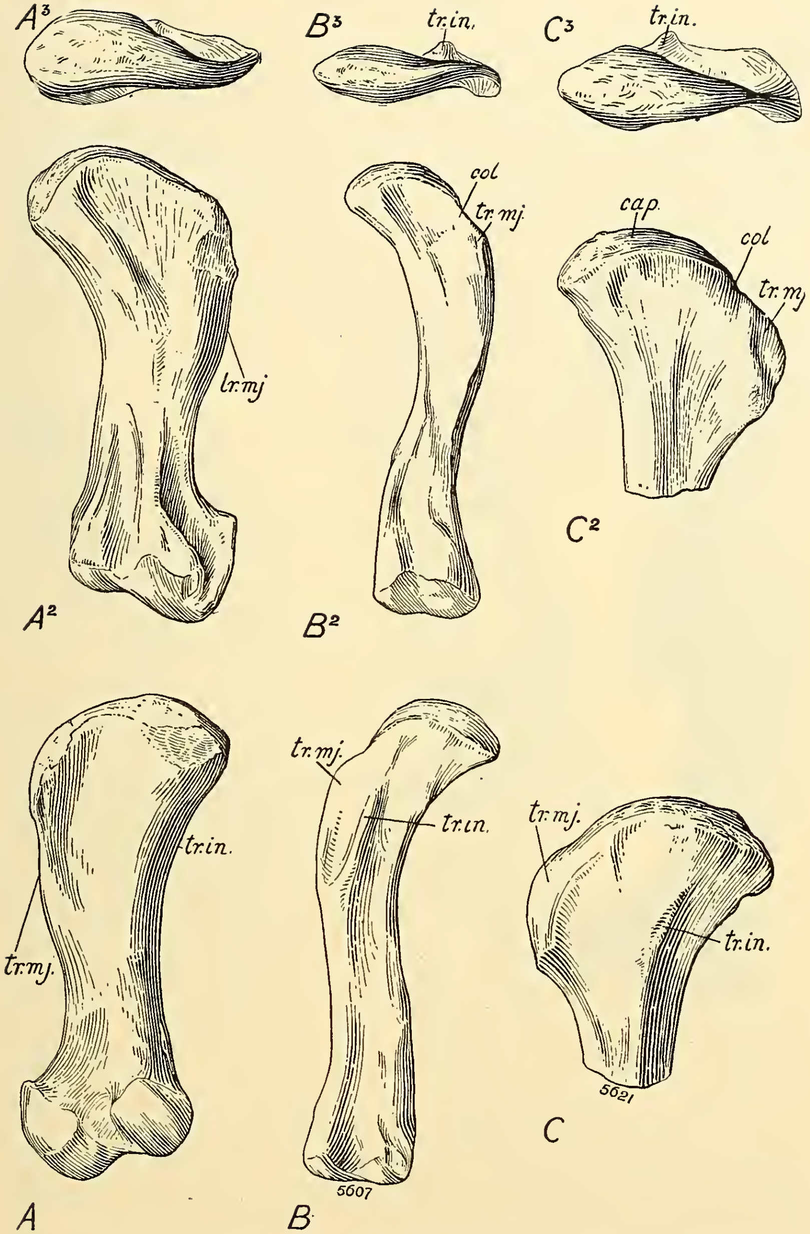

FIG. 132. Therapsid femora: A, *Moschops;* B, *Aelurosaurus;* C, *Cynognathus.* After Gregory and Camp. Scales various. Upper row, proximal end; middle row, dorsal; lower row, ventral.

ing below the middle, there is, especially in crawling forms, a rugosity or eminence, the *lesser trochanter*,[1] from which usually a more or less pronounced ridge or roughening descends toward, or nearly to, the postaxial condyle (Figs. 129 B, 132). It corresponds to the linea aspera of mammals and may be called the adductor ridge or crest. On the opposite side, and nearer the head, obsolete or even absent in ordinary crawling reptiles but well developed in the Chelonia (Fig. 154) [and in certain Therapsida, Fig. 132], is the *great trochanter*. Between the two there is a depression or fossa [intertrochanteric], at the upper extremity in turtles (Fig. 154), but broadly ventral in most other forms.

Fig. 132 bis. Dinosaur femur: *Camptosaurus*, right femur. After Gilmore. One sixth natural size.

The femora of the dinosaurs (Fig. 132 *bis*), especially the bipedal Predentata, but also indicated in the Sauropoda, have near the middle on the ventral preaxial side a rugosity or prominence, the *fourth trochanter*, sometimes, as in *Camptosaurus*, long and pendent.

The condyles, at the distal extremity of the femur, are separated by a groove in front and another behind (Fig. 129 B). The preaxial condyle, usually the smaller, gives articulation to the tibia; the postaxial condyle, to the fibula, and in part to the tibia behind. The shaft of the femur is sometimes markedly curved (Figs. 155, 157), sigmoidally in the more slender kinds. It is always longer and more slender than the humerus, its distal width seldom if ever equal to more than half the length of the bone.

The femur of the temnospondylous amphibians (Fig. 151 A) is sometimes indistinguishable from that of the cotylosaurs, but usually the adductor ridge is more strongly developed, and the articular ends are less well ossified.

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[1] [Recent evidence (Romer, 1924) indicates that this process is not homologous with the true "lesser trochanter" of mammals. A better name for it is "internal trochanter."—Ed.]

EPIPODIALS

Radius and Ulna. The two bones of the forearm or *antibrachium* are always complete in reptiles and movable upon each other, freely in most terrestrial reptiles, flexibly in the aquatic types, that is, without rotation of the radius; they may be more or less fixed in the chelonians (Fig. 145 A), though not crossed. The forearm in this order has a peculiar twist on the humerus by which the dorsal surface of the forearm, wrist, and hand is turned forward at right angles to the humerus without pronation or rotation of the radius (Fig. 145 A).

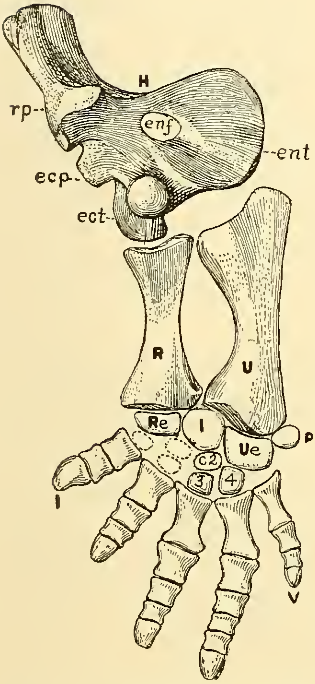

FIG. 133. Cotylosaur limb: *Limnoscelis*, left foreleg, ventral side. One fourth natural size.

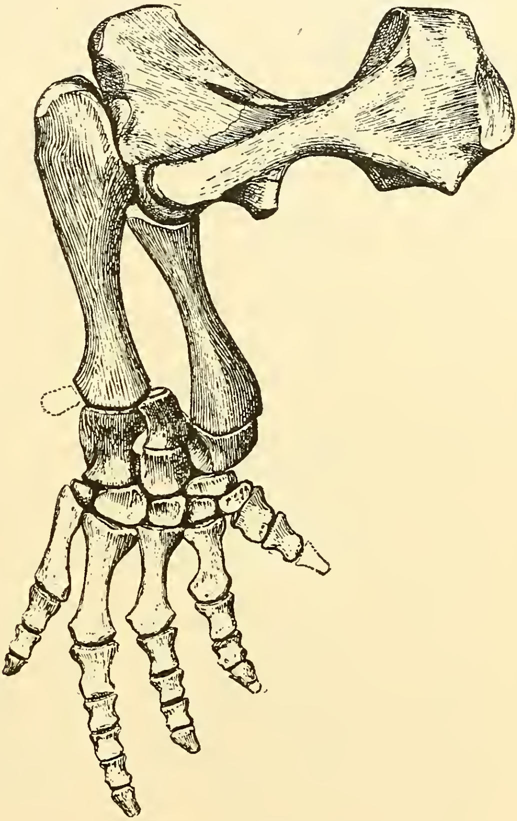

FIG. 134. *Ophiacodon:* Anterior extremity, as mounted. One half natural size.

The radius (Figs. 133, 134), on the thumb, radial or preaxial side, articulates with the preaxial condyle of the humerus by a more or less concave and rotating joint, as in the pentedactylate mammals; distally, normally with the radiale of the carpus. The ulna (Figs. 133, 134), on the postaxial side, articulates with the trochlear condyle of the humerus, as in mammals, by a hinge, but somewhat spiral joint; distally, normally with the intermedium and ulnare of the carpus, usually also at its distal postaxial angle with the pisiform. In terrestrial reptiles the ulna is produced more or less into an *olecranon*, or elbow.

In the aquatic reptiles the two bones, like the posterior epipodials, are shortened, sometimes losing all resemblances to the terrestrial forms. They retain some of their land characters in the early plesiosaurs and ichthyosaurs, but in the more specialized of both groups (Figs. 158 C, D, 159), they are wider than long, articulating with each other throughout their adjacent sides. In some of the later plesiosaurs a third and even a fourth bone, whose homologies are ill understood, may articulate with the distal end of the humerus on the postaxial side. A third bone is also known in some ichthyosaurs — an accessory epipodial (Fig. 158 C).

The radius and ulna of the temnospondylous amphibians (Fig. 136) present no characters by which they can be distinguished from those of the Cotylosauria; the olecranon is but feebly or not at all produced.

Tibia and *Fibula*. The tibia on the preaxial or big-toe side of the hind-leg is always the larger in terrestrial reptiles (Fig. 135), unlike the radius, which is more often the smaller. It articulates with both condyles of the femur, though chiefly with the preaxial, especially in bipedal forms. Its proximal extremity is expanded into a more or less prominent *cnemial* crest on the dorsal side for the immediate attachment of the extensor muscles, since there is no patella, and rarely sesamoid bones of any kind, in reptiles. The distal extremity (Figs. 135, 151, 153) articulates exclusively with the astragalus, or the astragalar part of the fused bone. This joint in the early reptiles was extensive and loose, permitting a wide range of lateral movement in the foot; in later reptiles it is closer and firmer.

The fibula, on the postaxial or little-toe side, is more slender than the tibia in land reptiles. It articulates proximally exclusively with the postaxial condyle (Figs. 135, 151). It has more of a sliding or arthrodial joint in land reptiles rotating the foot in extension. It articulates distally — primitively with the calcaneum and astragalus. Its lower end in those reptiles, especially cursorial reptiles, in which the astragalus is closely united or fused with the tibia, is obsolete or lost; in the later pterodactyls (Fig. 155 c) the whole bone has disappeared, as a separate ossification at least.

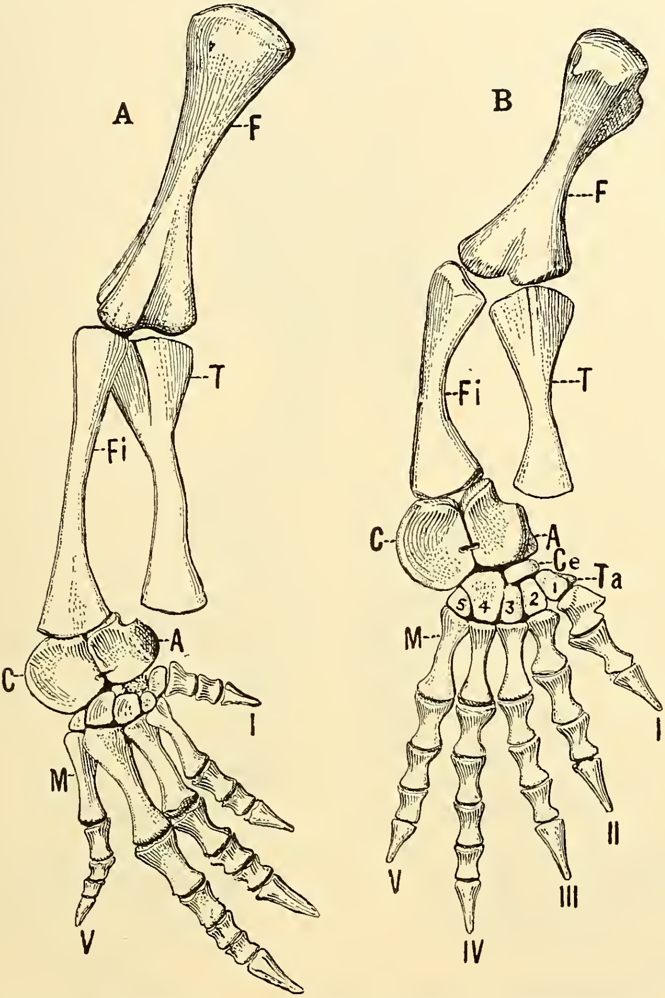

Fig. 135. Theromorph limbs: A, *Varanops*; B, *Casea*. One half natural size.

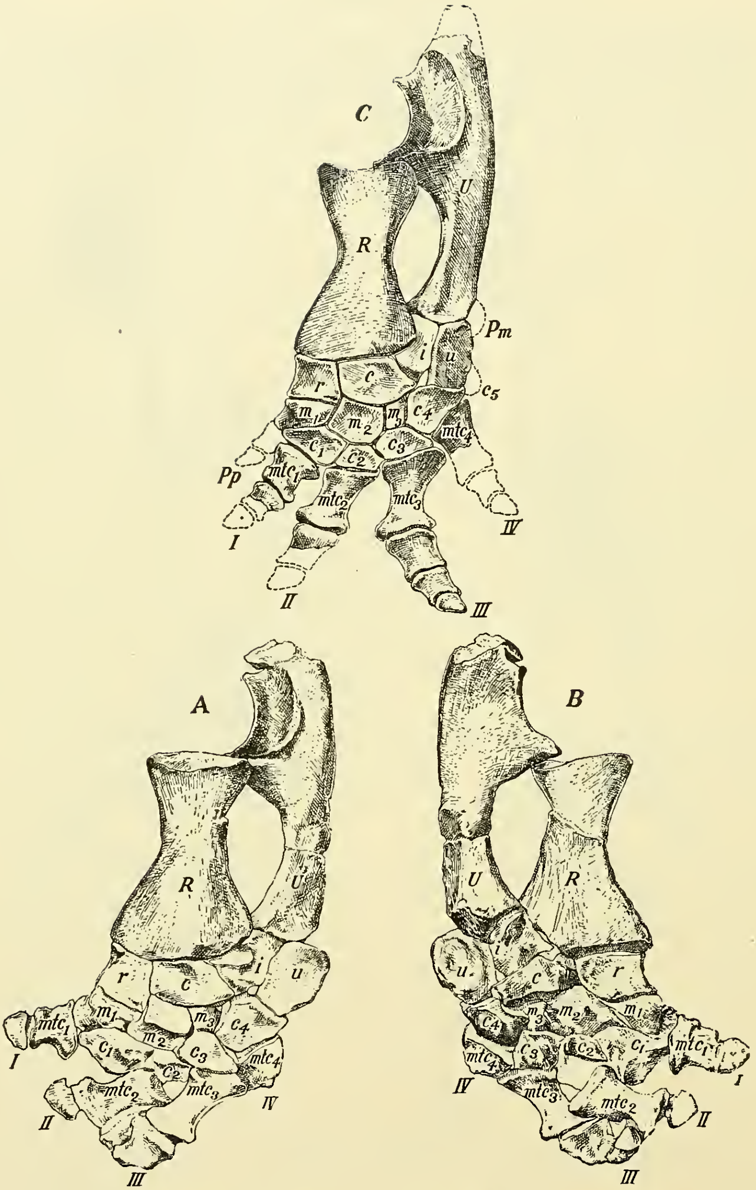

Fig. 136. Temnospondyl limb: *Eryops*, left foreleg. A, Cope's original specimen, in American Museum of Natural History; dorsum, or upper side. B, under side. C, reconstruction. After Gregory, Miner, and Noble. One third natural size.

The posterior epipodials in aquatic reptiles (Figs. 159, 158) are almost indistinguishable from the anterior ones, except that they are somewhat, or much, smaller. As in the front leg there may be accessory epipodials in both the plesiosaurs and ichthyosaurs. This shortening of the epipodials, so characteristic of aquatic animals, is seen to a moderate extent in the earliest known reptile, *Eosauravus* (Fig. 151 B) from the middle Pennsylvanian, as also in the Proganosauria (Fig. 153 A) and Choristodera. It is much more pronounced in the Mosasauria (Figs. 146–148, 158 A, B), Aigialosauria, Thalattosauria, and Thalattosuchia (Fig. 150). The elongation of the tibia and fibula, so characteristic of the cursorial or leaping forms, reached the maximum in the Pterosauria (Fig. 155 C).

The tibia and fibula of some temnospondylous amphibians are quite indistinguishable from those of many Cotylosauria.

MESOPODIALS

Numerous modifications have occurred in the structure of the carpus and tarsus of reptiles in adaptation to diverse habits of life. The *carpus* (Fig. 134) or wrist of the earliest known reptiles is composed of eleven freely articulated bones, none small: four in the first row, called respectively, from the preaxial to the postaxial side, the *radiale*, *intermedium*, *ulnare*, and *pisiform*, corresponding quite to the scaphoid, lunar, pyramidal, and pisiform of the human wrist; two in the second row, the radial or first, and the ulnar or second, *centrale;* and five in the third row, the carpalia, the first four corresponding to the trapezium, trapezoid, magnum, and unciform of the human wrist. Watson has recognized a small third centrale in the curious genus *Broomia* (Fig. 137 E) from South Africa, unknown as an ossified element in other reptiles, though perhaps represented by a cartilage in the young of the modern *Sphenodon.*

Carpus

The carpus is known in but two temnospondylous amphibians, *Eryops* (Fig. 136) and *Trematops*. In both, the preserved bones are the same in number as in the early reptiles and some modern ones. The radius of *Eryops*, however, articulates with three bones, the supposed radiale, intermedium, and ulnare, while the pisiform is large, and an articular surface on the postaxial distal margin of the ulna seems to indicate the original presence of another bone that would correspond better in position with the real pisiform. Unfortunately, the single known specimen of the carpus of *Trematops* has but two bones preserved in the proximal row. Two centralia, and two only, were present in *Trematops*, while the specimen of *Eryops*, here figured by the kindness of Dr. Gregory, has a small space which may represent a small third centrale. There are five well-developed carpalia in both forms, proving conclusively the presence of five digits in the hand.[1]

In some of the early cotylosaurs and anomodonts, supposed water habits have delayed the ossification of some of the mesopodial bones —supposedly, but it is a curious fact that all have similar feet, short, broad toes and ungual phalanges, very broad humeri, and short epipodials. It is not impossible, it seems to the author, that similar walking or digging habits, more after the mode of the tortoises, had, even this early, brought about a modified structure in the carpus and tarsus of *Limnoscelis* (Fig. 133), *Diadectes*, and *Lystrosaurus*.

It is the general belief that the loss of mesopodial bones has been due to their fusion with adjacent ones; it is doubtless true for the most part, but not always. That there has been an actual loss of the first centrale and fifth distale, the first to be lost in both carpus and tarsus, seems certain, as shown in specimens of various early reptiles, where unoccupied spaces for cartilaginous elements have been preserved. Moreover, their actual loss in living reptiles has long since been affirmed. Primitively both centralia were large (Figs. 133, 134, 137 E), as was also the fourth carpale, as correlated with the longest and strongest digit. And this carpale is the most persistent bone in the carpus, as it also is the first to be ossified in the human wrist. Every other bone of the carpus may be absent in different reptiles, but not the fourth carpale, unless it be in certain quadrupedal dinosaurs like the Sauropoda (Fig. 141 F) and Stegosauria (Fig. 141 I, J).

There was a perforating foramen between the second centrale, intermedium, and ulnare that was very persistent, retarding or preventing the fusion of these three bones (Fig. 134).

The first centrale and fifth carpale are always absent in mammals, at least since early Eocene times, but the second centrale is often

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[1] [For a different interpretation of the manus of *Eryops* see Gregory, Miner, and Noble in *Bulletin*, Amer. Mus. Nat. Hist., 1923, vol. XLVIII. — ED.]

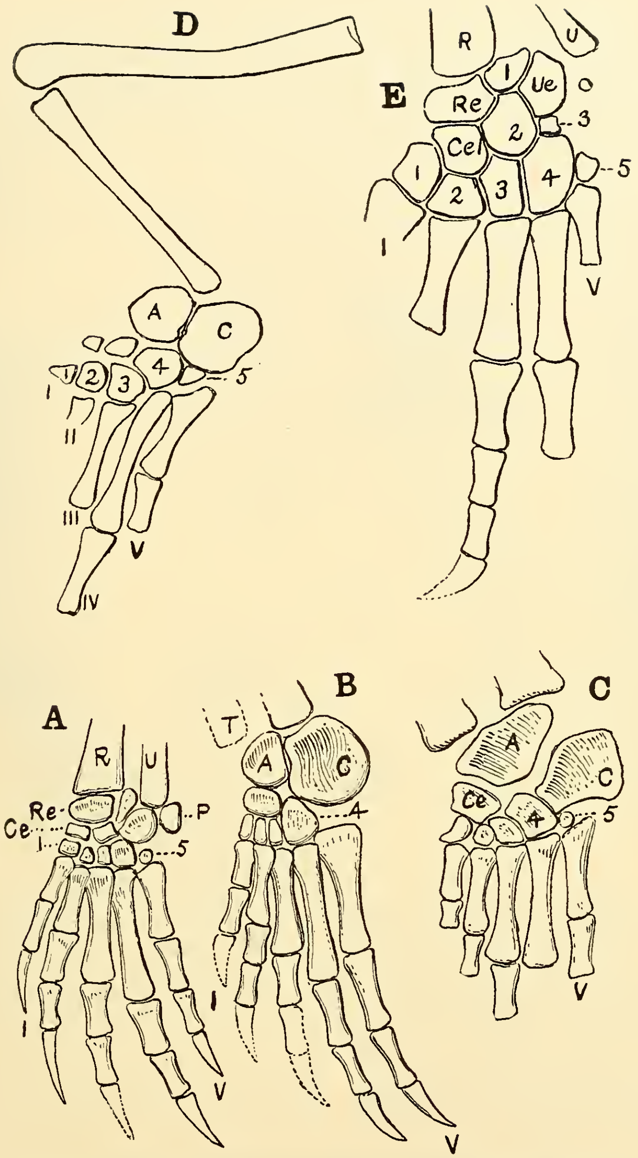

Fig. 137. Therapsid limbs: A, B, *Galechirus*, front and hind feet. After Broom. Natural size. C, *Galesphyrus*, left tarsus. After Broom. Natural size. D, *Broomia*, left tarsus. After Watson. Natural size. E, *Broomia*, left carpus. After Watson. About twice natural size.

present. In *Procolophon* only, of the Cotylosauria, is this centrale absent, as is also affirmed of the radiale. Throughout the Theromorpha, as known in numerous forms, the carpus is primitively complete, save that the first centrale and fifth carpale remained cartilaginous in one known genus, *Varanops*.

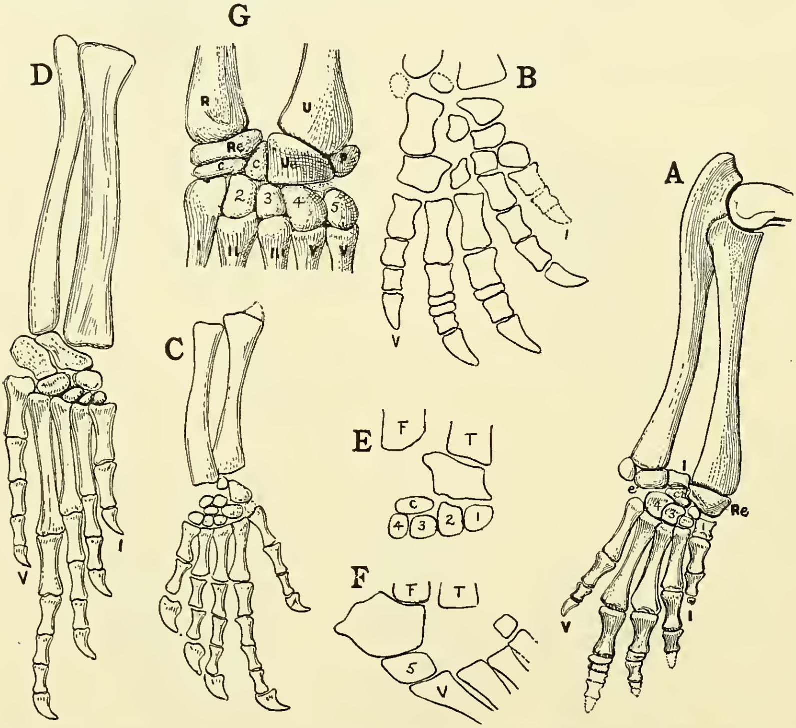

Fig. 138. Limbs: A, *Theriodesmus* (Therocephalia), front leg, dorsal side (rearranged from Seeley). One half natural size. B, *Scymnognathus* (Therocephalia), front foot. After Broom. One third natural size. C, *Protorosaurus* (Protorosauria), front leg. After von Meyer. One half natural size. D, hind leg of same. E, F, *Araeoscelis* (Protorosauria), part of tarsus, F probably immature. Nine eighths natural size. G, *Sceloporus* (Lacertilia). Enlarged.

Among the reptiles collectively known as the Therapsida, the carpus is ill known. In *Galechirus* of the Dromasauria (Fig. 137 A) as figured by Broom, the primitive structure is retained, as it also is in *Dicynodon* and its allies of the Anomodontia. The carpus of *Scymnognathus* of the Theriodontia, as figured by the same writer (Fig. 138 B) has a small intermedium, and the fifth carpale is represented as fused with the fourth, an error. A small element found near the first carpale was referred to a possible prepollex, or a radial sesamoid. Among reptiles there is no evidence of a lost prepollex.[1] *Theriodesmus* (Fig. 138 A) of the same group, as restored by the author from Seeley's figures, also lacks the fifth carpale, though the intermedium is not small. The complete carpus is unknown in other members of the Therapsida.

Sphenodon (Fig. 139 B) of the Rhynchocephalia is the only modern reptile which has retained the primitive structure and arrangement of the carpal bones. Extinct members of the order and its allies of the Diaptosauria are not sufficiently well known to determine whether this primitive structure is general, though doubtless it has been for the most part. In *Rhynchosaurus*, in a specimen figured by Newton, traces of the missing bones have been shown in dotted lines, indicating a primitive carpus save for the pisiform which was doubtless present.

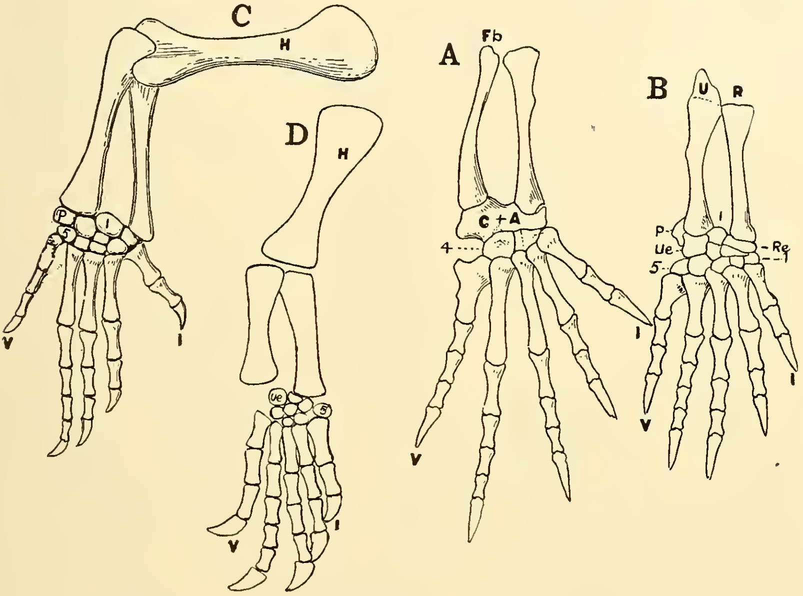

FIG. 139. Rhynchocephalian limbs: A, B, *Sphenodon*. After Howes and Swinnerton. About seven eighths natural size. C, *Sauranodon*. After Lortet. Nine eighths natural size. D, *Pleurosaurus*. After Lortet. Nine eighths natural size.

The carpus of the Crocodilia has been strangely modified (Fig. 140 A). It is composed of four bones only in all forms so far as known:

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[1] [But see Steiner, *Acta Zoöl.*, 1922, pp. 307–360. — ED.]

the radiale, ulnare, pisiform, and fourth carpale, as they are usually called. The radiale is very large and elongate, dilated at its ends and articulating with the radius and preaxial border of the ulna. It is supposed to be the fused radiale and intermedium but possibly is the intermedium only. The ulnare, of similar shape, but smaller, is approximated to the middle part of the distal border of the ulna, articulating also with the pisiform and radiale; distally with the fourth carpale only. The pisiform, of considerable size, articulates with the postaxial border of the ulna and ulnare. The first three carpalia, and perhaps also the centrale, are represented by cartilage, which fills out the interval between the end of the radiale and the metacarpals. This structure is a very ancient one as shown in the carpus of *Alligatorellus* (Fig. 140 B) and *Crocodeleimus* from the Jurassic, where, indeed, the two carpals are yet more elongate.

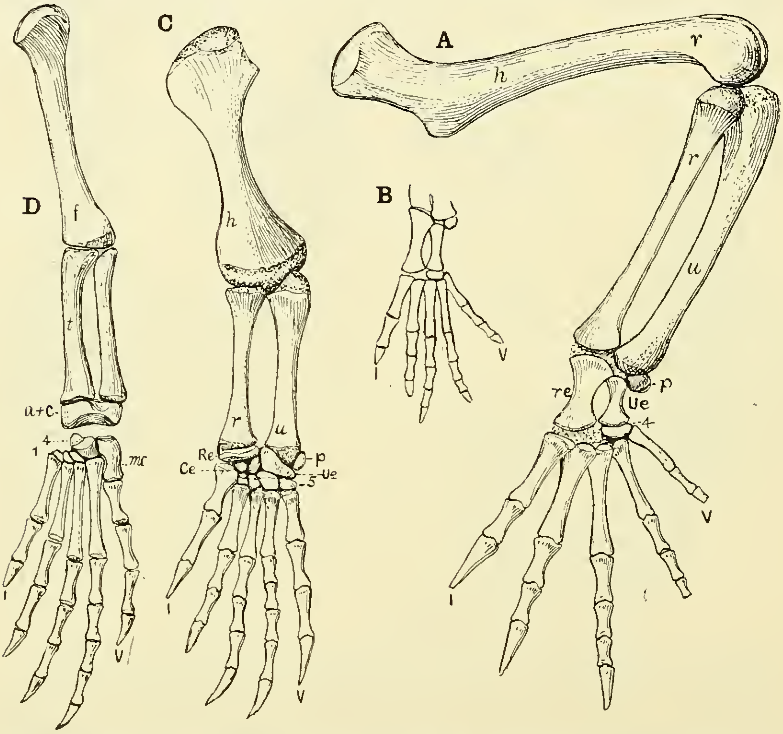

FIG. 140. Limbs: A, *Alligator* (Crocodilia). One half natural size. B, *Alligatorellus* (Crocodilia). Twice natural size. C, D, *Amblyrhynchus* (Lacertilia). Natural size.

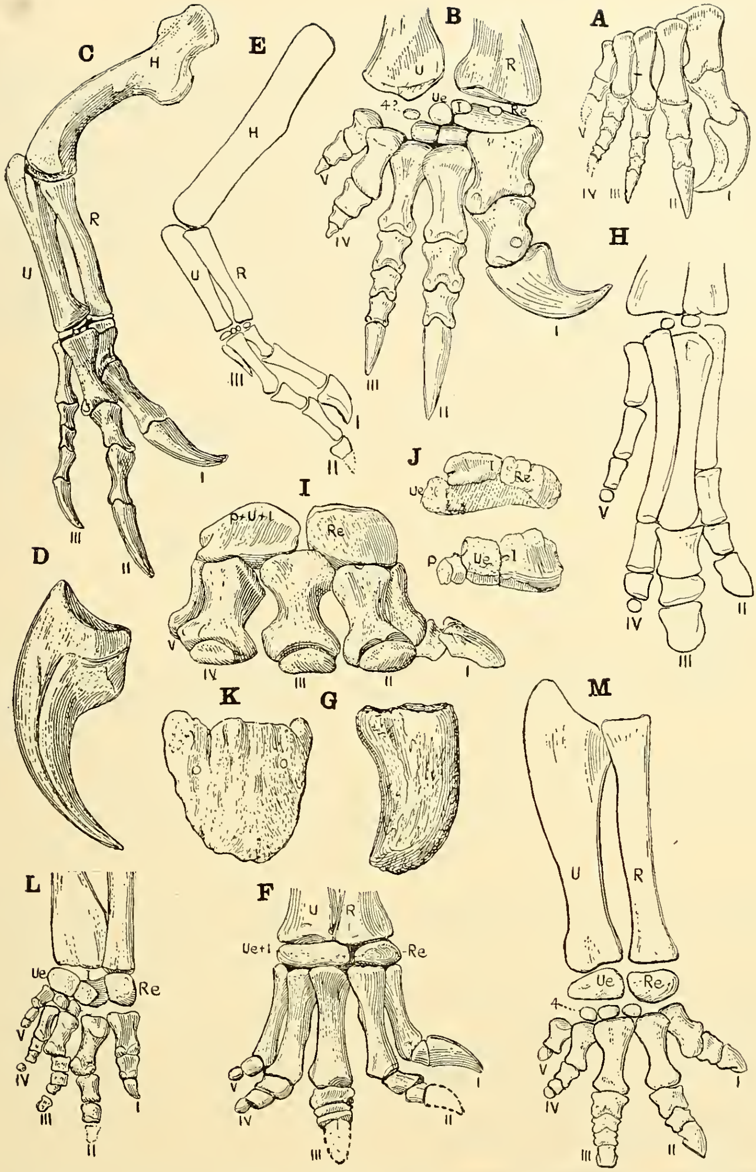

Fig. 141. Dinosaur pedes: A, *Plateosaurus* (Saurischia). After von Huene. One eighth natural size. B, *Gryponyx* (Saurischia). After Broom. One fifth natural size. C, *Allosaurus* (Saurischia). After Gilmore. About one sixth natural size. D, *Allosaurus* (Saurischia). After Gilmore. One fourth natural size. E, *Gorgosaurus* (Saurischia). After Lambe. One twelfth natural size. F, *Morosaurus* (Saurischia). After Riggs. One twelfth natural size. G, *Morosaurus* (Saurischia). After Marsh. One eighth natural size. [Should be *Brontosaurus*.] H, *Trachodon* (Ornithischia). After Brown. One ninth natural size. I, J, K, *Stegosaurus* (Ornithischia). After Gilmore. One eighth, one eighth, and one fourth natural size. L, *Thescelosaurus* (Ornithischia). After Gilmore. One fourth natural size. M, *Leptoceratops* (Ornithischia). After Brown. One half natural size.

The carpus in the Dinosauria (Fig. 141) has suffered greater reduction than in any other order of terrestrial reptiles, doubtless because of the upright posture. In no form has a centrale been reported, and the fifth carpale is doubtfully present in any (*Camptosaurus*), as would be expected from the constantly reduced fifth finger. In the quadrupedal forms there are but two proximal bones, both large and massive. In *Stegosaurus* (Fig. 141 I, J) the postaxial one of the two has been found in young specimens in three parts, the intermedium, ulnare, and pisiform; perhaps that was also the case in the Sauropoda (Fig. 141 F). A small bone may possibly represent a vestigial intermedium in *Leptoceratops* (Fig. 141 M) of the Ceratopsia. In the Theropoda, and iguanodont orthopods, that is, bipedal forms, the radiale, intermedium, and ulnare seem distinct in all, though not large. The second row of carpals has disappeared in the Sauropoda (Fig. 141 F) and Stegosauria (Fig. 141 I). Two have been found in all other known forms, except the Trachodontidae; in most cases the third and fourth carpale, though identified as the first and second in *Ornitholestes* and its immediate allies of the Theropoda. The carpus in the Trachodontidae (Fig. 141 H) is more reduced than in any other

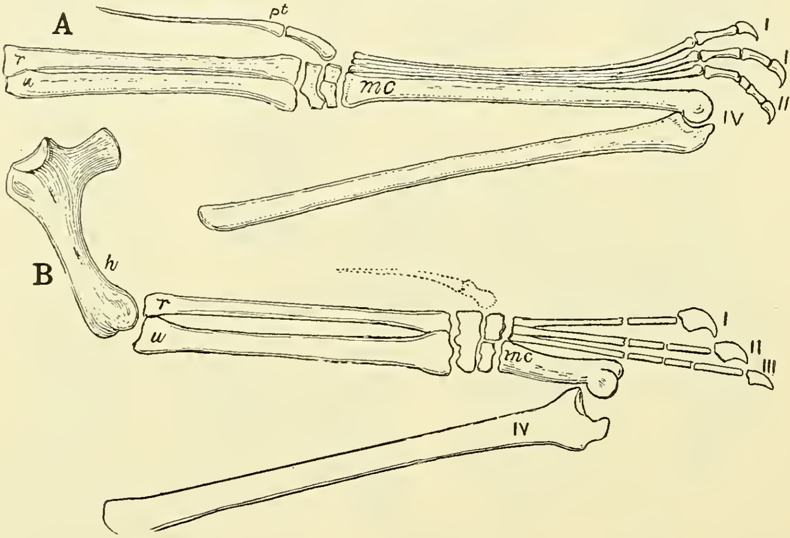

Fig. 142. Pterosaur limbs: A, *Pterodactylus*. American Museum of Natural History. Nearly three times natural size. B, *Rhamphorhynchus*. After Plieninger. One half natural size.

reptiles, unless it be some aquatic mosasaurs, but two small bones remaining, probably the radiale and fourth carpale.

The most remarkable modifications of the carpus are those of the volant Pterosauria (Fig. 142). The earliest stages we do not know, though certain progressive modifications are observable from the earlier to the later. In *Pteranodon* and its allies of the Upper Cretaceous, the carpus is reduced to three bones: a proximal one, articulating with both radius and ulna, and perhaps to be homologized with all the bones of the proximal row except the pisiform; a distal one, composed either of the greatly enlarged fourth carpale, or a fusion of two or three, probably the former; a third carpale, on the radial side, articulating chiefly with the [distal] carpale, may be either the first carpale, the centrale, or possibly neither. In the earlier *Rhamphorhynchus* (Fig. 142 B), there are two distal carpals, the first articulating with the first three metacarpals, the second with the fourth or wing metacarpal. This is also the structure in *Pterodactylus* (Fig. 142 A), except that in some forms there are five bones, two in the proximal, two in the distal row, and the usual lateral one supporting the pteroid. This great consolidation of the carpus in

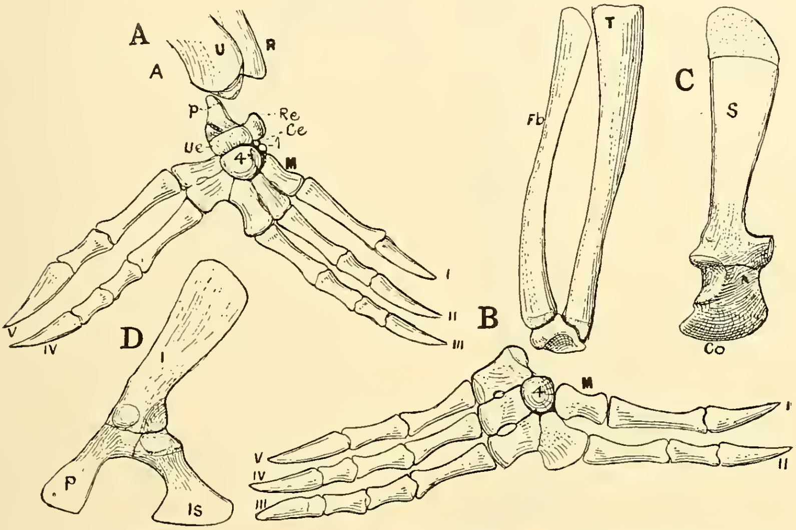

Fig. 143. Squamata, Rhiptoglossa. Limbs, etc., of Chameleon, much enlarged. A, right hand, dorsal; B, right hind foot, dorsal, with tibia, fibula, and tarsus; C, right scapulocoracoid; D, left innominate.

pterodactyls resulted in a maximum of firmness with but little mobility, which was not needed in the volant hand.

The carpus of the Pseudosuchia and Phytosauria is practically unknown.

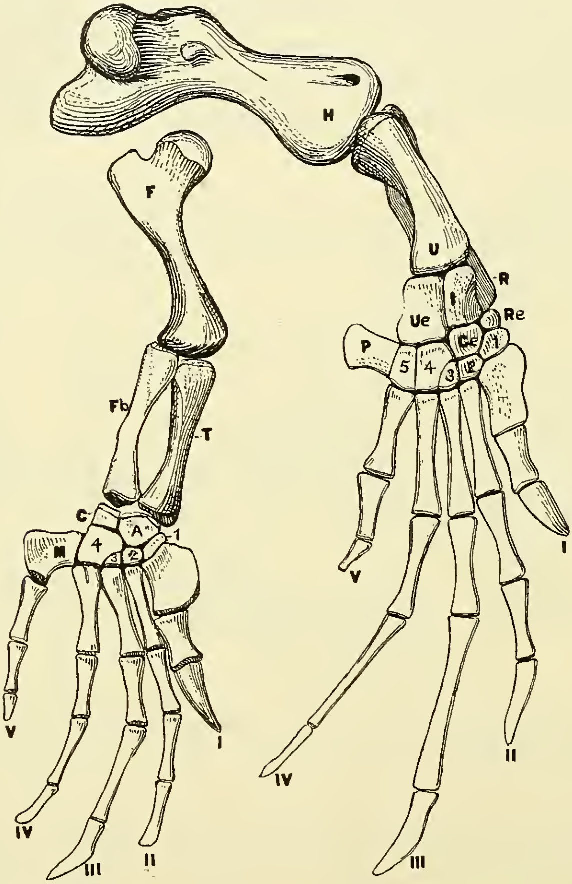

Fig. 144. Chelonia, Pleurodira: *Thalassochelys*, right front and hind legs.

Marked modification in the structure of the carpus is also characteristic of the Lacertilia (Fig. 140 c). There are but three bones in the proximal row, which may also be interpreted as the radiale, ulnare, and pisiform. No intermedium is visible in the various forms examined. It is reported to be present only in the family Lacertidae. A centrale is usually present, though sometimes small. The first centrale is also identified in some lizards. The fourth centrale [carpale], as usual, is large; the second, third, and fifth are usually large. The first is absent, unless it be the element sometimes called the first centrale.

In the curious hands of the highly specialized perching Rhiptoglossa (Fig. 143 A) the carpus is reduced to four functional bones, the radiale, ulnare, and posteriorly placed pisiform in the first row, and a large, hemispherical, fused third and fourth carpale in the distal row, around which the metacarpals revolve. Between the first metacarpal and radiale there are in the more specialized types two minute bones, which may represent the first and second carpalia, or the second and the centrale, probably the latter.

In the marine Chelonia (Fig. 144) the carpus is broad and flat, and is least reduced, though much modified. The radiale and intermedium are more or less elongate, the ulnare is small, the centrale large. The pisiform is greatly enlarged and has lost its primitive location between the ulna and ulnare, becoming attached to the ulnare and fifth metacarpal or the latter alone. This was the structure of the marine turtles as far back as the Cretaceous in *Protostega*, except that the proximal bones were less elongate.

At the opposite extreme, among the terrestrial tortoises (Fig. 145 A) the radiale has disappeared until nothing is left of it but a nodule of cartilage united with the first centrale, which has usurped its place. At least, this is the explanation given by Baur, who found in *Emydura* the two centralia in their normal positions, though enlarged. The two centralia are often present, often fused into the large single bone. The fused centralia in such early forms as *Idiochelys*, from the Jurassic, reached almost to the radius, and the radiale was doubtless cartilaginous. The fifth carpale may be absent, fused with the fourth, or separate and distinct. Indeed, in some old animals the third, fourth, and fifth carpalia and the pisiform may all be coössified.

The changes of the wrist and hand in adaptation to aquatic life are more profound than those of terrestrial reptiles. The earliest observed effect of water habits is delayed ossification, not only of the mesopodial bones, but of the bones of the skeleton in general, a large amount of cartilage remaining in the joints. Partial chondrification of the wrist and ankle occurred as early as the cotylosaurian *Limnos-*

celis (Fig. 133) and *Diadectes*, probably marsh animals. In *Clidastes* (Fig. 146) of the Mosasauria, essentially a surface-swimming lizard, the four proximal bones of the wrist are ossified, but the centralia, first and fifth carpalia were not. In *Platecarpus* (Fig. 147) a more advanced aquatic type, the ulnare, pisiform, and second carpale have also disappeared, leaving only the radiale, intermedium, third and fourth carpalia. In *Tylosaurus* (Fig. 148) the most highly specialized of all mosasaurs, there are but one or two bony nodules left, one of which is certainly the fourth carpale. All the others disappeared as bones but remained as cartilage, since space is left for them in many specimens as they have been found in the rocks.

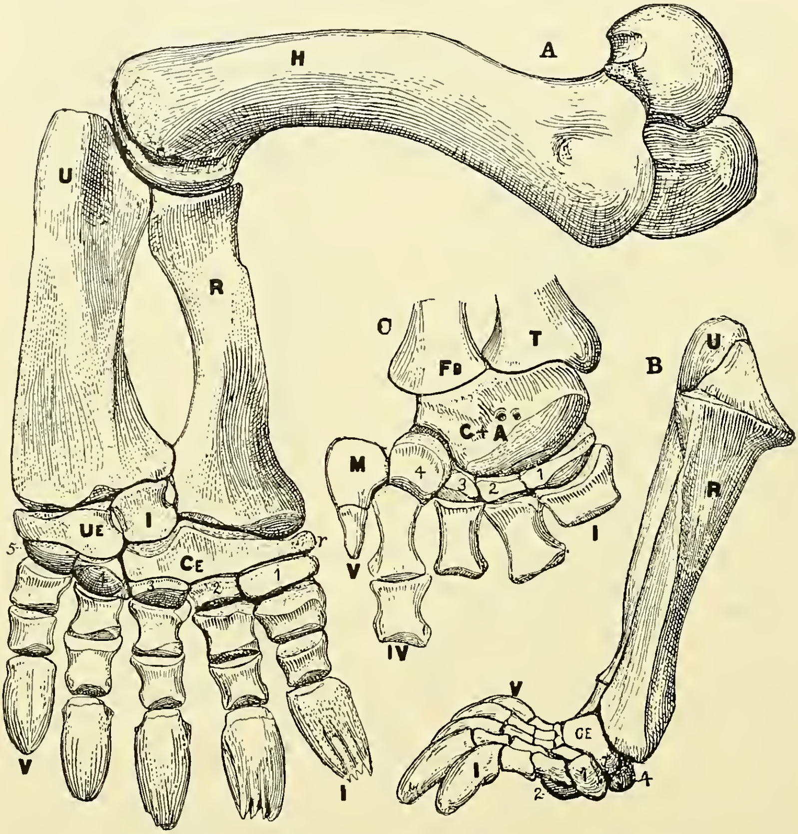

FIG. 145. Chelonia, Pleurodira: *Testudo*, A, front leg, dorsal side; B, the same, radial side; C, hind foot (tarsus, etc.) dorsal side.

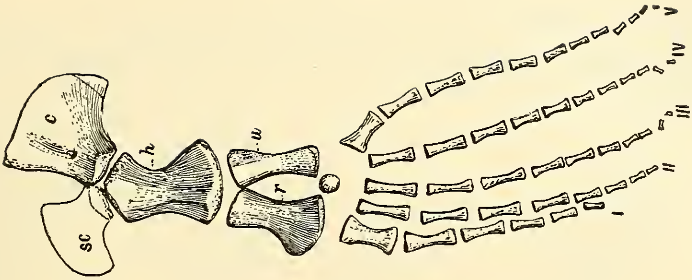

FIG. 148

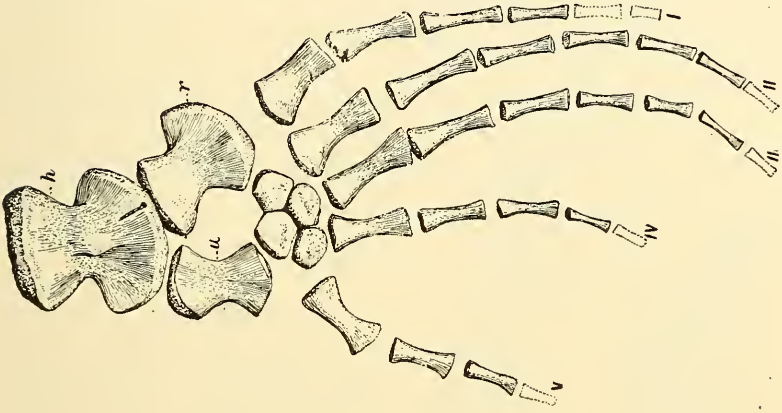

FIG. 147

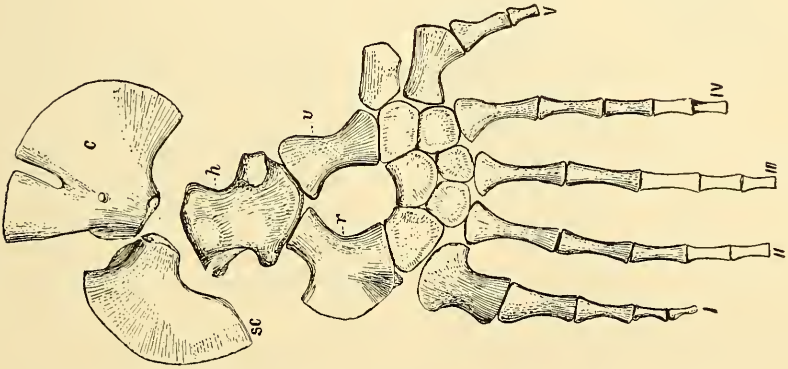

FIG. 146

FIG. 146. *Clidastes* (Mosasaur), left front paddle: *c*, coracoid; *h*, humerus; *r*, radius; *sc*, scapula; *u*, ulna.
FIG. 147. *Platecarpus* (Mosasaur), right front paddle.
FIG. 148. *Tylosaurus* (Mosasaur), left front paddle.

In the swimming feet of *Lariosaurus* (Fig. 149) of the Nothosauria the carpus is also reduced, the radiale apparently the most conspicuous for its absence.

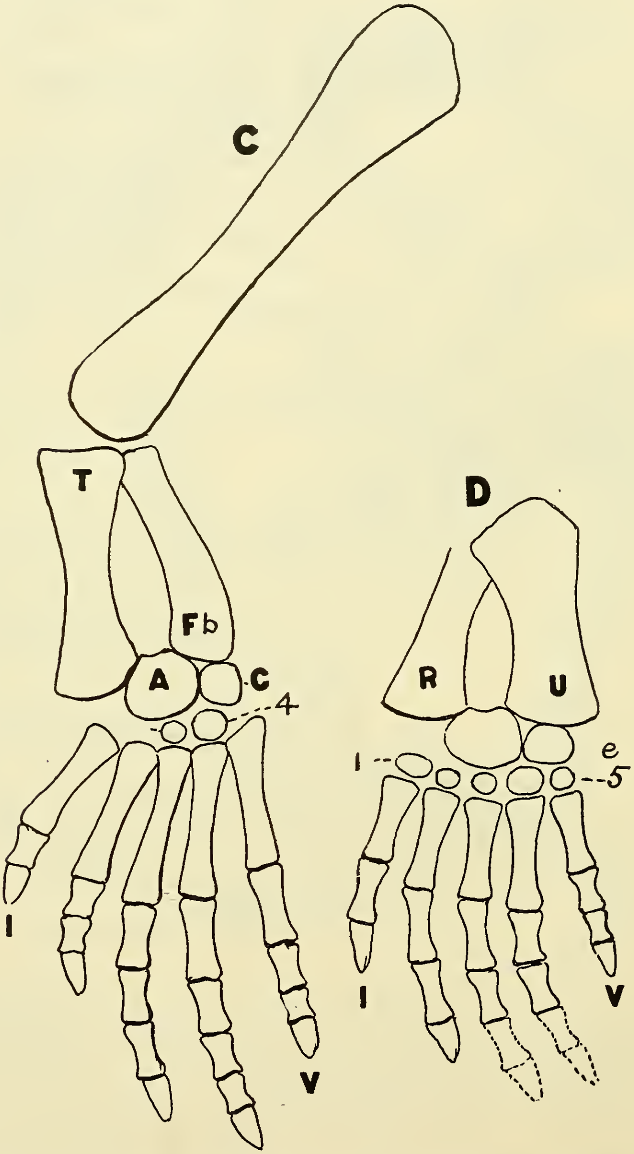

Fig. 149. Nothosaurian limbs: *Lariosaurus*. About four times natural size.

Very interesting are the modifications of the wrist and hand in the marine Crocodilia (Fig. 150). But two carpals remain, corresponding to the elongated ossified bones of the terrestrial forms; the first of them, the supposed radiale, is very broad and flat.

The carpus and hand of the strictly aquatic or marine reptiles are so like the ankle and foot that they may be discussed together (p. 193).

Tarsus

The earliest known tarsus is that of *Eosauravus* (Fig. 151 B), presumably a cotylosaur reptile, though the skull is not known, from the middle Pennsylvanian. It has but two bones in the proximal row, corresponding quite to the astragalus and calcaneum of mammals and the typical reptiles. Beyond these, six, and only six, bones are visible, five of which are undoubted tarsalia; one may be a centrale. The whole number, eight, was the most known in any reptile until recently. Nine bones are present in the tarsus of *Ophiacodon* (Fig. 152), from the uppermost Pennsylvanian or basal Permian of New Mexico: two in the proximal row, the astragalus and calcaneum, two centralia in the middle row on the tibial side; and five tarsalia in the distal row, one corresponding to each metatarsal. Since this discovery two centralia have also been found by Watson in the genus *Broomia* (Fig. 137 D), from the Permian of South Africa; and probably also two in the cotylosaurian genus *Labidosaurus*. The second

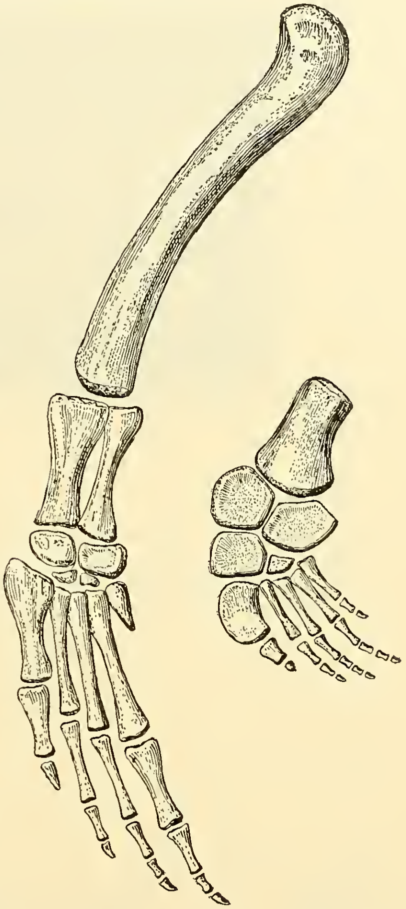

FIG. 150. *Geosaurus* (Thalattosuchia). Elongate left hind leg, and paddle-like left front leg. After Fraas.

centrale is usually retained in later reptiles, but the fifth tarsale is absent in all reptiles since Triassic times, and a free centrale is absent in all living reptiles, though present in most mammals.

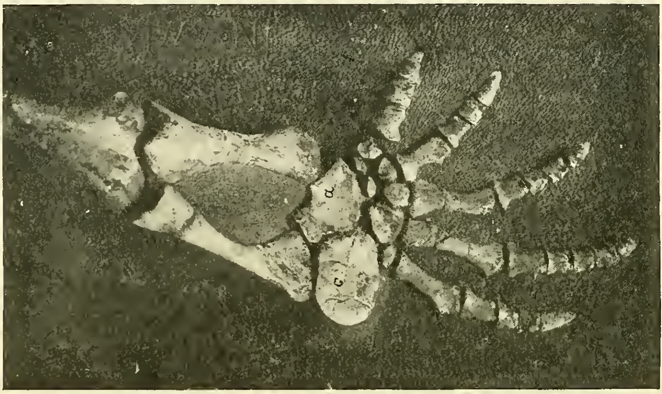

Fig. 152

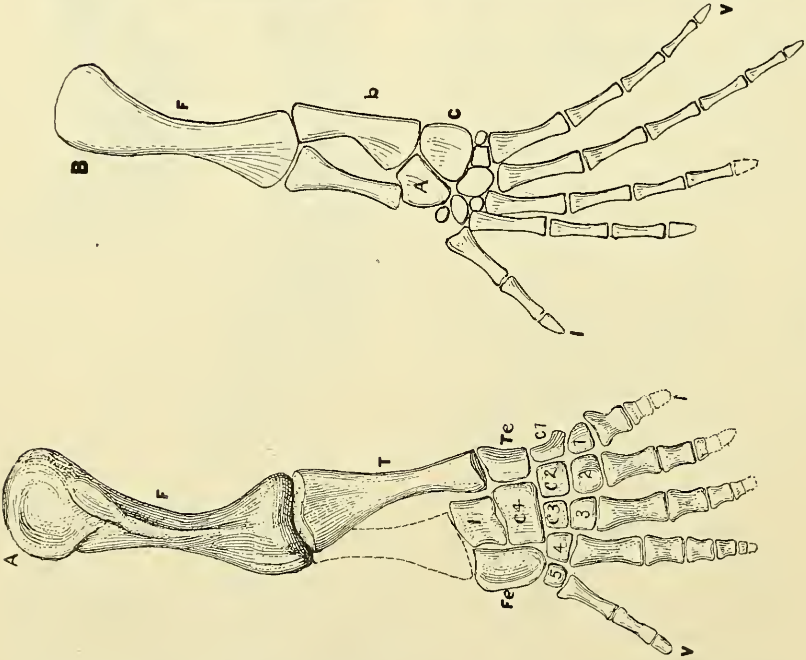

Fig. 151

Fig. 151. Limbs: A, *Trematops* (Temnospondyli). One half natural size. B, *Eosauravus* (Cotylosauria). About twice natural size.

Fig. 152. *Ophiacodon* (Theromorpha): right hind leg, from mounted skeleton. A little less than one third natural size. *a*, astragalus; *c*, calcaneum.

The mammalian foot, in this respect, is even more primitive than that of the lizards, turtles, and crocodiles, the navicular corresponding to the second centrale, the cuneiforms and cuboid to the four tarsalia. The fourth distale, primitively, as in the carpus and as a general rule in all reptiles, is the largest of the series, corresponding to the greater length and strength of the fourth toe.

The tarsus is known in but two temnospondylous amphibians, both from later rocks than *Eosauravus*, *Trematops* (Fig. 151 A), and *Archegosaurus*. In the former, and according to Baur in the latter also, there are three bones in the proximal row, the tibiale, intermedium, and fibulare; four centralia in the middle row; and five tarsalia in the distal — twelve in all.

Three of these have been lost in all known reptiles, the intermedium, or tibiale, and the third and fourth centralia. Nine bones, then, we may assume was the primitive number of tarsal bones in the reptiles. A separate intermedium has been accredited to certain reptiles, *Howesia* of the Rhynchocephalia, *Oudenodon* (*Dicynodon*) of the Anomodontia, and the ichthyosaurs and plesiosaurs. But, unless such forms have enjoyed an uninterrupted and independent descent of which we have no knowledge from the Amphibia, it is altogether improbable that both intermedium and tibiale have ever been present as separate bones in reptiles since early Pennsylvanian times. Otherwise we must assume that there has been a reversion from the specialized to the generalized condition of the Amphibia in these animals, a seeming impossibility in evolution. Moreover, there are but two bones in the proximal row of the tarsus of the Nothosauria (Fig. 149), and these reptiles are generally supposed to have a real genetic relationship with the plesiosaurs.

There have been various theories as to what has become of the additional bones of the amphibian tarsus.[1] Since Gegenbaur, it is generally believed that the intermedium is fused with the tibiale to form the astragalus. This is denied by Baur, who says there is no evidence of such union. Others have thought that the intermedium alone forms the astragalus, the tibiale represented by the tibial sesamoid, which occurs in certain mammals but is unknown as such in lower animals. In this uncertainty it is better to use the two mam-

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[1] [For an excellent review of this subject see Broom, 1921, in *Proc. Zoöl. Soc.*, London, pp. 143–155.—Ed.]

malian names astragalus and calcaneum and abandon the names tibiale, fibulare, and intermedium for the reptilian tarsus. Of the

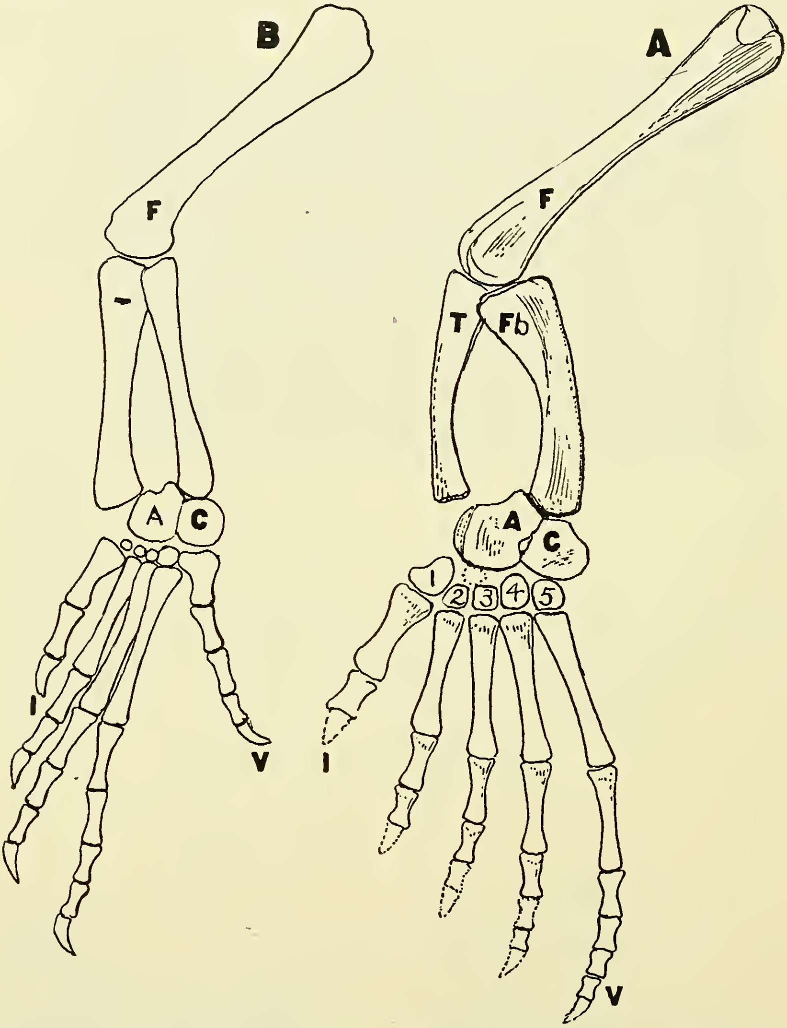

FIG. 153. Limbs: A, *Mesosaurus* (Proganosauria). Modified from McGregor. Natural size. B, *Sauranodon* (Protorosauria). Modified from Lortet. Three fourths natural size.

centralia the most probable theory is that the fourth of the amphibian tarsus has united with the astragalus, the third with the fourth tarsale. The second is known to fuse with the astragalus in the modern Chelonia (Fig. 154 C); perhaps at other times it is lost. And it is very probable that the first centrale of the amphibian and reptilian tarsus ceased very soon to be ossified, and is not represented, even in a fused condition, in any later reptilian tarsus. It has been shown by Baur and others that the fifth tarsale is not fused with the fourth, but has disappeared.

Among the Cotylosauria there are usually eight tarsal bones.[1] In *Pariasaurus* the centrale and fifth tarsale are not known with certainty. In the Theromorpha eight are present in all known forms except *Ophiacodon* (Fig. 152), which has nine. The centrale has not been recognized in the Proganosauria (Fig. 153 A), but there are five tarsalia; until their discovery four were the most known in any reptile. Indeed, Baur based the order Proganosauria chiefly upon this character. All other known reptiles, except certain Therapsida (like the mammals), have not more than seven tarsal bones, the fifth tarsale being invariably absent.

In *Pariasaurus*, *Sclerosaurus*, and *Telerpeton* of the later Cotylosauria, *Sphenodon* (Fig. 139 A) of the Rhynchocephalia, and most Lacertilia (Fig. 140 D) and Chelonia (Figs. 145 C, 154 D, G), the astragalus and calcaneum are fused into a single bone, and the calcaneum is either fused or lost in the Pterosauria (Fig. 155 D) and some Dinosauria (Fig. 156 I). A free centrale is absent in all modern reptiles, though sometimes suturally fused with the astragalus in the Chelonia (Fig. 154 C).

In the Chelonia the small calcaneum is sometimes free (Fig. 154 C). The centrale is never free. Four tarsalia are usually present, the third sometimes suturally united with the fourth. The fourth tarsale is always large.

In the kionocrane Lacertilia (Fig. 143 B) there is a similar condition, the small calcaneum either indistinguishably fused with the astragalus, or suturally attached in the adult. There is no centrale or fifth tarsale, and the first and second tarsalia are either vestigial or lost. The tarsus of the chameleons (Rhiptoglossa), like the wrist, is very curiously modified (Fig. 143 B). But two bones remain in the

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[1] [Watson (*Proc. Zoöl. Soc.*, 1919) reports the presence of three bones in the proximal row of the tarsus of the very primitive *Seymouria*, and adopts the view that the true tibiale has disappeared in later reptiles, the astragalus representing the intermedium only. — Ed.]

highly specialized species, the astragalo-calcaneum and the large, hemispherical fourth tarsale, articulating together enarthrodially, around which all the short metatarsals closely articulate in two groups of two and three.

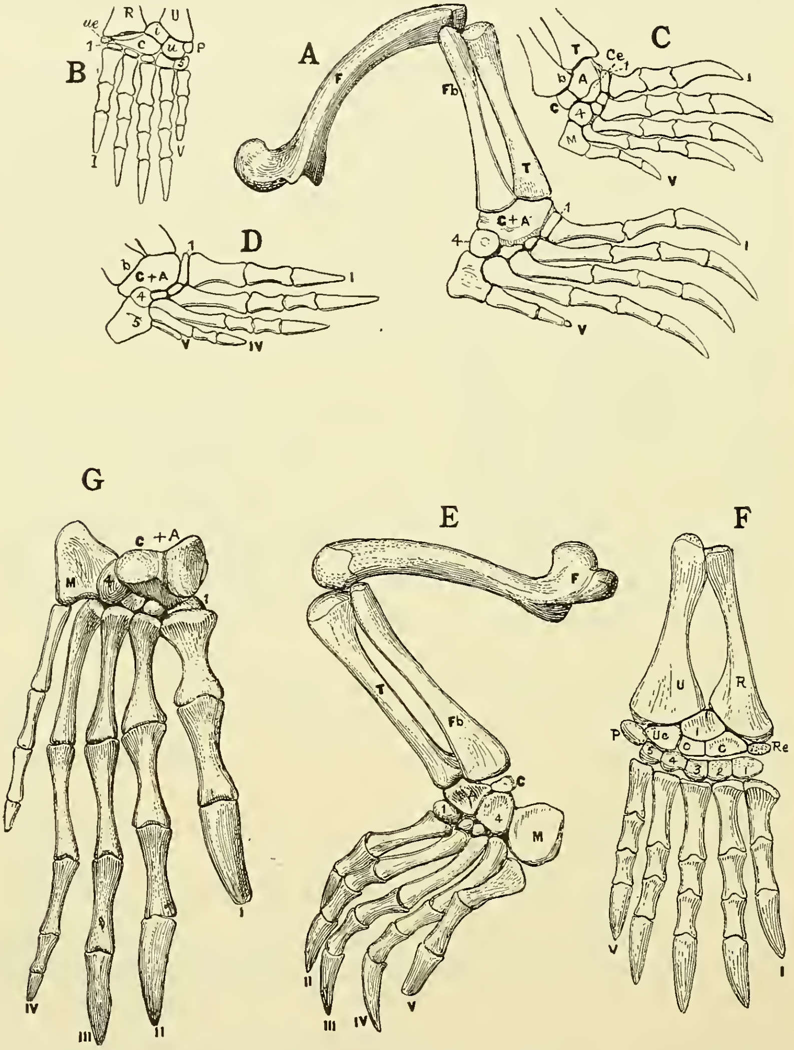

Fig. 154. Limbs and feet of Chelonia. Natural size. A, *Chrysemys*, hind leg from postaxial side. B, *Chrysemys*, front foot, dorsal side. C, *Chelydra*, hind foot, dorsal side. D, *Cistudo*, hind foot, dorsal side. E, *Podocnemys*, left hind leg, postaxial side. F, *Podocnemys*, right front forearm and foot, dorsal side. G, *Trionyx*, left hind foot, dorsal side.

The hind foot is poorly known in the Therapsida. In *Galechirus* (Fig. 137 B) of the Dromasauria the fifth tarsale is lost, but a small one has been recognized in the related genus *Galesphyrus* (Fig. 137 C). The Anomodontia have the astragalus and calcaneum, four tarsalia, and a small, frequently unossified centrale; the fifth tarsale is absent. The tarsus is unknown in other groups.

The tarsus of the modern *Sphenodon* (Fig. 139 A), unlike the carpus, is highly specialized. In addition to the fused calcaneum and astragalus, the centrale and fifth tarsale have disappeared and the first three tarsalia are fused in the adult.

The tarsus of the Pterosauria (Fig. 155 D), like the carpus, is highly specialized. In the early forms the astragalus is suturally united with the tibia, the calcaneum fused with the astragalus. In the later forms the astragalus is indistinguishably united with the end of the tibia, the calcaneum fused or lost as in birds, forming a large, pulley-like articulation. In the early pterodactyls there were at least three other tarsals; in the later ones, like *Pteranodon* or *Nyctosaurus*, there are but two free tarsalia, probably the fourth and the fused second and third, or fused first, second, and third. Centralia are unknown in all.

The tarsus of the dinosaurs (Fig. 156), like the carpus, has been much modified in adaptation to upright-walking habits. There is a tendency in all for the two proximal bones, the astragalus and calcaneum, to articulate closely with the leg bones. The astragalus of the Theropoda (Fig. 156 B, C, E) fits more or less closely in a depression or groove on the under and anterior side of the tibia; in the later forms (*e. g.*, *Ornithomimus*, Fig. 156 E) developing a high ascending process in front, as in the young of birds — a parallel character which has no genetic value. In the Sauropoda (Fig. 156 I) there is a less close union, perhaps due to the larger amount of cartilage in the joints of these animals. The centrale and first and fifth tarsalia are always absent. The second and third tarsalia are often fused, apparently; the fourth is always single when present. The tarsalia, like the carpalia, are absent in the Trachodontidae (Fig. 156 G); even the fourth is said to be wanting — possibly a vestige yet remains. If really absent it is the only known example among reptiles of the absence of all the bones of the distal row.

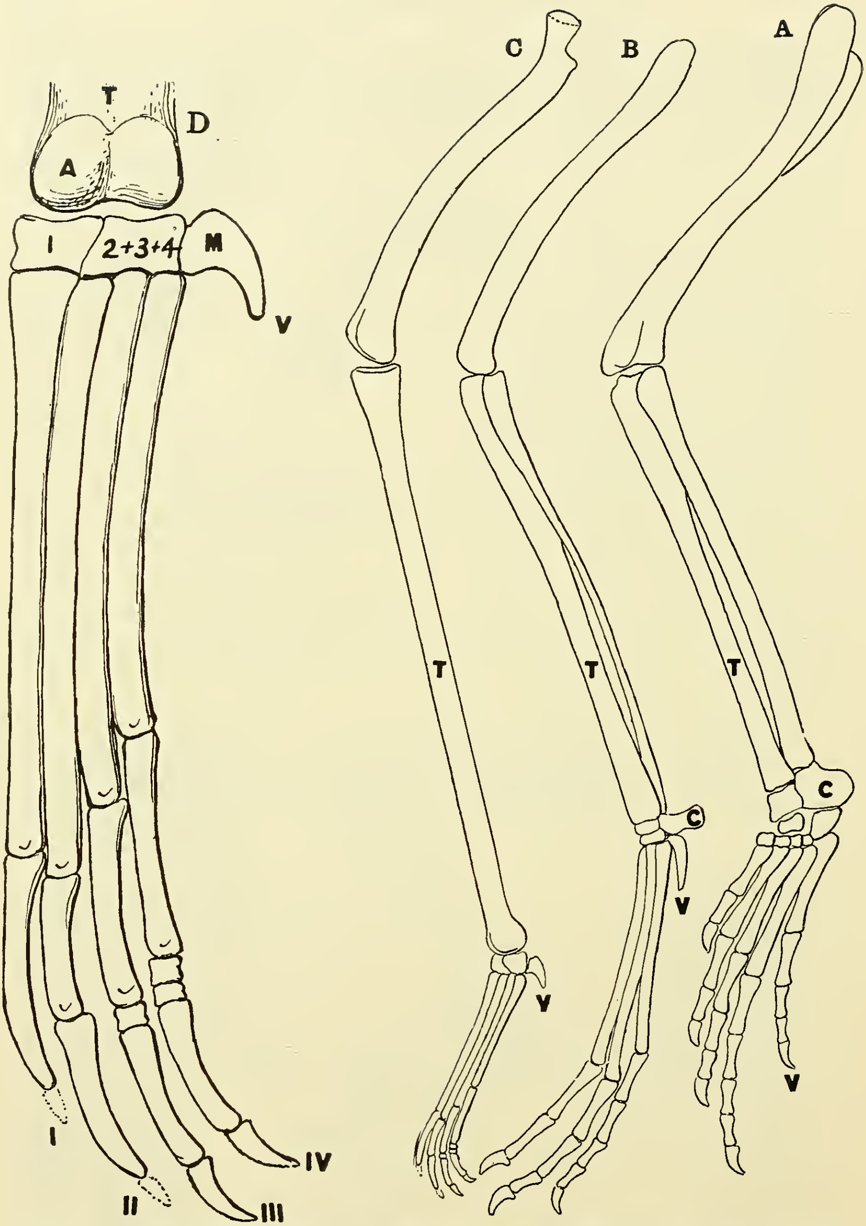

Fig. 155. Limbs: A, *Araeoscelis* (Protorosauria). Three fourths natural size. B, *Hallopus* (Dinosauria). After Marsh. One half natural size. C, *Pteranodon* (Pterosauria). About one third natural size. D, *Pteranodon*. About five sixths natural size.

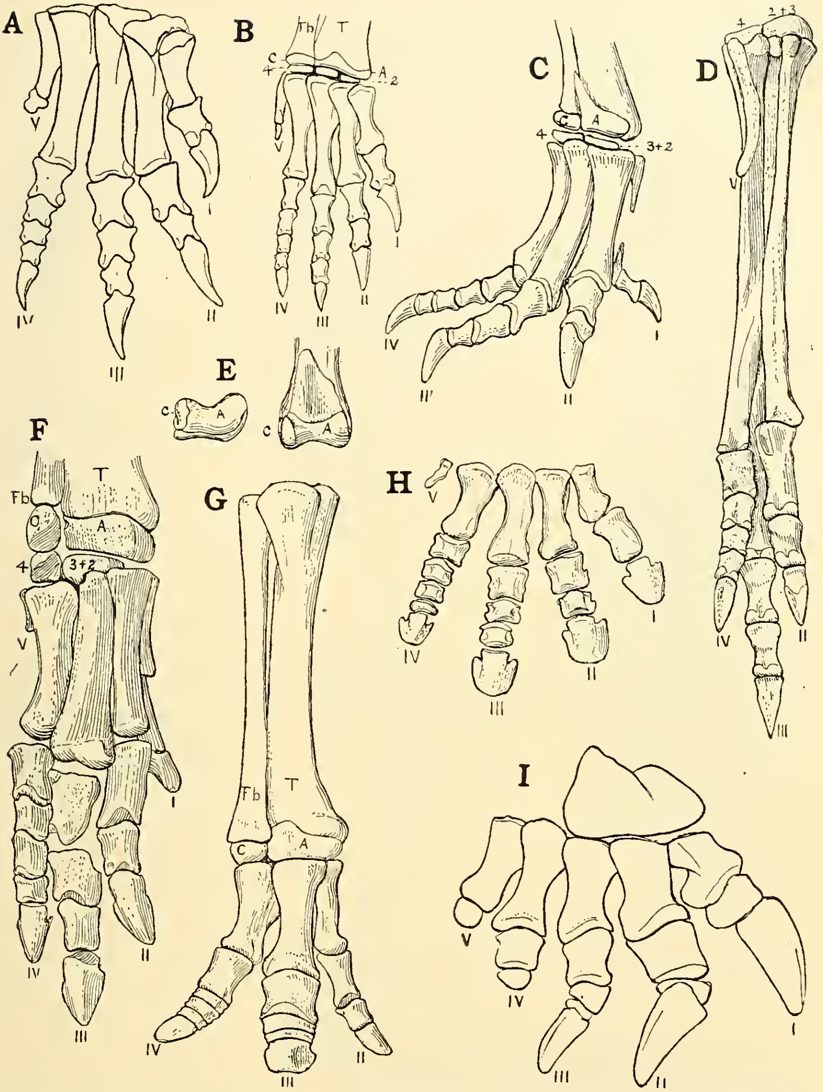

Fig. 156. Dinosaur pedes: A, *Plateosaurus* (Saurischia). After Huene. One twelfth natural size. B, *Anchisaurus* (Saurischia). After Marsh. One eighth natural size. C, *Allosaurus* (Saurischia). After Osborn. One seventeenth natural size. D, *Struthiomimus* (Saurischia). After Osborn. A little more than one sixth natural size. E, *Ornithomimus* (Saurischia). After Marsh. One sixth natural size. F, *Thescelosaurus* (Ornithischia). After Gilmore. One fifth natural size. G, *Trachodon* (Ornithischia). After Brown. About one nineteenth natural size. H, *Monoclonius* (Ornithischia). After Brown. One sixteenth natural size. I, *Morosaurus* (Saurischia). After Hatcher. About one eighth natural size. [*Brontosaurus.*]

The calcaneum of the Crocodilia (Fig. 157 A, B) is produced into a heel-like process; the first and fifth tarsalia and the centrale are absent, the second tarsale is small. *Hallopus* (Fig. 155 B), usually referred to the Dinosauria, also has a heel-like calcaneum, as is the case in *Scleromochlus*, and other genera of the Pseudosuchia, *Araeoscelis* (Fig. 155 A), *Broomia* (Fig. 137 D), and other leaping or springing reptiles.

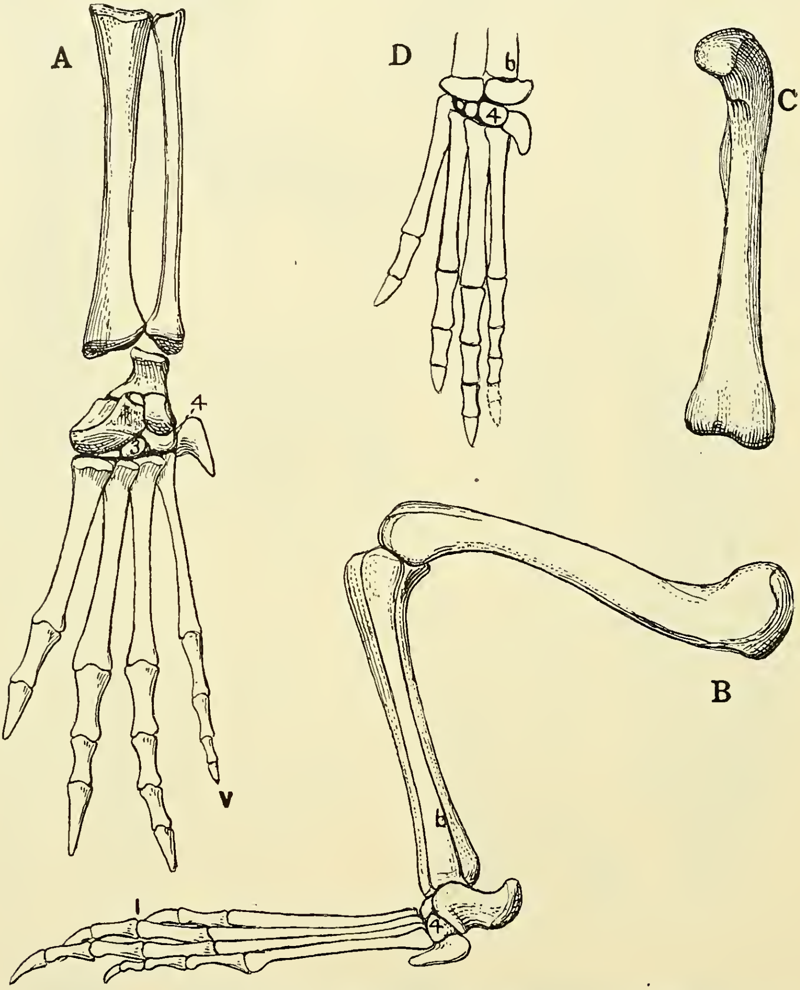

Fig. 157. Crocodilian limbs: A, B, left hind limb of *Alligator*, dorsal and postaxial; C, left femur dorsal; D, *Alligatorellus*. After Lortet. About three fourths natural size.

In the web-footed Mosasauria the tarsus, like the carpus (Figs. 146–148), progressively became more cartilaginous. In *Platecarpus* (Fig. 158 A) and *Clidastes* (Fig. 158 B) the astragalus, calcaneum, and fourth tarsale alone remain, with the divaricated fifth metatarsal, as in land lizards. In *Tylosaurus*, the most specialized of mosasaurs, but one, or at most two, small bones remain. Other tarsal bones remained unossified, though represented by cartilage in the adult.

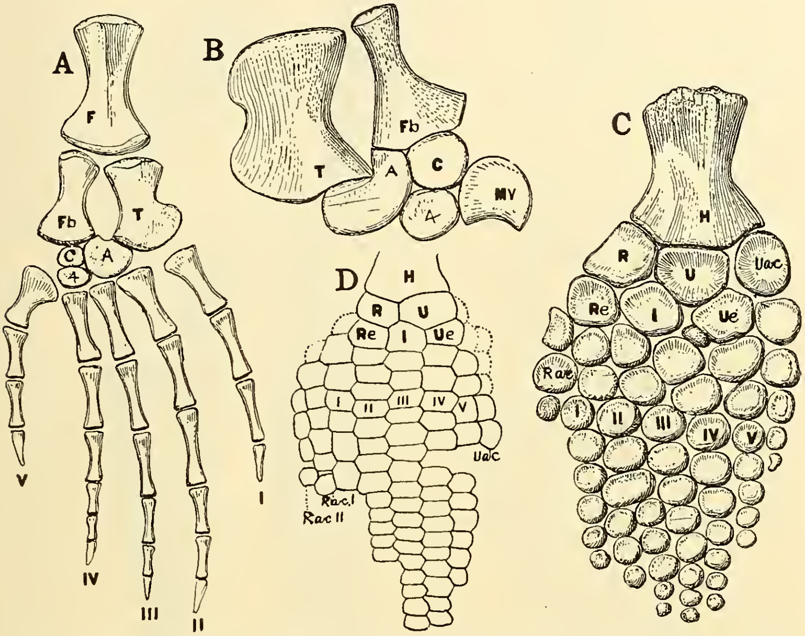

Fig. 158. Limbs of aquatic reptiles: A, *Platecarpus* (Mosasauria), right hind leg. About one sixth natural size. B, *Clidastes* (Mosasauria), right hind leg and tarsus. One third natural size. C, *Ophthalmosaurus* (Ichthyosauria), left front paddle. One eighth natural size. D, *Ichthyosaurus platydactylus* (Ichthyosauria), left front paddle. One sixth natural size.

Not more than six bones of the plesiosaurs can be called tarsals, and their homologies are doubtful (Fig. 159 B, C). They have the same shapes and relations as the carpal bones and cannot be distinguished from them except by their smaller size. The three in the first row are usually called the tibiale, intermedium, and fibulare; a fourth, on the postaxial side, has sometimes been called the pisiform in both front and hind limbs, but as there never was in any terrestrial reptiles a pisiform in the tarsus, that name is of course incorrect.

There are valid reasons for doubting the reappearance of the intermedium after its loss in the terrestrial ancestors of the plesiosaurs. It may be the enlarged centrale. The bones in the distal row may be the first, fused second and third, and the fourth tarsalia. The homologies of the mesopodial bones of the Ichthyosauria (Fig. 158 C, D), where a like similarity between the front and hind limbs exists, are even more doubtful. There is the same objection to the recognition of an intermedium tarsi in this order as in the plesiosaurs, whatever may be the corresponding bone in the carpus.

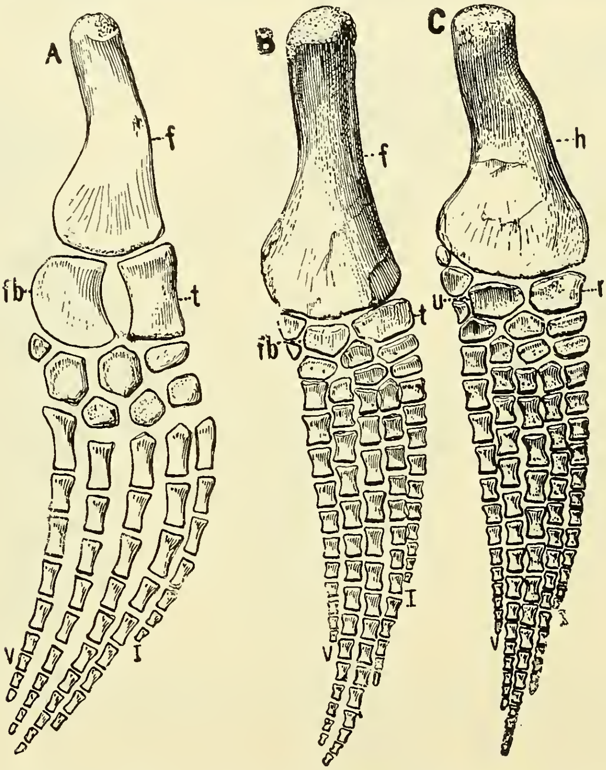

Fig. 159. Paddles of Plesiosaurs: A, right hind paddle of *Thaumatosaurus*, after Fraas. B, right hind paddle of *Trinacromerum*. C, right front paddle of same individual. *f*, femur; *fb*, fibula; *t*, tibia; *h*, humerus; *r*, radius; *u*, ulna.

Metapodials and Phalanges

The most primitive hand or manus known is that of the Cotylosauria, from the Permocarboniferous (Figs. 128, 133). The five metacarpals increase in length to the fourth; the fifth is shorter, but is not markedly divaricated. There are two phalanges in the thumb or *pollex*, three in the second digit, four in the third, five in the fourth, and but three in the fifth. The first and fifth metacarpals are more freely movable on the wrist than are the other three.

Of the Temnospondylous amphibians no complete hand is known. That there were five functional digits is certain,[1] since there are five functional carpalia in both *Eryops* (Fig. 136) and *Trematops*. It is often assumed that all amphibians of the past, as of the present, had but four fingers, as is known to be the case in some of the ancient Stegocephalia. The phalangeal formula was either 2, 3, 4, 4, 3 or 2, 3, 3, 4, 3, in the rhachitomous temnospondyls. It must be remembered, however, that we know nothing whatever of the hands or feet of the earliest amphibians, and it is purely an assumption that the reptilian hands and feet were evolved from forms like the later ones of Permocarboniferous times. In all probability the embolomerous ancestors of the reptiles had the phalangeal formulae of both front and hind feet like those of the known earliest reptiles. We can hardly conceive of an increase either of the number of digits or number of phalanges in the earliest reptiles.

In crawling reptiles the structure of the digits, it is seen, has not changed much to the present time, the modern *Sphenodon* (Fig. 139 A, B) as well as most modern lizards (Fig. 140 C, D) having the same number of bones arranged in the same ways. This primitive phalangeal formula is that of the Cotylosauria, Therocephalia, Theromorpha, Phytosauria, Pseudosuchia, Rhynchocephalia, Nothosauria, or at least some members of the group, and the group called by the author the Acrosauria, that is, the early *Araeoscelis* (Fig. 155 A), *Protorosaurus* (Fig. 138 D), *Pleurosaurus* (Fig. 139 D), and *Sauranodon* (Fig. 139 C). In the Crocodilia (Figs. 140 A, 157 A, B), the postaxial fingers are in all cases shorter and weaker, with fewer phalanges.

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[1] [For a different interpretation, however, see Gregory, Miner, and Noble in *Bulletin*, Amer. Mus. Nat. Hist., 1923, vol. XLVIII.—Ed.]

In no other reptiles has there been as great modification of the fingers as in the Pterosauria (Fig. 142), so great indeed that there is dispute as to the homologies of the ones that remained. The maximum of changes was reached in the latest forms, especially *Nyctosaurus* and *Pteranodon*, where there are three very short and weak fingers on the preaxial side, with two, three, and four phalanges, the terminal ones in the shape of strong claws. On the postaxial side the fourth finger is very long and strong, with four phalanges for the support of the patagium. This wing finger has generally been supposed to be the fifth, the first finger or pollex represented by a slender bone turned backward from the wrist toward the humerus and known as the *pteroid*. It seems more probable that the wing finger is the fourth, as originally so called by Cuvier, the fifth being absent. In the development of the patagium the claw of the wing finger would in all probability disappear, as in the bats, leaving the normal number for the fourth digit. If it is really the fifth, not only has the claw been converted into a long membrane-supporting phalange, but an additional phalange has been added; while each of the preceding three digits has lost one phalange. We can conceive of no cause for such hypo- and hyper-phalangy in the hand in these volant reptiles. One of the phalanges of the third finger is short, as in the third digit of the foot.

The first three metacarpals of the early pterodactyls articulated normally with the carpus (Fig. 142); in the later ones they were mere splints lodged loosely in the flesh at the distal end of the fourth metacarpal, only the first of them retaining a very slender connection with the wrist. The fourth metacarpal, on the other hand, progressively increased in length till it much exceeded the length of the forearm. Its distal articulation is a very perfect pulley-like joint, permitting flexion of the first phalange through almost one hundred and eighty degrees.

A general reduction of the postaxial digits of both front and hind feet is characteristic of the Dinosauria (Figs. 141, 156). Only in the primitive *Anchisaurus* and *Plateosaurus* (Fig. 141 A) is a nearly complete hand recognized, and even in these, two phalanges of the fifth finger are gone. The fifth finger is absent in all Theropoda since the early Jurassic, the fourth usually, the third sometimes. In *Gorgosaurus* (Fig. 141 C), from the uppermost Cretaceous, the hand is functionally didactyl, the extreme of specialization among reptiles. In the Theropoda (Fig. 141 A–E) the thumb is the stoutest digit, its claw the largest. In the herbivorous dinosaurs (Fig. 141 F, H, I, L, M) the hand is less preaxial, the first and second fingers being the larger. In the Trachodontidae (Fig. 141 H), indeed, the first finger is absent. In all herbivorous forms the outer fingers are reduced, though the fifth is seldom entirely absent, the phalangeal formula never exceeding 2, 3, 4, 3, 2, the claws lacking in the two postaxial digits. In *Trachodon* a greater reduction has occurred, almost the maximum among reptiles, the formula, according to Lambe, being 0, 3, 3, 2, 2. The ungual phalanges of both front and hind feet are characteristic, curved and sharply pointed in the Theropoda (Fig. 141 A–D), more obtuse in the Sauropoda (Fig. 141 F, G), for the most part hooflike in the Predentata (Fig. 141 H–M).

The foot or *pes* of reptiles is similar in structure to the hand, the reduction of the toes being usually anticipatory of the fingers in the terrestrial forms. There was one more phalange in the fifth toe than in the fifth finger primitively. In *Pariasaurus*, only, of the Cotylosauria, the phalangeal formula is slightly reduced, though primitive in *Propappus*, a related genus.

The loss of the fifth toe is rare among reptiles, aside from the Dinosauria. The crocodiles (Fig. 157 A, B, D) have only the fifth metatarsal left, and the fourth toe has but four phalanges. A very few lizards also have lost the fifth toe. It is often reduced among the Chelonia (Fig. 154 C, D); usually one, sometimes two, of the normal phalanges are lost. The greater strength of the foot in this order as in the dinosaurs is more to the preaxial side, unlike most other reptiles.

The foot of dinosaurs (Fig. 156), so far as the reduction of phalanges is concerned, is less specialized than the hand, the Theropoda (Fig. 156 A–E) retaining the original formula, except in the fifth toe. *Plateosaurus* (A) and *Anchisaurus* (B), from the Trias, have the formula 2, 3, 4, 5, 1; *Allosaurus* (C), from the lower Cretaceous, and *Struthiomimus* (D), from the uppermost Cretaceous, 2, 3, 4, 5, 0, the fifth metatarsal a vestige. The known Sauropoda (I) have 2, 3, 4, 3, 1 phalanges. Among the Predentata (F–H) the phalanges of the fifth toe are invariably absent in known forms, the formula, 2, 3, 4, 5, 0 being the usual one, and in *Trachodon* (G), 0, 3, 4, 5, 0. Among the quadrupedal Sauropoda (1) the axis of the foot is more to the preaxial side; in other dinosaurs it is the third toe that is the stoutest, though less so in the oldest theropods (A, B), this arguing perhaps a more sauropod-like mode of progression.

The earliest pterodactyls had two or three phalanges in the fifth toe; the later ones (Fig. 155 D) have only the hook-shaped metatarsal left. The greatly elongated feet were adapted more for perching or clinging than for locomotion. A striking peculiarity is seen in the greatly reduced second phalange of the third toe and the second and third of the fourth toes, singularly identical with the corresponding phalanges of the hand of the therocephalian *Scymnognathus* (Fig. 138). Similar reduced phalanges are seen in the hand of the theropod *Struthiomimus* and the tree sloths among mammals, in all cases doubtless to be ascribed to the grasping or clinging habits.

A peculiarity of the fifth metatarsal among the Diapsida (Figs. 139 A, 153 B), or many of them, and the Sauria (Fig. 140 D) and Chelonia (Figs. 144 B, 145 C, 154) is the more or less hook-like shape, proximally, a character which has been adduced in proof of their phylogenetic relationships. In all such cases the metatarsal articulates with the fourth tarsale, and the fifth tarsale is absent. In those reptiles which have a fifth tarsale, either ossified or cartilaginous, the metatarsal is straight, and perhaps also in those reptiles in which the foot had become more or less erect or digitigrade before its entire loss.

Hypophalangy. In the Chelonia (Figs. 144, 145, 154), Dromasauria (Fig. 137 A, B), Anomodontia, Cynodontia, as in the mammals, the primitive phalangeal formula suffered a reduction to 2, 3, 3, 3, 3 in both front and hind feet, with a further reduction to 2, 2, 2, 2, 2 (1) (Fig. 145 A) in many tortoises. The river turtles (Trionychoidea, Fig. 154) have normally four phalanges in the fourth and the fifth digits, which may rather be ascribed to a secondary hyperphalangy. More than three phalanges have also been observed in some Pleurodira. The chameleon lizards have the phalangeal formula 2, 3, 4, 4, 3 for both fore and hind feet (Fig. 143), and various examples of partial reduction of the postaxial digits occur among the Cotylosauria (*Pariasaurus*), Crocodilia, and especially the Dinosauria, as has been mentioned above.

Hyperphalangy and *Hyperdactyly.* An increase of the phalanges above the normal number (hyperphalangy) and of the digits (hyperdactyly) is known only in swimming animals. In some if not all Proganosauria (Fig. 153 A) the fifth toe has two extra phalanges, that is, 2, 3, 4, 5, 6, possibly but very improbably a primitive character, as the earliest foot known (*Eosauravus*, Fig. 151 B) from the middle Pennsylvanian has the same number and arrangement of the phalanges as in the Cotylosauria (Figs. 128, 133) and modern lizards (Fig. 140). In *Trionyx*, a river turtle, five phalanges have been observed in the fourth toe, and as many as six in the fifth, certainly an acquired character, and the only examples of hyperphalangy in the order Chelonia. In web-footed swimming animals there is sometimes a tendency toward the elongation of the fifth toe, as observed in *Eosauravus* (Fig. 151 B), *Lariosaurus* (Fig. 149), and especially *Mesosaurus* (Fig. 153 A), and *Tylosaurus* (Fig. 148). It may perhaps indicate the use of the hind legs more as sculling organs after the manner of seals, sea otters, and the Cretaceous bird *Hesperornis*, in all of which the fifth toe is very long and strong, though without additional phalanges.

In all strictly aquatic reptiles (Figs. 158, 159) the digits are elongated, and except in the Chelonia, there was an increase of the number of phalanges in both front and hind feet, sometimes far beyond the normal number. A like hyperphalangy is observed in the marine mammals, one or two additional cartilaginous phalanges in the sirenians, and from two to ten ossified ones in the Cetacea. Various theories have been proposed to account for their origin. That they cannot be due to the ossification and separation of the normal epiphyses in reptiles is quite evident, for these reptiles at least had no epiphyses. Like the additional epipodials of the plesiosaurs and ichthyosaurs, they are accessory, new ossifications in the mesenchyme and not reversions to a primitive fish-like fin.

In the Mosasauria there was a progressive increase in hyperphalangy as observed in the genera *Clidastes* (Fig. 146), *Platecarpus* (Fig. 147), and *Tylosaurus* (Fig. 148) from one or two to as many as six or eight additional phalanges, concomitant with the progressive chondrification of the mesopodials. In certain plesiosaurs as many as twenty-two phalanges are known in the third digit, and certain ichthyosaurs have even more. Hyperdactyly, due to the same causes, is known in the ichthyosaurs only among reptiles (Fig. 158 C, D).

More usually the feet are pentedactylate, but certain early forms have but three digits, while other later ones may have as many as nine. It is a question whether three was the primitive number, and that all above that number are accessory; more probably the hypodactyly occurred after the ichthyosaur paddle was essentially evolved. Some of these accessory digits seem to have arisen at the sides of the paddles; others by a splitting of the digits, as shown in Figure 158 C. The paddles of both the plesiosaurs and ichthyosaurs were oar-like and flexible; the feet of the mosasaurs were webbed, more like the feet of ducks and frogs.

In crawling reptiles (Figs. 1, 128) the feet are directed more outwardly, and the motion of the foot upon the epipodials is largely lateral. The structure of the feet in the early forms, even as late as *Sauranodon* (Fig. 153 B), with a large astragalus and calcaneum, shows an extensive lateral movement of the foot upon the leg in locomotion. In the modern lizards (Fig. 140 D) and *Sphenodon* (Fig. 139 A) the angle between the leg and foot in locomotion is acute, probably much more so than in the early forms, and this may account for the coössification of the heel bones. In such reptiles the toes always are and must be long, with the main axis of the foot more postaxial. On the other hand, the direction of the foot in the turtles, and especially the tortoises (Fig. 145), is more forward than lateral; the digits of the feet on the two sides are brought more nearly parallel in locomotion. The same acute angle between the foot and leg and the elevation of the heel bones have also resulted in the firmer ossification of the tarsal bones and their fusion. In such locomotion long toes would be a hindrance, and they have been shortened, both by a reduction in the numbers and by a shortening of the segments.

Doubtless this same more mammal-like or turtle-like mode of progression was characteristic of the Dromasauria, Anomodontia, and Theriodontia, and likewise resulted in the reduction of the phalanges and shortening of the toes. One can imagine the difficulties of locomotion if our toes were six inches long! The Cotylosauria have short and broad feet, and many of the later ones, like *Pariasaurus* and *Telerpeton* have the astragalus and calcaneum fused. Possibly the mode of progression was more turtle-like than lizard-like, and the results began to be seen in the reduced phalangeal formula of *Pariasaurus*. Except among the Sauropoda and Stegosauria, in which the toes have become shortened and the phalanges on the postaxial side reduced, the dinosaurs have rather long digits, but they had become distinctively digitigrade, shortening the portion resting upon the ground, like the reduction of the digital formula in the plantigrade reptiles. In all such reptiles with the more mammal-like mode of locomotion, the foot is more mesaxial or preaxial, as in the mammals, where the fourth is very seldom the strongest toe.

The chief joint between the foot and legs in mammals is between the end of the tibia and the first row of the tarsals. In reptiles it is intratarsal, that is, between the first and second rows of the tarsus. In those reptiles which walked more or less upon the toes, digitigrade, there was a progressively closer articulation between the tibia and the astragalus, giving a firmer and closer ankle which otherwise would have been subject to injury with the heel elevated far above the ground. In the bipedal Theropoda (Fig. 156 A, C), the astragalus, while perhaps never fully fused with the tibia, acquired a long ascending process which fitted closely into a groove in front of the distal end of the tibia. In the still more elongated feet of the pterodactyls (Fig. 155 C, D) the astragalus became indistinguishably fused with the tibia, as in birds, and the joint, while actually, as formerly, intratarsal, was functionally between the leg and tarsus as in mammals.

Short toes and reduction of phalanges, then, mean a more mammal-like mode of locomotion and posture of the feet. In the turtles this has been produced by the exigency of the immovable shell, and by the greater or lesser twisting of the epipodials upon the propodials.

PART II

THE CLASSIFICATION AND RANGE OF REPTILES

CHAPTER VI

THE PROBLEM OF CLASSIFICATION

One who has studied attentively the skeleton of reptiles cannot fail to be impressed with the fact that similar or even apparently identical structures have arisen in different orders. Procoelous vertebrae, for instance, occur in crocodiles, pterodactyls, lizards, and frogs when it seems impossible that all should have been evolved from the same common ancestor with procoelous vertebrae. Snakes, some lizards, and certain Stegocephalia have a peculiar mode of articulation of the vertebrae, called zygosphenal, but their evolution from a common ancestor is impossible. For such resemblances the convenient term homoplasy has been proposed. Did they occur rarely in organisms they would not trouble us much; but they are everywhere in nature, and the problem of all classification is to distinguish between them and those characters due to heredity. Until we have learned to distinguish them our classification must remain more or less artificial.

The true end of all classification is genealogy. Some time in the Carboniferous period there was but a single kind of reptile, differing very slightly from its ancestors, and from this reptile has descended all the kinds that have ever lived. In the adaptation of its progeny to various provinces and modes of life they have divided into innumerable branches. Many of these branches were feeble and of short duration; others have continued to modern times, but none has ever reunited with another branch, even though small. Our object in classification is to determine these branches, and especially the early or primary ones. The twigs we call species, the lesser branches genera and families, the limbs orders, and the main boughs subclasses. It is easy enough relatively to distinguish the twigs and smaller branches, but it is often very difficult to determine where the limbs united with the boughs and where the boughs joined the trunk. A perfect classification would be dichotomous, each bough, limb, and branch dividing first into two, and each division again into two; but an approximation even to such a classification cannot be attained, and we must often treat groups of organisms as though radiating from a common center. And it is also evident that such divisions occurred rapidly. Many of the first groups of species that branched as twigs from the common stem were the ancestors of orders, for they held, all of them, possibilities of great developments; succeeding species became more and more restricted in their potentialities.

Our chief object, then, in classification is to trace the history of each species, genus, family, and order to its separation from allied forms, and to give to each minor and major group a name and place. And our chief difficulty in doing this is to determine whether the resemblances that they show to each other have been due to descent and common heritage, or have been the result of common environmental influences. The problems are hard and always will be hard because actual proofs of heredity must ultimately rest on the facts of paleontology, and paleontological history is and always will be imperfect. In all probability the earth since remote ages has always been as densely populated with living organisms as it is at the present time, and rapidly or slowly in different kinds of organisms evolution and extinction have replaced the faunas and floras many times. There are to-day living upon the earth about twenty thousand species of air-breathing vertebrate animals, and doubtless there has been no time since the first general invasion of land by air-breathers that the number has been less; it may have been greater, since man has exerted a powerful influence upon them. As the only air-breathers of paleozoic times were amphibians and reptiles, there must have been, during the time that they reigned supreme,— from the Mississippian to the Jurassic, millions of years,— scores of thousands of their kinds; we know but a few hundreds. Had we records of all that have lived, the major problems would be much easier, the minor ones greatly increased.

Nevertheless, in tracing the genealogies of organisms, that is, in classifying them, we are aided by general laws which have obtained recognition among students of extinct animals. First of all, by the law that evolution is irreversible, that organs or functions once lost can never be regained by descendants; similar organs or similar functions often, but never the original ones. By the general law that there has been a continuous loss of parts; we can trace, for instance, probably every bone of the human skull back to the primitive reptilian or amphibian skull, but there were twice or thrice as many bones in the older forms as there are in recent ones. And there has been in general an increase in bodily size in every phylum. The largest animals have always lived at or near the end of their race, and a race of small animals has never been evolved from a race of large animals. Furthermore, horns, spines, protuberances, and excrescences occur only in the later history of any race, never at its beginning.

The two chief factors of evolution have been environment and heredity. There is more or less impulse due to heredity, a sort of *vis a tergo* that seems to influence evolution along parallel lines in related forms, though we are never sure how much is due to it and how much to similar environmental influences.

The chief problem, then, in any classification is the relative importance of structural characters in the absence of the actual connecting links insensibly uniting different forms, that is, the determination of the more conservative hereditary characters of the skeleton, those which have been influenced less by environmental conditions. Some parts of the skeleton are very variable even in nearly related forms. The number of vertebrae in the spinal column, we have seen, may vary extraordinarily within an order. Chameleon lizards have only about sixty vertebrae; other lizards may have a hundred and ninety-four, while snakes of the same order may have as many as four hundred and fifty. The number is seldom of more than generic value, and sometimes perhaps not more than specific. It would be absurd, for instance, to unite in the same group a lizard and a turtle because each happens to have eight cervical vertebrae.

And the teeth of reptiles, unlike those of mammals, have little value as criteria of relationships, so adaptable are they in shape and number to food habits, though their location may be more conservative. The pectoral and pelvic girdles have been influenced less by environmental conditions; the structure of the feet still less in adaptation to life conditions. More conservative is the arrangement and mode of articulation of the ribs. Most conservative of all has been the structure of the cranial region of the skull, that surrounding the brain, and in consequence it furnishes the most reliable characters for the discrimination of the larger groups, the subclasses or superorders.

The most primitive reptiles that we know had no less than thirty-seven pairs and four single bones in the skull. The crocodiles have but twenty-four pairs and six unpaired bones in the adult; the turtles have twenty-two or twenty-three pairs and five or six unpaired bones; the lizards have at the most twenty-nine pairs and five single bones. But not all are the same. The crocodiles have three or four pairs that have been lost in the turtles; the turtles, one pair that is fused in the crocodiles; the lizards, several bones lost or fused in the turtles, and so on. All reptiles since Triassic times have lost four bones in the pectoral girdle, and all have lost some bones of the feet. The persistence or loss of bones furnishes many certain evidences of relationships and descent. Each order must have descended from ancestors that had the persistent bones; they could by no possibility have regained them when once lost.

The relative importance of all such characters in classification is, however, largely a matter of the classifier's personal opinion. No two persons see them from the same viewpoint and consequently no two persons whose opinions deserve consideration ever wholly agree as to the value of characters in classification. It is only in the gradual crystallization of opinions that stability finally results, and this crystallization is never complete. So long as science endures, new facts will be discovered to influence our opinions. Any system of classification, then, merely represents the present state of our knowledge and the consensus of the opinions of those best qualified to decide as to their value, more or less influenced by the classifier's individual opinions. No classification will ever be perfect, for perfection postulates complete knowledge. Fortunately, however, the increase of knowledge affects less and less the major principles, and more and more subordinate details.

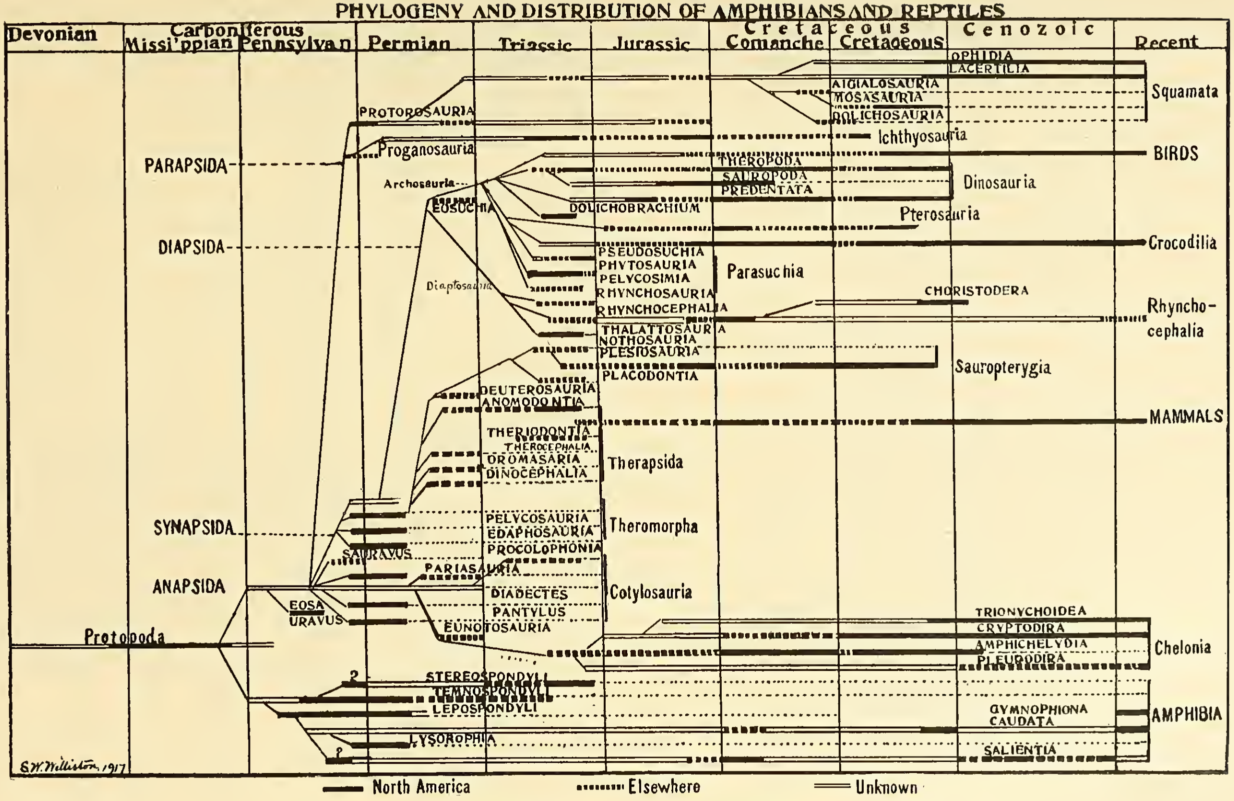

Fig. 160. Phylogeny and distribution of Amphibians and Reptiles.

CHAPTER VII

A SYNOPTIC CLASSIFICATION OF THE REPTILIA

I. **ANAPSIDA.** Temporal region of skull roofed over, or secondarily emarginated, not perforated.

  1. **Cotylosauria.** Skeleton primitive; two coracoids[1]; at least eighteen dorsal vertebrae, their ribs not expanded.
     - A. SEYMOURIA. Most primitive; teeth conical, in single row; intertemporal and otic notch. Insectivorous. Lower Permian.
     - B. DIADECTOSAURIA. Teeth heterodont, the posterior transversely molariform, crushing. Malacophagous. Lower Permian.
     - C. LABIDOSAURIA. Teeth anisodont, in two or more rows posteriorly; no supratemporal; interparietal on posterior surface. Lower Permian.
     - D. LIMNOSCELIS. Teeth anisodont, conical, in single row; interparietal on dorsal surface. Tail long. Lower Permian.
     - [E. PANTYLOSAURIA. Teeth blunt or pebble-like, in single rows in upper jaw and dentary, numerous on palate and coronoid; interparietals large on dorsal surface. Lower Permian.]
     - F. PARIASAURIA. Teeth anisodont, the posterior flattened [compressed] and crenulate; an acromion. Middle and Upper Permian.
     - G. PROCOLOPHONIA. Incisors conical, posterior teeth transverse, crushing; no supratemporal; interparietal obsolete or absent. Triassic.
  2. **Eunotosauria.** Skeleton primitive; two coracoids, ten dorsal vertebrae, their ribs expanded to meet on the dorsum, *and* a dermal layer of bony plates. Middle Permian.
  3. **Testudinata** (*Chelonia*). Skeleton not primitive; a single coracoid; ten dorsal vertebrae, their ribs expanded to meet on the dorsum *or* a dermal layer of bony plates.
     - A. AMPHICHELYDIA. No mesoplastra. Cervical vertebrae amphicoelous or concavo-convex, neck not retractile. Upper Triassic to Cretaceous.
     - B. PLEURODIRA. Neck retracted laterally; pelvis united with plastron. Jurassic to Recent.
     - C. CRYPTODIRA. Neck retracted vertically; carapace with peripheral plates. Jurassic to Recent.
     - D. TRIONYCHOIDEA. Neck retracted vertically; no peripheral plates. River turtles. Cretaceous to Recent.

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[1] [But see footnote on page 126.—ED.]

II. **SYNAPSIDA.** A single temporal opening, primitively below the postorbito-squamosal arch; two coracoids.

4. **Theromorpha.** Skeleton primitive; vertebrae notochordal with persistent dorsal intercentra; teeth on palate bones; phalangeal formula primitive; propodials horizontal in locomotion.
   - A. PELYCOSAURIA. Carnivorous; teeth strongly anisodont with diastema; dorsal spines more or less elongated; interparietal and tabulars present. Lower Permian.
   - B. EDAPHOSAURIA. Malacophagous; teeth small, isodont. Dorsal spines elongate, with bars; interparietal and tabulars present. Lower Permian.
   - C. POLIOSAURIA. Insectivorous; teeth small, conical, subisodont; dorsal spines not elongate. Lower Permian.
   - D. CASEASAURIA. Malacophagous; teeth small, isodont; dorsal spines short. Lower Permian.

5. **Therapsida.** Skeleton less primitive; vertebrae amphicoelous, rarely notochordal; dorsal intercentra absent or unknown; phalangeal formula often reduced; propodials turned more or less downward in locomotion.
   - A. DINOCEPHALIA. Skull massive; no secondary palate; quadrate large, temporal opening surrounded by postorbital and squamosal; phalangeal formula primitive [?]. Upper Permian.
   - B. DROMASAURIA. Dentition subisodont or absent; no secondary palate; phalangeal formula 2, 3, 3, 3, 3. Permian.
   - C. ANOMODONTIA. Edentulous or with long canine, or canine and molars; a rudimentary secondary palate; an acromion; phalangeal formula 2, 3, 3, 3, 3. Upper Permian, Triassic.
   - D. THERIODONTIA. Carnivorous; dentition more or less heterodont, at least one pair of caniniform teeth; phalanges and teeth variable. Temporal opening extending to parietal in later forms. Triassic.

III. **SYNAPTOSAURIA.** A single temporal opening bounded below by postorbito-squamosal arch; no supratemporal, interparietal or tabulars. A single coracoid (? Placodontia).

6. **Sauropterygia.** Vertebrae platycoelous; no dorsal intercentra; dorsal ribs single-headed, articulating with diapophysis; no teeth on palate. Neck more or less elongated.
   - A. NOTHOSAURIA. Amphibious; feet webbed; phalangeal formula primitive; no interpterygoidal opening in palate. Middle and Upper Triassic.
   - B. PLESIOSAURIA. Marine; limbs paddle-like, the propodials long; hyperphalangic; palate with openings. Triassic to close of Cretaceous.

7. **Placodontia.** Jaws and closed palate with heavy pavement teeth; vertebrae deeply amphicoelous; dorsal ribs double-headed; body with dermal bones; coracoids and feet unknown. Upper Triassic.

IV. **PARAPSIDA.** A single temporal opening, between parietal and postorbito-squamosal arch; supratemporal (tabular) persistent. Ribs articulating more or less exclusively with centrum. A single coracoid.

8. **Proganosauria.** Skeleton largely primitive. Aquatic, the neck and tail elongate. Phalangeal formula 2, 3, 4, 5, 4 (6). Skull imperfectly known; the quadrate fixed. Lower Permian.
9. **Ichthyosauria.** Marine reptiles with short neck and all aquatic adaptations. Vertebrae amphicoelous; no dorsal intercentra. Quadrate fixed. Middle Triassic to Upper Cretaceous.
10. **Protorosauria.** Aquatic or terrestrial. Not more than seven cervical vertebrae. Vertebrae amphicoelous (? Saphaeosauridae). Quadrate fixed. Phalangeal formula primitive. Lower Permian to Jurassic.
11. **Squamata.** Quadrate freely articulated proximally (streptostylic) or secondarily fixed.
    - A. LACERTILIA (*Sauria*).[1] Parietals never united to basisphenoid by descending plates, the brain-case more or less membranous anteriorly.
        - (*a*) *Kionocrania.* An epipterygoid present[2]; vertebrae amphicoelous with persistent dorsal intercentra, or procoelous and no dorsal intercentra; eight cervical vertebrae; limbed or limbless. Phalangeal formula primitive. Cretaceous to Recent.
        - (*b*) *Platynota.* An epipterygoid. Vertebrae procoelous. Nine or more cervical vertebrae. Phalangeal formula primitive. Lower Cretaceous to Recent.
        - (*c*) *Pythonomorpha.* Marine reptiles; limbs paddle-like, hyperphalangic; seven cervical vertebrae, procoelous; an epipterygoid present. Upper Cretaceous.
        - (*d*) *Amphisbaenia.* No epipterygoid or temporal arch, the quadrate secondarily fixed; limbless or with vestigial front legs; vertebrae procoelous. Oligocene to Recent.
        - (*e*) *Rhiptoglossa.* No epipterygoid or clavicles[3]; five cervical vertebrae; vertebrae procoelous; phalangeal formula 2, 3, 4, 4, 3. Oligocene to Recent.
    - B. OPHIDIA (*Serpentes*). Brain-case enclosed by descending plates from parietals and frontals; no epipterygoids; no temporal arch; mandibles united by ligament. Vertebrae procoelous, with zygosphenes; no chevrons. Limbless. Cretaceous to Recent.

V. **DIAPSIDA.** Two temporal openings, separated by postorbito-squamosal arch; no supratemporals or tabulars (? *Youngina*). A

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[1] [For a more comprehensive classification of the Lacertilia, see C. L. Camp, 1923, *Bulletin*, Amer. Mus. Nat. Hist., XLVIII, 289–481.—ED.]

[2] [Absent in Dibamidae. — G. K. N.]

[3] [Sometimes present, but small. — ED.]

single coracoid; no cleithrum. Phalangeal formula primitive. Often reduced postaxially.

12. ? **Proterosuchia.** Skull elongate, with palatal teeth; an antorbital vacuity. Skull only known. Triassic.

13. ? **Eosuchia.** No antorbital vacuity[1]; interparietal and tabulars present; a parietal foramen. Only skull known. Upper Permian.

A. *DIAPTOSAURIA.* No antorbital foramen in skull; no supratemporal, tabulars or interparietals; palate with teeth. Vertebrae amphicoelous. Dorsal ribs articulating with intercentral space or centrum and arch, holocephalous.

14. **Rhynchocephalia.** Teeth protacrodont or acrodont.
    - A. RHYNCHOSAURIA. Skull broad, with decurved premaxillae and crushing teeth on palate. No epicondylar foramina; pubo-ischiatic opening small. Littoral reptiles. Upper Triassic.
    - B. SPHENODONTIA. Premaxillae beak-like; pelvis with large pubo-ischiatic vacuity; an entepicondylar foramen; dorsal intercentra persistent. Littoral reptiles. Upper Jurassic to Recent.
    - C. CHORISTODERA. Face elongate, the nares terminal; no pubo-ischiatic vacuity; teeth labyrinthine. Subaquatic. Uppermost Cretaceous and Lowermost Eocene.
    - D. ? THALATTOSAURIA. Skull elongate, with external nares posterior. Ribs attached by single head to centrum. Limbs paddle-like. Imperfectly known. Aquatic. Triassic.

AA. *ARCHOSAURIA.* Dorsal ribs, anteriorly at least, articulating with arch only, dichocephalous; no teeth on palate; no parietal foramen; no supratemporal, interparietal, or tabulars; vertebrae variable; dorsal intercentra not persistent; usually an antorbital opening. Typically with large pubo-ischiatic vacuity.

15. **Parasuchia.** Pelvis more or less plate-like with small pubo-ischiatic vacuity; vertebrae amphicoelous; no false palate; phalanges not reduced; body with dermal scutes.
    - A. PSEUDOSUCHIA. External and internal nares near extremity of face; legs elongate, the epipodials long. Cursorial reptiles. Triassic.
    - B. PELYCOSIMIA. External and internal nares terminal. Legs short and stout. Terrestrial or marsh reptiles. Triassic.
    - C. PHYTOSAURIA. External and internal nares remote from extremity of slender face. Triassic.

16. **Crocodilia.** Pubes excluded from acetabulum, not meeting in ventral symphysis. A secondary palate. External nares terminal; vertebrae amphicoelous or procoelous; postaxial digits reduced.
    - A. EUSUCHIA. With dermal plates; no sclerotic plates. Amphibious. Jurassic to Recent.

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[1] [According to Broom, a well-preserved antorbital vacuity is present. — ED.]

B. THALATTOSUCHIA. Neck shorter; no dermal plates; sclerotic plates in orbits. Vertebrae amphicoelous; a terminal caudal fin. Front legs reduced, paddle-like. Marine. Jurassic.

DINOSAURIA. More or less upright-walking reptiles.

17. **Saurischia.** Pelvis normal, the pubes meeting in a ventral symphysis; presacral vertebrae amphicoelous, or some or all opisthocoelous. No predentary or rostral bones in skull. Postaxial digits reduced. No dermal ossicles.

A. THEROPODA. Carnivorous or secondarily herbivorous, bipedal in gait, the front legs more or less reduced. Triassic to close of Cretaceous.

B. SAUROPODA (CETIOSAURIA, OPISTHOCOELIA). Herbivorous, quadrupedal, the front legs but little or not at all reduced; limb bones not hollow; neck and tail elongate. Jurassic, Cretaceous.

18. **Ornithischia** (*Orthopoda*). Herbivorous, a predentary bone in mandible; pubes composed of a spatulate anterior process not meeting in symphysis, and a more or less elongate posterior process. Postaxial digits reduced.

A. ORNITHOPODA. Upright-walking, bipedal. Without dermal bones. Lower Jurassic to close of Cretaceous.

B. STEGOSAURIA. Quadrupedal, with dermal armor of plates and spines; skull small; bones solid. Jurassic to close of Cretaceous.

C. CERATOPSIA. Quadrupedal. Skull very large with bony horns and a posterior expansion fringed with scutes or spines. Uppermost Cretaceous.

19. **Pterosauria.** Volant reptiles, the bones pneumatic. Fourth finger greatly elongated to support patagium. Vertebrae procoelous.

A. PTERODERMATA (RHAMPHORHYNCHOIDEA). Wing metacarpal not longer than forearm; tail long. Skull with teeth. Jurassic.

B. PTERODACTYLOIDEA. Wing metacarpal longer than forearm; tail short. Skull with or without teeth. Upper Jurassic to Upper Cretaceous.

CHAPTER VIII

THE SUBCLASS ANAPSIDA

Temporal region of skull wholly roofed over, or secondarily emarginated from the sides, not perforated.

1. ORDER COTYLOSAURIA

Temporal roof complete, not emarginated: skeleton primitive. An order of reptiles, not only the oldest geologically, but more primitive in structure than any other; probably the ancestral stock of all later Amniota. They were very variable in size, structure, and habits: as known, subaquatic, lowland, or marsh reptiles, never cursorial or climbing; invertebrate feeders for the most part, varying in size from less than one to about ten feet in length. The body was never slender, nor the legs long; the neck was always short. Dermal ossifications of any kind are known in but a few genera, *Diadectes*, *Pantylus*, and the Pariasauridae; the body was probably covered with horny plates or scales. The earliest known member of the order dates from the Middle Pennsylvanian, the latest from the Middle Triassic.

None has all the primitive characters given in the list, but the losses or modifications in any form are few. They may be discussed under three groups, which include their chief evolutional modifications.

1. *Carboniferous and Lower Permian*

The intertemporal bone and the otic notch are known in but one or two genera, the Seymouriidae; the supratemporals are absent in the Captorhinidae, the tabulars also in *Labidosaurus*. The ectopterygoid has not yet been certainly demonstrated in any genus, though probably present. The parietal foramen is absent in *Pantylus*, and possibly also in some others. Free ribs are present to the sacrum and in the tail in *Seymouria* only, absent wholly in the lumbar region of the Captorhinidae. Parasternal ribs are known only in the last-named family and *Sauravus*. Two pairs of sacral ribs are present in all genera except *Seymouria* and *Diadectoides*. There are from twenty-two or twenty-three to twenty-six presacral vertebrae; the tail of

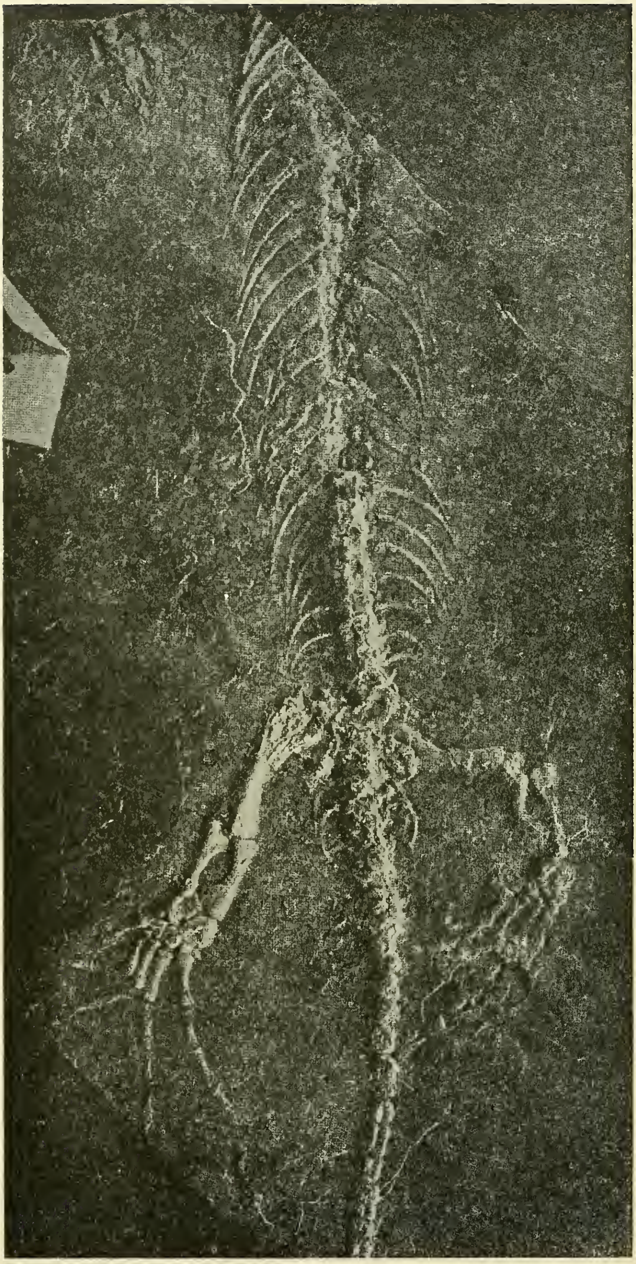

Fig. 161. *Eosauravus:* Part of skeleton, from above. Enlarged. Specimen in National Museum.

moderate or considerable length. Two centralia pedis are doubtfully known only in *Labidosaurus*. Dichocephalous ribs are known only in *Seymouria* and *Pantylus*. The cleithrum is vestigial in some.

FAMILY SEYMOURIIDAE. Primitive, terrestrial, insectivorous reptiles less than three feet in length. Teeth conical in a single row on jaws and dentaries. Cleithrum vestigial or absent. Vertebral spines vestigial, the vertebrae with broad arches.

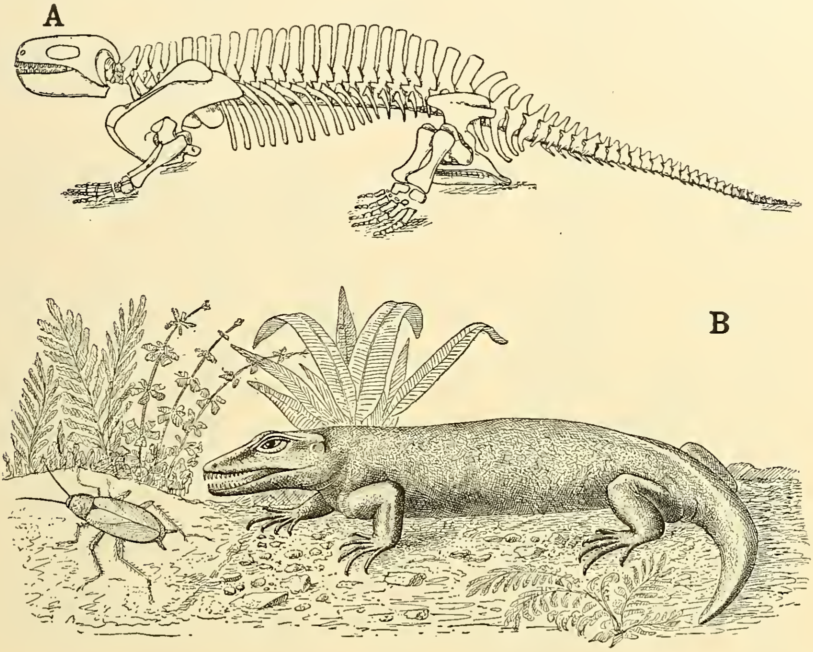

FIG. 162. Skeleton and life restoration of Cotylosaurs: A, *Diasparactus*. After Case. One twentieth natural size. B, *Seymouria*. About two feet long.

Seymouria Broili (? *Conodectes* Cope). United States.

FAMILY SAURAVIDAE. Slender reptiles about one foot in length. Skull and intercentra unknown.

Eosauravus (Middle Pennsylvanian). United States.

Sauravus. Thevenin, France.

FAMILY GYMNARTHRIDAE. Small reptiles six to eight or ten inches in length, insectivorous or invertebrate feeders. Teeth obtusely pointed. Parasphenoid large and broad. Appendicular skeleton unknown, and the skull imperfectly known.

Gymnarthrus Case, *Cardiocephalus* Broili, United States.

FAMILY DIADECTIDAE (Diadectosauria). From about five to about eight feet in length. Skull short and high. Teeth incisiform in front, transversely molariform posteriorly. Vertebrae with hyposphene and hypantrum. Cleithrum rather large.

Diadectes Cope, *Animasaurus* Case and Williston, *Bolbodon* Cope, *Chilonyx* Cope, *Desmatodon* Case, *Diadectoides* Case, *Diasparactus* Case, United States.

FAMILY BOLOSAURIDAE. Teeth subconical, cuspidate. Small reptiles. Teeth and part of skull only, known. *Bolosaurus* Cope, United States.

FAMILY CAPTORHINIDAE (Labidosauria). From one to three feet in length; invertebrate feeders. Dermosupraoccipitals confined to occiput. No supratemporals and, in *Labidosaurus*, no tabulars. Teeth obtusely flattened, conical, in two or more rows on maxillae, one or more on mandible. Cleithrum vestigial. Spines of vertebrae short, their arches broad. Parasternal ribs present.

Captorhinus Cope, *Pleuristion* Case, *Labidosaurus* Cope, United States.

FAMILY PARIOTICHIDAE. Small terrestrial reptiles about one foot in length, insectivorous or invertebrate feeders. Teeth obtusely pointed, in one or more rows. Imperfectly known.

Pariotichus Cope, *Ectocynodon* Cope, *Isodectes* Cope, *Puercosaurus* Williston, United States.

FAMILY STEPHANOSPONDYLIDAE. Maxillae with two rows of transverse teeth. Cleithrum large. Skull short, imperfectly known, as also the skeleton.

Stephanospondylus Stappenbeck, *Phanerosaurus* Meyer, Saxony, Germany.

GENERA INCERTAE SEDIS: *Chamasaurus* Williston, *Archeria* Case, *Bathyglyptus* Case, *Helodectes* Cope, United States.

FAMILY LIMNOSCELIDAE. Elongate, subaquatic or marsh reptiles seven or eight feet in length. Teeth conical, recurved in single rows.

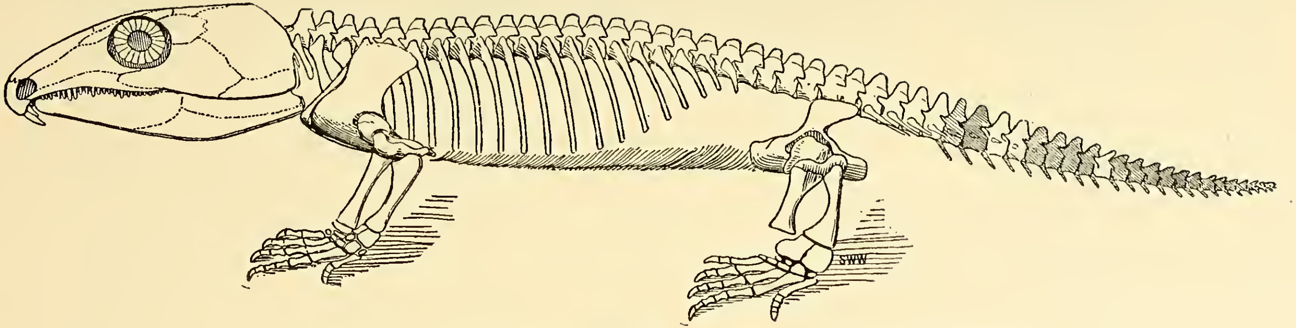

Fig. 163. Skeleton of *Labidosaurus* (Cotylosauria) from the side. One fourth natural size.

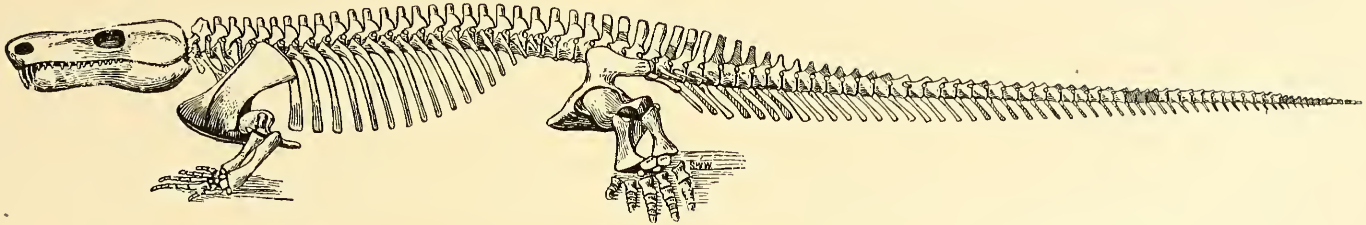

Fig. 164. *Limnoscelis*, a subaquatic cotylosaur, from the Permocarboniferous of New Mexico, One twelfth natural size,

Skull elongate and compressed in front. Cleithrum small, tail elongate.

Limnoscelis Williston, United States.

Family Pantylidae (Pantylosauria). Terrestrial reptile less than two feet in length. Skull low, short, flat, with palatal and coronoid teeth; a single row of short teeth in [upper] jaws and mandible. Skeleton imperfectly known. No parietal foramen. Body covered with small bony scutes.

Pantylus Cope (? *Ostodolepis* Williston), United States.

2. *Middle and Upper Permian*

Family Pariasauridae (Pariasauria). Large lowland cotylosaurs reaching nine or more feet in length. Skull with protuberances, broad and short, its intimate structure not well known. Teeth in a single row, convex on the outer side with six or seven cusps arranged around their borders. Scapula with acromion and screw-shaped glenoid fossa. Phalangeal formula of front feet unknown. Astragalus and calcaneum fused; centrale and fifth tarsale unknown, possibly absent. Phalangeal formula believed to be 2, 3, 3, 4, 3 in one genus, primitive in others. Body with several rows of bony dermal scutes.

Pariasaurus Owen, *Propappus* Seeley, *Anthodon* Owen, *Bradysaurus* Watson, *Embrithosaurus* Watson, *Pariasuchus* Haughton and Broom, South Africa. *Pariasaurus* or an allied genus, Russia.

3. *Lower and Middle Triassic*

Family Procolophonidae (Procolophonia). Small reptiles a foot or more in length. Skull triangular, relatively smooth. Teeth in front conical, behind transverse, in a single row. Orbits very large, elongate anteroposteriorly. Parietal foramen large. Dermosupraoccipitals small or vestigial. Tabulars large, including between them and the squamosal a large otic notch. No supratemporals. Post-temporal openings of considerable size. Ectopterygoids distinct. Spines of vertebrae small. Two or three sacrals. Coracoids free in maturity. No cleithrum. Astragalus and calcaneum sometimes fused. Radiale and fifth carpale unossified, also centrale and fifth tarsale, so far as known. Lacrimals small, sometimes excluded from nares. Parasternals sometimes present.

Procolophon Owen, *Saurosternon* Huxley, *Thelegnathus* Broom, South Africa. *Koiloskiosaurus* Huene, *Leptopleuron* Owen (*Telerpeton* Mantell), *Sclerosaurus* Meyer, Europe.

Family Elginiidae. Skull triangular, broad behind, with long horns in tabular region and numerous conical protuberances. Orbits not elongate. Crowns of teeth denticulate. Intimate structure and skeleton unknown.

Elginia Newton, Scotland.

2. ORDER EUNOTOSAURIA

Primitive terrestrial reptiles with reduced dorsal vertebrae, expanded ribs, and an incomplete carapace of dermal bones.

The skull is doubtless wholly roofed over; the palatine is primitive, with numerous teeth. Maxillae and premaxillae with a single row of small teeth. External nares terminal. Vertebrae slender, notochordal, with vestigial spines; capitular attachment of ribs on anterior part of centrum, the second to ninth ribs with a vestigial tubercle, progressively broadened, contiguous at their borders. Pectoral and pelvic girdles primitive. Tail probably small. Femur slender, sigmoidally curved; feet unknown. Dorsal region strongly convex, covered with dermal ossifications, apparently in median and lateral rows.

This group at present is known by a single species, *Eunotosaurus africanus* Seeley, from the Middle Permian of South Africa, represented by incomplete specimens which have recently been described by Watson, from whom the above characters are taken. That the genus is intermediate between the true Cotylosauria and the Chelonia seems very probable, as Watson has urged. To locate it with either order will require many modifications in their definitions. For that reason it may be left in an independent position until further discoveries furnish more details regarding the skull, limbs, and carapace. The known characters ally it more closely with the Cotylosauria than with the Chelonia.

Middle Permian. *Eunotosaurus* Seeley, South Africa.

3. ORDER TESTUDINATA OR CHELONIA

Temporal region of skull usually exposed by the emargination of the roof bones, the supratemporals, dermosupraoccipitals, and tabulars absent. Eight cervicals. Ten dorsal vertebrae enclosed in a more or less complete carapace; an ossified plastron. A single coracoid; pelvis with large openings. Phalangeal formula always reduced.

No order of reptiles is so unequivocally distinguished from all others as the Chelonia, the turtles and tortoises. Jaws are always [beaked], and except in *Stegochelys* of the Trias they are wholly toothless; a short, broad body, a rather short skull, a flexible neck of eight vertebrae, and an osseous carapace and plastron.

In addition to the bones mentioned above, the postfrontals and ectopterygoids and usually the lacrimals are absent, the temporal region, when roofed over, covered by the large postorbitals, jugals, squamosals, and quadratojugals. The prevomers are united; there is no interpterygoidal opening, and there may be an incipient secondary roof to the palate. The prefrontals meet in the median line, the nasals are often absent; the stapes is slender. The pectoral girdle is composed of a furcate scapula and a single coracoid, usually without a supracoracoid foramen. The carpus and tarsus are much modified, and the phalangeal formula is always reduced, to 2, 3, 3, 3, 3 or 2, 2, 2, 2, 2, with the fifth toe usually still more so. Because of the inflexible carapace the structure and posture of the limbs are much modified. The forearm is so twisted upon the humerus that the foot is brought more or less directly forward in walking. As in the dinosaurs there is a greater or less reduction of the postaxial fingers and a strengthening of those on the other side of the feet. Only rarely, in certain aquatic types, have the outer fingers of the hand more than three phalanges, probably because of an incipient hyperphalangy.

Regarding the general classification of the Chelonia there is still dispute. According to Cope, Dollo, and Hay there are two chief divisions or suborders, the Athecae and Thecophora, dependent upon the character of the carapace, the former with but a single living species, the latter with more than two hundred. The more generally accepted classification recognizes four suborders, the Cryptodira (including the Athecae), the Pleurodira, Amphichelydia, and Trionychoidea. The definitions of the Athecae and Thecophora given by Hay are as follows:

Athecae. Turtles which retain the primitive dermal armor, with at least traces of the subdermal expansions connected with the ribs. A single living species, *Dermochelys coriacea.*

Thecophora. Turtles in which the primitive dermal armor is obsolete or abolished, the carapace formed by expansions of the ribs, neural plates, and usually peripheral plates.

Evidences of this primitive external series are found as vestiges, perhaps, of various Cretaceous Thecophora, but they have been accounted for in other ways. If however, the interpretation of the characters of *Eunotosaurus*, as given on a preceding page, is correct, this theory is much strengthened, since the Eunotosauria have both the expanded dermal ribs corresponding with the ordinary carapace of the turtles, and an overlying carapace composed of rows of plates like those of *Dermochelys.*

A. SUBORDER AMPHICHELYDIA

Mesoplastra present. Nasals and lacrimals distinct. Skull wholly roofed over. Neck short, not retractile, the cervical vertebrae amphicoelous or concavo-convex.

FAMILY PROGANOCHELYDIDAE. Vomer and parasphenoid with small teeth. Nine dorsal ribs (costals) and seven cervical vertebrae, with ribs. Neck with free dorsal plates. Scapular girdle with short proscapular process or acromion; coracoid short, more or less fused with scapula; a supracoracoid foramen. One sacral vertebra. (Jaekel.)

Upper Trias. *Stegochelys* Jaekel,[1] *Proterochersis* Fraas, *Proganochelys* Baur, ? *Chelyzoum* Meyer, Germany.

FAMILY PLEUROSTERNIDAE. Cervical vertebrae amphicoelous. Skull elongated; coracoid distally expanded. Carapace united to plastron by narrow buttresses.

Upper Jura. *Platychelys* Wagler, *Pleurosternum* Owen, Europe.

Cretaceous. *Glyptops* Marsh, North America. *Helochelys* Meyer, Germany.

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[1] [=*Triassochelys* Jaekel.—ED.]

Family Baënidae. Carapace united to plastron by strong buttresses. Skull short. Cervical vertebrae for the most part with but one end concave.

Lower Cretaceous. *Probaëna* Hay, *Naomichelys* Hay, United States.

Upper Cretaceous. *Baëna* Leidy, *Eubaëna* Hay, *Boremys* Lambe, ? *Neurankylus* Lambe, *Thescelus* Hay, *Charitemys* Hay, ? *Polythorax* Cope, United States.

Eocene. *Baëna* Leidy, North America.

B. SUBORDER PLEURODIRA

Peripheral bones of carapace present. Neck withdrawn laterally. Mesoplastra absent or present. Temporal roof of skull complete or much emarginated. Pubes and ischia suturally united with plastron. Pterygoids not separating quadrates from basisphenoid.

Family Pelomedusidae. Mesoplastron present. No nasals. Vomers present or absent.

Upper Cretaceous. *Bothremys* Leidy, *Taphrosphys* Cope, *Amblypeza* Hay, *Naiadochelys* Hay, North America.

Eocene. *Podocnemis* Wagler, Europe, Africa. *Stereogenys* Andrews, Africa.

Pliocene. *Sternothaerus* Bell, *Pelomedusa* Wagler, Africa.

Family Chelydidae. No mesoplastron. Vomer distinct, the prefrontals separated.

Eocene. *Hydraspis*, India. Recent South America.

Pleistocene and Recent. *Chelodina* Fitzinger, Australia.

Family Miolanidae. Skull roof complete with horn-like protuberances. Very large turtles.

Uppermost (?) Cretaceous. *Miolania* Owen, South America.

Pleistocene. *Miolania*, Australia.

C. SUBORDER CRYPTODIRA[1]

Head withdrawn in a vertical flexure. Carapace with marginal plates. Pelvis not united with plastron. Epiplastra in contact with hyoplastra. Pterygoids separating quadrates and basisphenoid.

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[1] [Many genera omitted.—G. K. N.]

Family Thalassemyidae. Temporal region of skull more or less over-roofed. Neck short. Plastron loosely connected with carapace, usually with one or more fontanelles. Ambulatory turtles.

Upper Jura. *Eurysternum* Wagler, *Thalassemys* Rütimeyer, Europe.

Upper Jura and Wealden. *Tropidemys* Rütimeyer, *Pelobatochelys* Seeley, Europe. *Chitracephalus* Dollo, Europe.

Upper Cretaceous. *Osteopygis* Cope, *Catapleura* Cope, *Lytoloma* (*Rhetechelys*, *Erquelinnesia*) Dollo, North America. *Erquelinnesia* (*Pachyrhynchus*) Dollo, Europe, Africa.

Eocene ?*Lytoloma* Cope, Europe.

Family Toxochelyidae. Temporal region largely over-roofed. Palatines entering into internal nares. Plastron loosely articulated. Carapace with shields. Subaquatic, at least two claws on front feet.

Cretaceous. *Toxochelys* Cope (? *Cynocercus* Cope), *Porthochelys* Williston, North America.

Family Desmatochelyidae. Skull almost wholly roofed over. Internal nares far forward. Small palatine foramen. Nasals present. Plastron loosely connected with carapace. Limbs paddle-like, aquatic.

Upper Cretaceous. *Desmatochelys* Williston, *Neptunichelys* Wieland, *Atlantochelys* Agassiz, North America.

Family Protostegidae. Marine turtles of large size, the limbs paddle-like without claws. Carapace greatly reduced, the plastron loosely attached. Skull large; temporal region wholly roofed over. Internal nares far forward, not under-roofed.

Upper Cretaceous. *Protostega* Cope, *Archelon* Wieland, North America.

Family Cheloniidae. Marine turtles with paddle-like limbs and elongate fingers. Skull mostly roofed over. Head not retractile. Plastron loosely united to carapace.

Upper Cretaceous. ? *Allopleuron* Baur, North America. *Allopleuron* Baur, Europe. *Peritresius* Cope, North America.

Eocene. *Lembonax* Cope, North America. *Argillochelys* Lydekker, *Eosphargis* Lydekker, *Eochelone* Dollo, Europe.

Miocene. *Scyllomus* Cope, *Procolpochelys* Hay, North America.

Oligocene. *Chelyopsis* Beedin, Europe.

[FAMILY DERMOCHELYIDAE. Leathery turtles. Marine turtles, with mosaic of small, polygonal, bony plates, in the dermis of the back, not ankylosed to the ribs.

Eocene. *Psephophorus*, Egypt, North America.

Recent. *Dermochelys*.]

FAMILY CHELYDRIDAE. Marsh and river turtles, with reduced plastron loosely joined to carapace, the skull incompletely roofed. Entoplastron T-shaped. Caudals mostly opisthocoelous. Feet elongate, webbed.

Upper Jurassic. *Tretosternum* Owen (*Peltochelys* Dollo), Europe.

Eocene. *Gafsachelys* Stefano, Europe.

Miocene. ? *Acherontemys* Hay, North America. *Chelydra*, Europe.

Pleistocene and Recent. *Macrochelys* Gray, *Chelydra* Schweiger, North America.

FAMILY DERMATEMYIDAE. Temporal region not roofed. Plastron suturally united to carapace. No parietosquamosal arch. Caudals procoelous. Marsh turtles, the carapace well ossified.

Upper Cretaceous. *Adocus* Cope, *Homorophus* Cope, *Zygoramma* Cope, *Agomphus* Cope, *Compsemys* Leidy, *Basilemys* Hay, North America.

Eocene. *Anosteira* Leidy, *Baptemys* Leidy, *Pseudotrionyx* Dollo, *Kallistira* Hay, *Notomorpha* Cope, *Alamosemys* Hay, *Basilemys* Hay, *Hoplochelys* Hay, North America.

Oligocene. *Xenochelys* Hay, ? *Anosteira* Leidy, North America. *Anosteira* Leidy, Europe.

Trachyaspis Meyer, Eocene, Miocene, Europe, Africa.

FAMILY EMYDIDAE.[1] Temporal region not roofed. Neck retractile. Carapace low-arched. Subaquatic, the feet webbed. Middle digit rarely reduced. Marsh tortoises.

Upper Cretaceous. ? *Gyremys* Hay.

Eocene. *Paleotheca* Cope, *Echmatemys* Hay, North America. ? *Chrysemys*, *Emys*, Europe.

Oligocene. *Graptemys* Agassiz, North America. ? *Clemmys* Gray, Europe.

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[1] [Many modern taxonomists unite the Emydidae with the Testudinidae, as the former grade into the latter. — ED.]

Miocene. *Trachemys* Agassiz, *Clemmys* Ritgen, North America.

Pliocene. *Terrepene* Merrem, *Trachemys* Agassiz, ? *Clemmys* Ritgen, *Deirochelys* Agassiz, *Pseudemys* Gray, North America.

Pleistocene. *Terrepene* Merrem, *Chrysemys* Gray, *Clemmys* Ritgen, ? *Pseudemys*, North America.

Ptychogaster Pomel, Oligocene, Miocene, Europe.

FAMILY TESTUDINIDAE. Temporal roof reduced. Neck retractile. Plastron suturally united with the highly arched carapace. Phalanges not more than two in number. Small to very large tortoises, herbivorous, terrestrial.

Eocene. *Hadrianus* Cope, *Achilemys* Hay, North America. *Testudo*, Africa.

Oligocene. *Testudo* Linné, *Stylemys* Leidy, North America.

Miocene to Recent. *Testudo* Linné, North America, Europe, Asia, Africa.

D. SUBORDER TRIONYCHOIDEA

Skull and neck as in the Cryptodira, the basiphenoid separating the pterygoids. Plastron ligamentously united with carapace, which lacks the peripheral bones and is covered with a leathery skin only and is flattened. More than three phalanges in third digit. River and lake turtles, the neck long.

FAMILY PLASTOMENIDAE. Hyoplastra, hypoplastra, and xiphiplastra closely united. Legs unknown.

Uppermost Cretaceous and Lower Eocene. *Plastomenus* Cope, North America.

FAMILY TRIONYCHIDAE. Openings between hyoplastra, hypoplastra, and xiphiplastra. Three claws only, feet elongate.

Uppermost Cretaceous. *Helopanoplia* Hay, North America.

Eocene. *Conchochelys* Hay, *Axestemys* Hay, *Aspideretes* Hay, *Amyda* Oken (= *Platypeltis* Fitzinger), North America.

CHAPTER IX

THE SUBCLASS SYNAPSIDA

A SINGLE, lateral, temporal opening, bounded primarily by the squamosal, jugal, and postorbital only. About seven cervical vertebrae, amphicoelous. Dorsal ribs double-headed, articulating intercentrally more or less and with the arch. Pectoral girdle with two coracoids on each side, sometimes with vestigial cleithrum; interclavicle and clavicles always present. Pelvis more or less plate-like. Feet always pentadactylate.

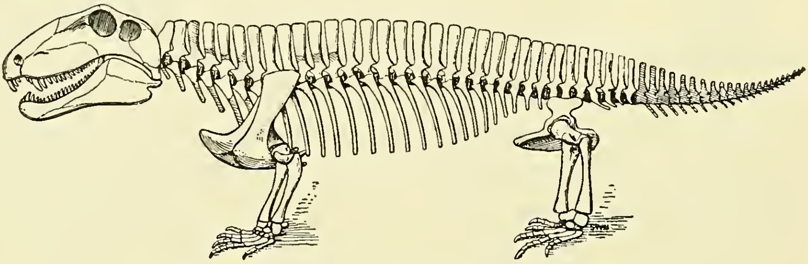

FIG. 164 *bis*. *Sphenacodon* (Theromorpha). Restored skeleton.

4. ORDER THEROMORPHA

Vertebrae notochordal or deeply biconcave, the intercentra persistent throughout. Limbs and palate primitive. Propodials in locomotion horizontal.

There has been much discussion as to the rank and limits of the Paleozoic genera included under the above definition. Nor can we hope to reach a very satisfactory solution of the numerous problems till much more is known of them and especially of the later Permian and Triassic forms included here in the same subclass.

The above definition will distinguish fairly well the Lower Permian forms from the Middle and Upper ones, and the order Theromorpha may be therefore accepted for the present with these limitations. Originally the name was proposed by Cope to include not only the Cotylosauria but all of the African genera of the order Therapsida as

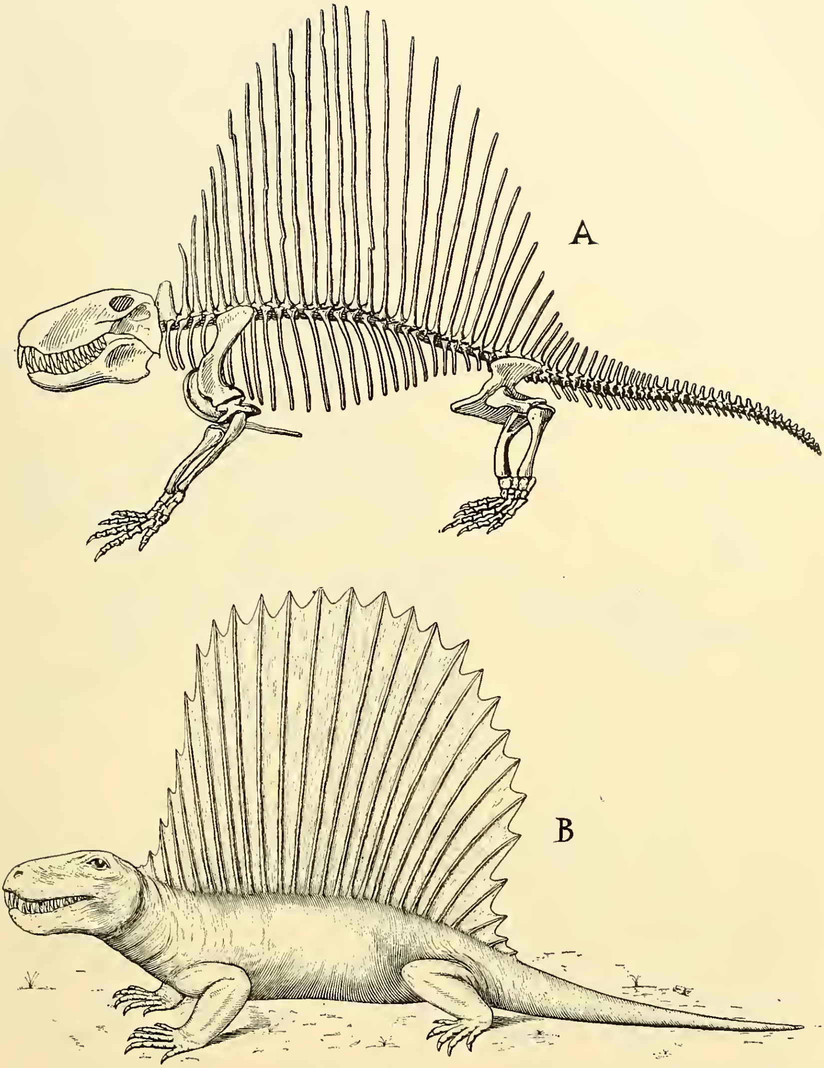

FIG. 165. Skeleton and life restoration of *Dimetrodon* (Theromorpha). About eight feet long.

well, and is still used often in that original sense or with the exclusion of the Cotylosauria.

There is greater diversity among the Theromorpha as thus distinguished than among the Cotylosauria, the only constant differences from which are the perforated temporal roof, the longer neck, and usually longer legs. Doubtless they were more active and agile animals, and their adaptive radiation was greater. But the primitive characters were less constant. The intertemporal bone is never present; the interparietals, tabulars, and supratemporals are always smaller; some may be wanting, and the two former are always confined to the occipital surface when present. The quadratojugal is smaller; the lacrimal seldom extends to the nares. The teeth are often wanting on the prevomers; the postsplenial is never present in the mandible though there is a possibility of an additional coronoid, the posterior one of which is always present. The humerus has an ectepicondylar foramen only in the Edaphosauridae; the entepicondylar foramen is always present. The plate-like pelvis never has a large pubo-ischiatic or a true thyroid foramen. There are two or three sacral vertebrae. The fifth tarsale is rarely unossified. No dermal bones have been discovered in any member of the order, and parasternal ribs are known only in the Poliosauridae and Ophiacodon-

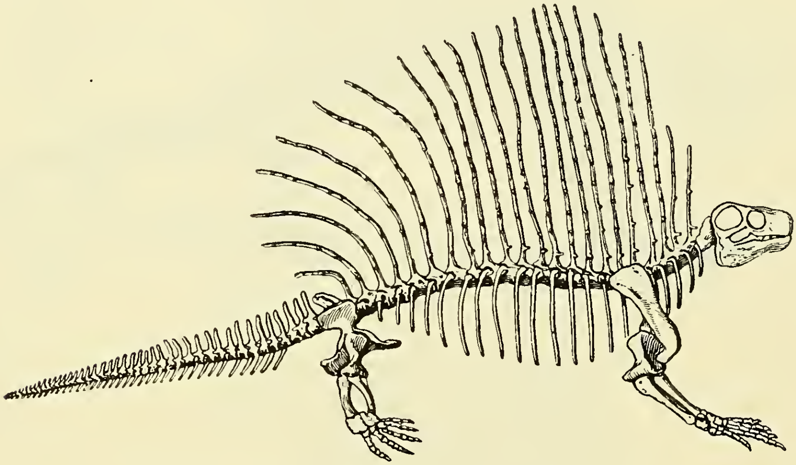

Fig. 166. Skeleton of *Edaphosaurus* (Theromorpha).

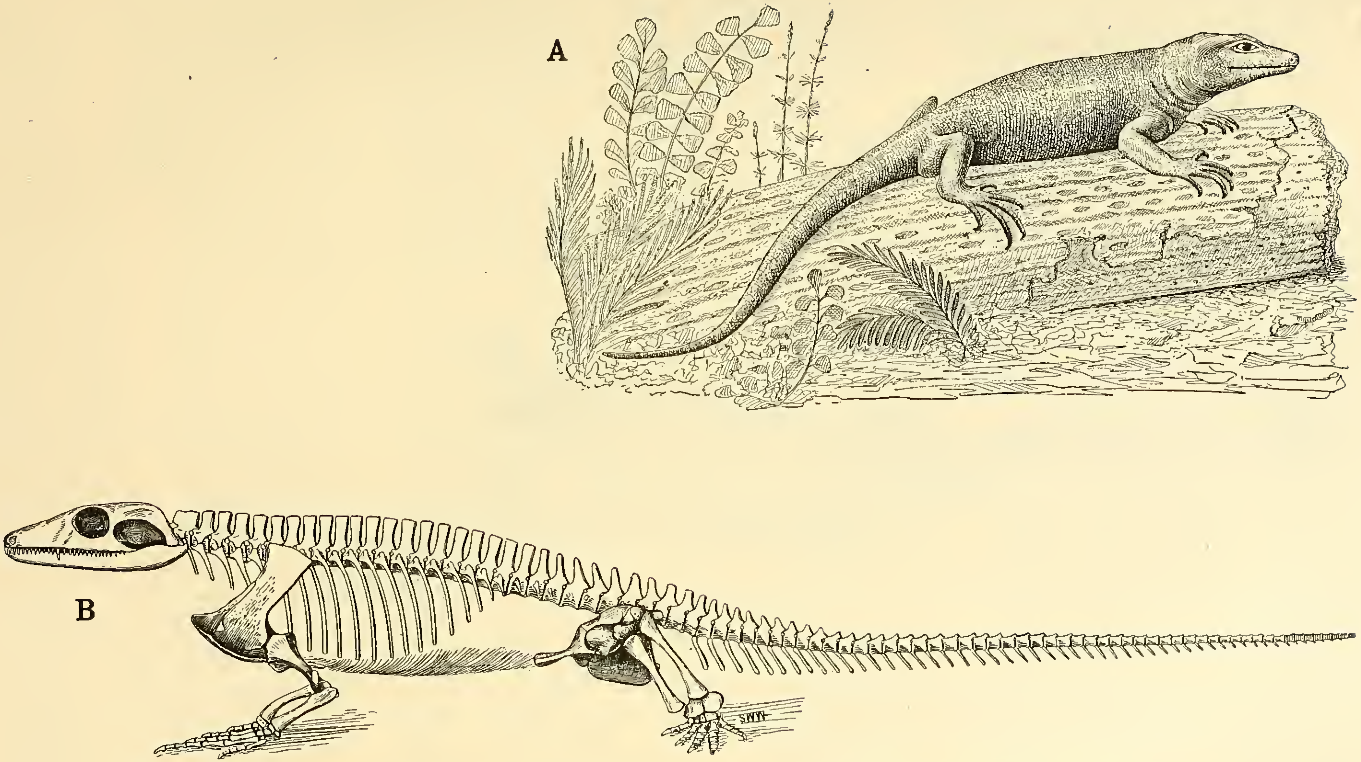

Fig. 167. Theromorph reptile *Varanosaurus*, from the Permian of Texas: A, restoration. B, skeleton. About one sixth natural size.

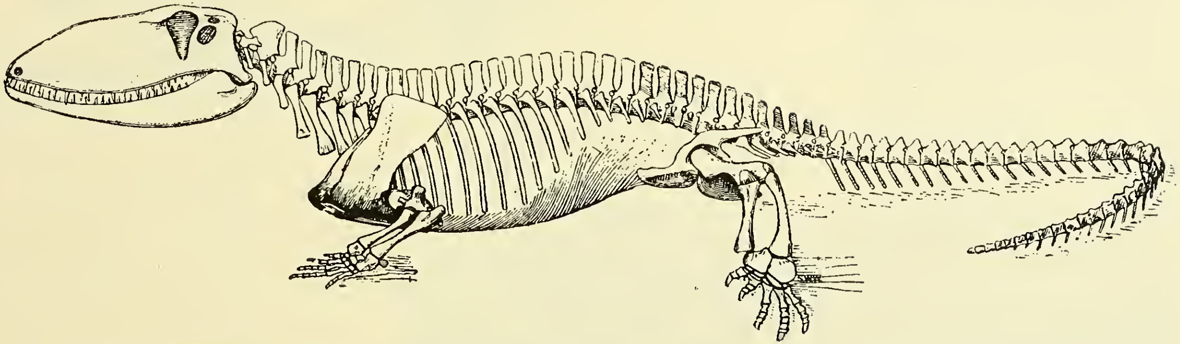

Fig. 168. Theromorph skeleton *Ophiacodon*, from mounted specimen in Walker Museum. About one twelfth natural size.

tidae. Permocarboniferous (Uppermost Carboniferous and Lowermost Permian).

A. SUBORDER PELYCOSAURIA

FAMILY SPHENACODONTIDAE (Pelycosauria). Carnivorous reptiles of from four to eight feet in length, with long, often very long, dorsal spines; three sacral vertebrae.

Sphenacodon Marsh, New Mexico. *Dimetrodon* Cope, Texas. *Clepsydrops* Cope, Illinois, Texas. *Tetraceratops* Matthew, Texas. *Bathygnathus* Leidy, Prince Edward Island.

B. SUBORDER EDAPHOSAURIA

FAMILY EDAPHOSAURIDAE (Edaphosauria). Subaquatic or terrestrial invertebrate feeding reptiles, from six to eight feet in length. Spines of dorsal vertebrae very long, each with transverse processes. Skull small, short, high, with numerous palatal and coronoid conical teeth.

Edaphosaurus Cope, Texas, New Mexico. *Naosaurus* Cope, Texas, New Mexico, Ohio, Germany, Russia.

C. SUBORDER POLIOSAURIA

FAMILY POLIOSAURIDAE. Lizard-like, insectivorous, four or five feet in length. Teeth conical; spines of vertebrae short; two sacral vertebrae. Texas and New Mexico.

Varanops Williston, *Varanosaurus* Broili, *Poliosaurus* Case, *Poecilospondylus* Case, *Arribasaurus* Williston, *Scoliomus* Williston and Case.

FAMILY OPHIACODONTIDAE. About six feet in length, carnivorous. Skull narrow; teeth slender and conical or flattened; temporal opening small, an upper one also in *Ophiacodon;* ribs holocephalous; limbs short and stout; two sacral vertebrae. Texas and New Mexico.

Ophiacodon Marsh, *Theropleura* Cope, *Diopeus* Cope, *Secodontosaurus* Williston.

D. SUBORDER CASEASAURIA

FAMILY CASEIDAE (Caseasauria). Thickset, crawling and probably burrowing, invertebrate-feeding reptiles about four feet long. Skull

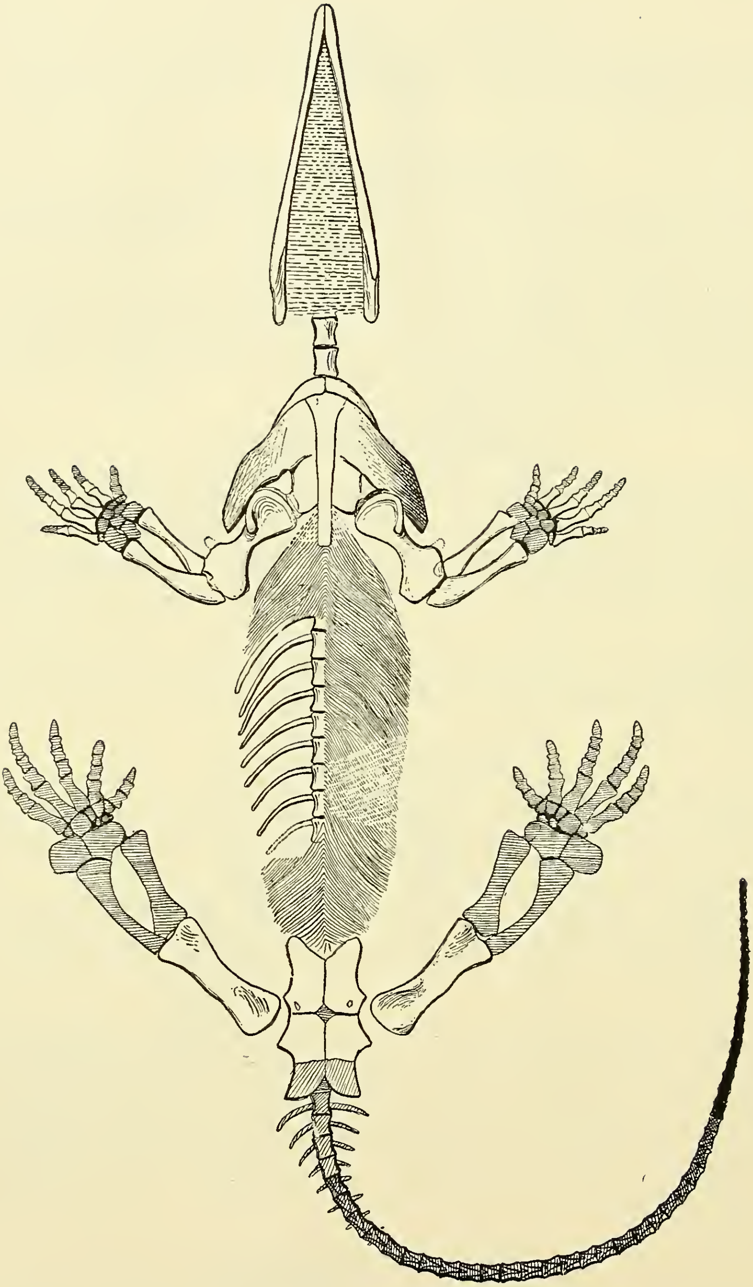

Fig. 169. Skeleton of *Theropleura* (Theromorpha), from below. One sixth natural size.

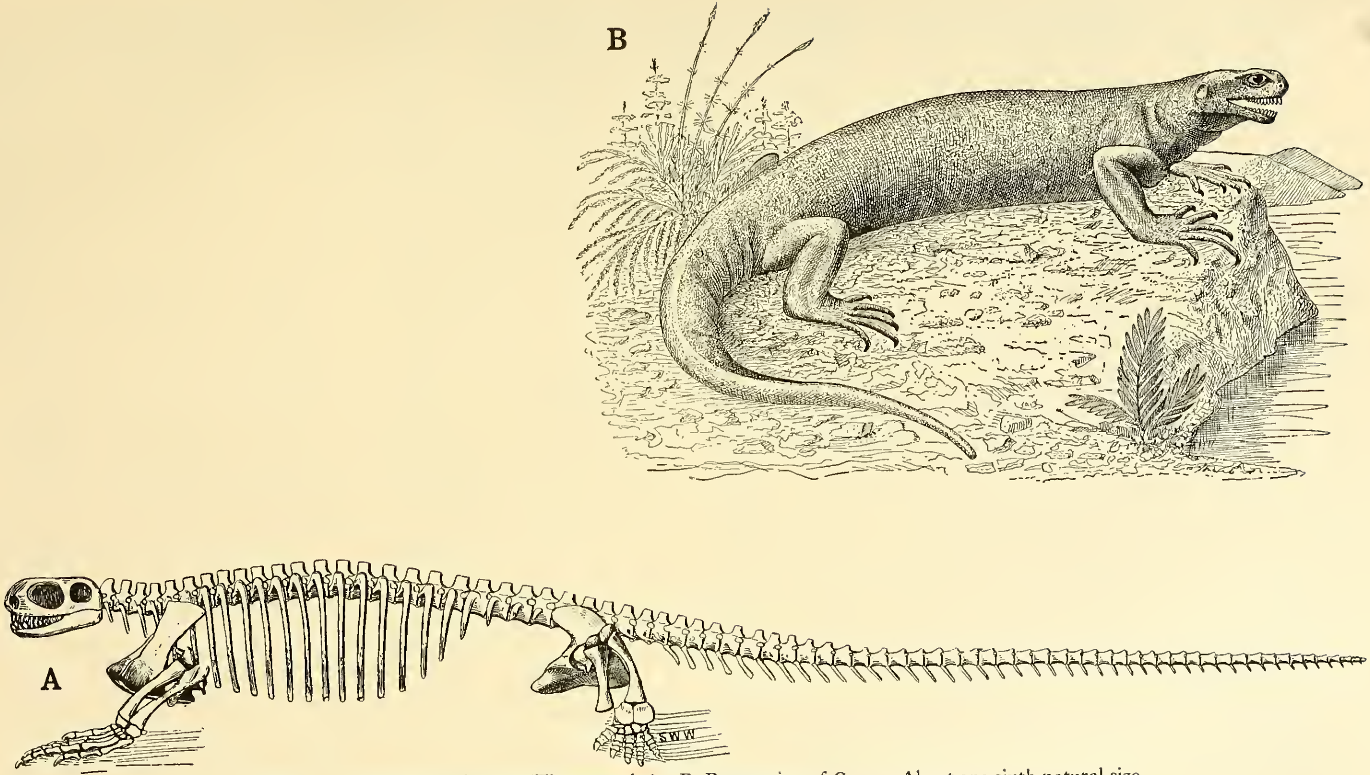

FIG. 169 *bis*. A, Skeleton of *Casea* (Theromorpha). B, Restoration of *Casea*. About one sixth natural size.

broad, short, with large pineal opening, and palate and coronoids covered with conical teeth. Three sacral vertebrae. Texas.

Casea Williston, ? *Trichasaurus* Williston.

E. SUBORDER UNCERTAIN

FAMILY PALEOHATTERIIDAE. Small, slender reptiles. Twenty-seven presacral vertebrae; three sacrals. Parasternal ribs present. Intimate structure of skull unknown. Skeleton feebly ossified, probably young animals, the metacoracoids not ossified. Vertebrae notochordal, ribs holocephalous. Lower Permian.

Paleohatteria Credner, Germany. *Haptodus* Gaudry, France. ? *Callibrachion* Boule, France.

INCERTAE SEDIS. *Mycterosaurus* Williston, *Glaucosaurus* Williston, *Tomicosaurus* Case, *Metamosaurus* Cope, *Embolophorus* Cope, Texas. *Archaeobolis* Cope, Illinois. *Aphelosaurus* Gervais, Autun, France. *Stereorhachis* Gaudry (? Sphenacodontidae), Autun, France.

Doubtfully members of the order: *Ammosaurus* Huene (Triassic). *Datheosaurus*.

5. ORDER THERAPSIDA

Less primitive, more upright-walking reptiles, the propodials more or less inclined in locomotion. Vertebrae amphicoelous, rarely notochordal, dorsal intercentra unknown. Palate and limbs less primitive; pelvis with larger pubo-ischiatic vacuity or thyroid opening.

As stated on a previous page, sharp distinctions between the members of this order and the preceding one cannot be made. The primitive characters common to both orders are largely included in the Synapsida. But the very great differences presented by the later, Triassic, forms, especially those included under the Cynodontia, differences as great as those between any other two orders of reptiles, render a division or divisions imperative, even though it may result, as is so often the case in other groups of animal and vegetable life, in the structural differences between members of the same group being greater than those limiting the groups themselves. This division, it seems to the writer, may be best made at the present time between the Lower and Middle Permian types, that is, based upon the stages of evolution chiefly. Perhaps when more is known of the various and diverse forms included in both orders, a better and more scientific division may be made on genealogical characters. But such are not available at present.

The characters, as a whole, of the Therapsida are primitive, but less so than those of the Theromorpha, and they are increasingly inconstant. The vertebrae are known to be notochordal only in the Dromasauria and Dinocephalia, and the intercentra are seldom if ever persistent throughout the column; there may be as many as seven sacral vertebrae; the boundaries of the temporal opening are less constant; in a few words, no characters seem to be more primitive than in the Theromorpha. The interparietals, when present, are fused into a single bone, which is rarely the case in the Theromorpha. The supratemporals are always, the postfrontals often, the quadratojugals usually, absent.[1] The palate and teeth undergo many changes; the pterygoids are less free, palatal teeth are less constant. The cleithrum is seldom present and always small, etc.

But to divide the various groups into orders seems not to solve but rather to add to the difficulties. For that reason, perhaps it is better at present to consider the whole group as one order, as Broom has suggested, clearly differentiated from all others save the Theromorpha by the skull and pectoral girdle, and to treat its characters under the chief divisions. Of course the distribution of some, perhaps many, of the genera is more or less provisional, as must be the case in any order of reptiles or other organisms until everything about them is fully known, a result greatly to be wished, but never within the limits of human endeavor. The classification adopted is that of Broom and Watson in numerous publications and *in literis*, with but few modifications.

A. SUBORDER DINOCEPHALIA

Powerful reptiles from the size of a boar to that of a rhinoceros. Skull very massive, especially in the cranial region. Temporal opening bounded by the postorbital and squamosal, the jugal sometimes intervening below. Lacrimals and quadratojugals small, the interparietal and tabulars large. No dermal bones fused in midline. Parietal opening large, opening in a protuberance or boss. Teeth

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[1] [The quadratojugal has recently been identified in anomodonts, gorgonopsians, and cynodonts, by Watson. — ED.]

more or less flattened and denticulated along their border,[1] not more than eighteen in either jaw, subisodont or with a large caniniform tooth; no teeth on palate. Prevomers, palatines, and pterygoids united in midline, concealing the parasphenoid. Quadrate large. Vertebrae deeply concave or notochordal. Atlanto-axis as in *Dimetrodon* (Theromorpha); four sacral vertebrae. Ribs dichocephalous, probably no parasternals. Shoulder girdle massive; procoracoid barely entering glenoid fossa; a feeble cleithrum sometimes, if not always, present. Large clavicles and interclavicle. No acromion. Pelvis with small pubo-ischiatic vacuity. An entepicondylar foramen. Legs stout; epipodials and digits short; phalangeal formula unknown, probably primitive.

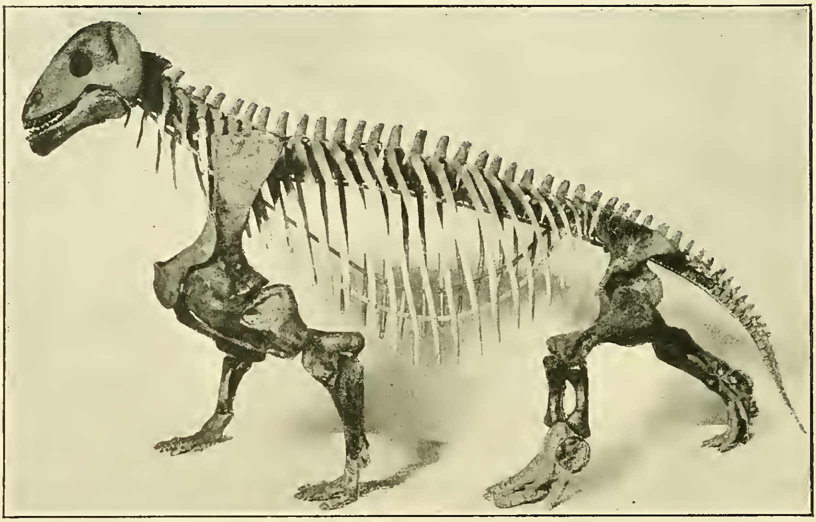

FIG. 170. Skeleton of *Moschops* (Dinocephalia). After Gregory. One twenty-second natural size. Skeleton in American Museum.

FAMILY TAPINOCEPHALIDAE. Middle and Upper Permian. *Delphinognathus* Seeley, *Lamiasaurus*[2] Watson, *Moschognathus* Broom, *Mormosaurus* Watson, *Moschops* Broom, *Moschosaurus* Haughton, *Phocosaurus* Seeley, *Pnigalion* Watson, *Struthiocephalus* Haughton,

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[1] [This statement refers only to the cheek teeth; the premaxillary teeth and the first three or four in the dentary have a long conical crown, greatly expanded posteriorly at the base, and long roots. — ED.]

[2] [Cranium, Fig. 170. — ED.]

Tapinocephalus Owen, *Taurops* Broom, *Archaeosuchus* Broom, *Scapanodon* Broom, *Eccasaurus* Broom, South Africa.

FAMILY DEUTEROSAURIDAE. Upper Permian. *Deuterosaurus*, Eichwald, Ural Mts.

FAMILY RHOPALODONTIDAE. Upper Permian. *Rhopalodon*, Eichwald, Ural Mts.

FAMILY TITANOSUCHIDAE.[1] Upper Permian. *Titanosuchus* Owen, South Africa. "*Lamiasaurus*" [snout].

B. SUBORDER DROMASAURIA

About the size of a rat. Skull short; orbits large; lacrimals continuous to septomaxilla; temporal opening bounded by postorbital, squamosal, and jugal; possibly the preparietal, and probably the interparietal, present; parietal foramen large; teeth isodont, subisodont, or absent; quadratojugals obsolete or absent; vertebrae notochordal, intercentra unknown; two or three sacrals, probably twenty-eight presacrals; parasternals present; no acromion and no cleithrum; pelvis plate-like, pubic foramen large; carpus primitive, tarsus with or without a fifth tarsale; phalangeal formula 2, 3, 3, 3, 3.

FAMILY GALECHIRIDAE. A single row of subisodont teeth.
Middle Permian. *Galechirus* Broom, *Galesphyrus* Broom, *Galepus* Broom, South Africa.

FAMILY GALEOPIDAE. Edentulous.
Middle Permian. *Galeops* Broom, South Africa.

FAMILY MACROSCELESAURIDAE. *Macroscelesaurus* Haughton.

C. SUBORDER ANOMODONTIA

From the size of a mouse to that of a tapir, vegetable or invertebrate feeders. Large temporal opening bounded by postorbital, squamosal, and jugal. Skull typically short and wide, the face short; quadrates and squamosals large; lacrimals small; quadratojugals small or obsolete.[2] Preparietal usually present, in front of, or sur-

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[1] [A number of new genera of South African Titanosuchidae were described by Broom in 1923 (*Proc. Zoöl. Soc.*, London). — ED.]

[2] [See page 243, below. — ED.]

rounding, parietal foramen. An interparietal and small tabulars. Premaxillae fused and always toothless, and in life covered with horny beak. Maxilla usually with an enlarged, permanently growing canine, which, however, is absent in the females of some genera, and generally with a number of small molars often irregularly arranged in more than one series. Molars are always present on the mandible if in the maxilla, but there is never any canine present. Prevomers fused. A rudimentary false palate, no teeth on palatal bones. Stapes large. Occipital condyle tripartite. Dentary, angular, and surangular large; no coronoid. A mandibular foramen. Sclerotic plates in orbits. Vertebrae amphicoelous; no intercentra back of atlas; four to seven sacrals. No parasternals. Legs short and stout, hands and feet short; an entepicondylar foramen. Phalangeal formula 2, 3, 3, 3, 3. A thyroid foramen in pelvis; ilium projecting in front of acetabulum. An ossified sternum. The shoulder girdle has the coracoid and precoracoid well developed, and a distinct but short acromion. There is a small cleithrum known in *Dicynodon* and *Cistecephalus*, and possibly present in most other genera.

Family Dicynodontidae. Middle Permian. *Dicynodon* Owen, *Pristerodon* Huxley, South Africa.

Upper Permian. *Tropidostoma* Seeley, *Diaelurodon* Broom, *Prodicynodon* Broom, *Eocyclops* Broom, *Emydops* Broom, *Diictodon* Broom, *Emydorhynchus* Broom, *Emyduranus* Broom, *Taognathus* Broom, *Cryptocynodon* Seeley, *Endothiodon* Owen, *Cistecephalus* Owen, *Chelyrhynchus* Haughton, South Africa, *Dicynodon* Owen, South Africa and Russia.

Lower and Middle Triassic. *Dicynodon* Owen, *Lystrosaurus* Cope, *Prolystrosaurus* Haughton, *Myosaurus* Haughton, South Africa.

Upper Triassic. *Kannemeyeria* Seeley, *Gordonia* Newton, *Geikia* Newton, Scotland. *Placerias* Lucas, *Brachybrachium* Williston, Wyoming.

D. SUBORDER THERIODONTIA

Carnivorous Therapsida with more or less differentiated dentition, including at least one pair of upper caniniform teeth; a prominent coronoid. Vertebrae never notochordal; few or no teeth on palate bones. No cleithrum. Manus and pes, so far as known, rarely primitive.

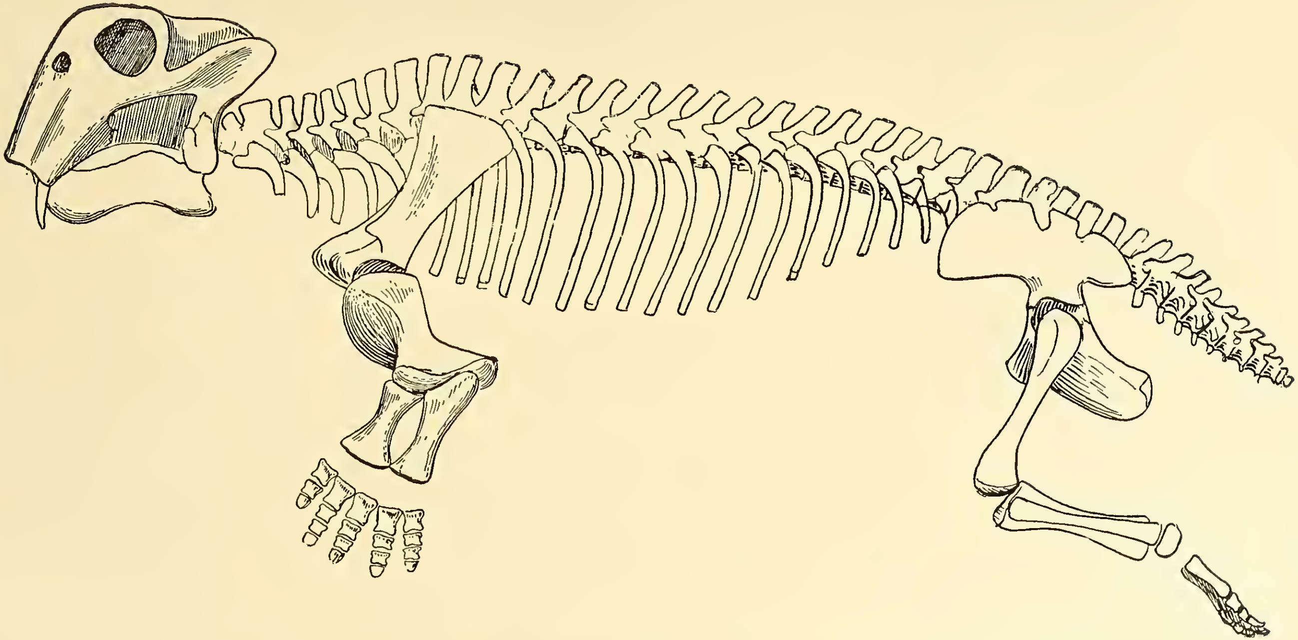

Fig. 171. Skeleton of *Lystrosaurus*, as restored by Watson, slightly modified. One fourth natural size.

1. Tribe Gorgonopsia

Prefrontals and large postfrontals contiguous over orbit. A distinct preparietal in front of small parietal foramen. Temporal opening bounded above by united postorbital and squamosal, below by squamosal and jugal or squamosal only. Parietal region wide. A single vomer (? fused prevomers). No secondary palate; an ectopterygoid. No acromion on scapula; no cleithrum; coracoids relatively small; a large proatlas. Phalangeal formula primitive 2, 3, 4, 5, 3.

A group intermediate, according to Broom, between the Therocephalia and Anomodontia.

Middle and Upper Permian.

Family Gorgonopsidae. *Gorgonops* Owen, *Scymnognathus* Broom, *Cyniscodon* Broom, *Cerdognathus* Broom, *Scymnosaurus* Broom, *Gorgonognathus* Haughton, *Scylacognathus* Broom, *Scylacops* Broom, *Galesuchus* Haughton, *Ictidomorphus* Broom, *Aloposaurus* Broom, *Aelurosaurus* Owen, *Cynodraco* Owen, *Tigrisuchus* Owen, *Arctosuchus* Broom, *Arctognathus* Broom, *Arctops* Watson, *Theriodesmus* Seeley, *Asthenognathus* Broom, South Africa. *Inostrancevia* Amalitsky, Russia.

Family Ictidorhinidae. Middle and Upper Permian. *Ictidorhinus* Broom, South Africa.

Family Burnetidae. Lower Triassic. *Burnetia* Broom,[1] South Africa.

2. Tribe Bauriasauria

A well-formed secondary palate; a median, unpaired vomer; single occipital condyle; the pterygoids extend to quadrates; no postfrontals; squamosal small; quadrate large; parietal foramen present or absent; strong incisors and grinding molars; large posterior palatine vacuities. No acromion on scapula.

Upper Triassic. *Bauria* Broom, *Microgomphodon* Seeley, *Melinodon* Broom, *Sesamodon* Broom, *Aelurosuchus* Broom, South Africa.

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[1] [Made the type of a new suborder, Burnetiamorpha, by Broom, 1923.—Ed.]

3. Tribe Therocephalia

Temporal opening large, bounded below by squamosal and jugal, above by the parietal or the connected postorbital and squamosal.[1] No quadratojugals[2]; quadrates small; a parietal foramen; squamosals large; no preparietal. Teeth conical, four or five in premaxilla; one or two large upper caniniform teeth, and five to nine smaller ones posteriorly; no secondary palate, or a rudimentary one (? *Scaloposaurus*); prevomers separated or fused (*Scaloposaurus*); an interpterygoidal opening; large posterior palatine vacuities; palate with few or no teeth; postfrontals small or absent; parietal region usually narrow. Mandible with loose symphysis, long dentary, and large coronoid; posterior elements not reduced. Postcranial skeleton largely unknown.

Family Scylacosauridae. Middle and Upper Permian. *Alopecodon* Broom, *Pardosuchus* Broom, *Glanosuchus* Broom, *Scylacosaurus* Broom, *Pristerognathus* Seeley, *Ictidosaurus* Broom, *Alopecognathus* Broom, *Scylacorhinus* Broom, South Africa.

Family Ictidosuchidae. Middle and Upper Permian. *Ictidosuchus* Broom, *Arnognathus* Broom, *Cerdodon* Broom, South Africa.

Family Lycosuchidae. Middle and Upper Permian. *Lycosuchus* Broom, *Trochosuchus* Broom, *Hyaenasuchus* Broom, South Africa.

Family Scaloposauridae. Middle and Upper Permian. *Scaloposaurus* Owen, *Ictidognathus* Broom, *Simorhinella* Broom, *Icticephalus* Broom, *Akidnognathus* Haughton, South Africa.

Family Alopecopsidae. Middle and Upper Permian. *Alopecopsis* Broom, *Scymnopsis* Broom, South Africa.

Family Whaitsidae. *Whaitsia* Haughton, South Africa.

Family doubtful. Middle and Upper Permian. *Lycosaurus* Owen, *Eriphostoma* Broom, *Lycorhinus* Broom, *Scymnorhinus* Broom, *Alopecorhinus* Broom, *Scylacoides* Broom, South Africa.

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[1] [In typical Therocephalia, as described by Broom, the postorbital and squamosal do not connect with each other.—Ed.]

[2] [See page 239, above.—Ed.]

4. Tribe Cynodontia

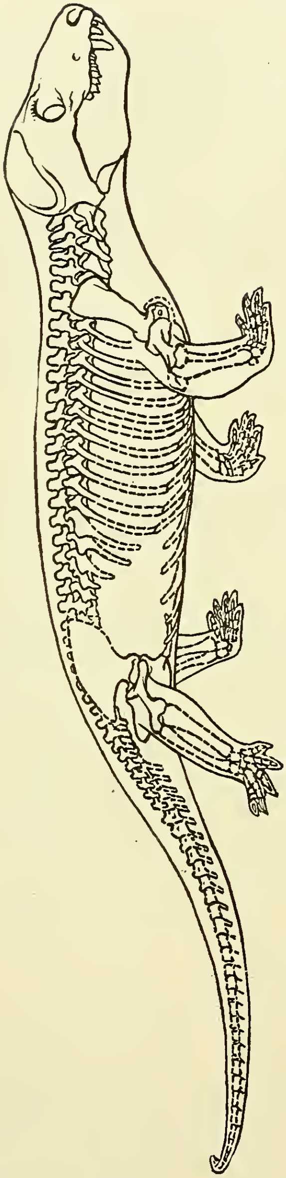

Fig. 172. Skeleton of *Cynognathus* (Therapsida). After Gregory. One fourteenth natural size.

Especially characterized by a heterodont dentition, a secondary palate, reduced posterior mandibular bones, and two occipital condyles. Dentition composed of from three to five incisors, a canine, and seven to nine, rarely thirteen, molars, secodont or gomphognath or cuspidate. Temporal opening bounded by parietal and postorbital above, usually by squamosal and postorbital only below; frontals small, excluded from orbital margin by the union of the prefrontal and postorbital; postfrontals absent; parietals narrow; a small parietal foramen, but no preparietal bone; tabular large; quadrate small; stapes long, stout or slender; the pterygoids do not reach the quadrate; probably a small ectopterygoid; vomer large, unpaired. Coronoid large. A small acromion on scapula; scapula with reflected anterior border; no cleithrum. Fifth carpale unossified; phalangeal formula 2, 3, 3, 3, 3, so far as known. A thyroid foramen in pelvis. Feet imperfectly known, the digits short. Vertebrae amphicoelous; no dorsal intercentra. Twenty-eight presacrals, four sacrals.

Family Nythosauridae. Septomaxillae on face; molars less cuspidate; posterior mandibular bones less reduced.

Middle Triassic. *Nythosaurus* Owen, *Ictidopsis* Broom, *Galesaurus* Owen, *Platycraniellus* v. Hoepen, South Africa.

FAMILY CYNOSUCHIDAE. ? Middle Triassic. *Cynosuchus* Owen, South Africa.

FAMILY CYNOGNATHIDAE. Septomaxillae within nares; molars cuspidate; [posterior] mandibular bones more reduced.

Upper Triassic. *Cynognathus* Seeley, *Lycochampsa* Broom, South Africa.

FAMILY DIADEMODONTIDAE. Upper Triassic. *Diademodon* Seeley, *Gomphognathus* Seeley, *Trirachodon* Seeley, South Africa. ? Upper Triassic *Cynochampsa* Owen, South Africa.

5. THERIODONTIA (?) INCERTAE SEDIS

Upper Triassic. ? *Dromotherium* Emmons, North Carolina. *Tribolodon* Seeley, *Karoomys* Broom, South Africa.

Lower Jurassic. *Tritheledon* Broom, *Pachygenelus* Watson, South Africa.

[May be either primitive mammals or cynodonts — too imperfectly known to enable one to decide. Probably each is the type of a distinct family. —R. Broom.]

CHAPTER X

THE SUBCLASS SYNAPTOSAURIA

6. ORDER SAUROPTERYGIA

A SINGLE, large temporal opening, bounded above by the parietal, below by the postorbital and squamosal. No dermosupraoccipitals, tabulars, or quadratojugals. Quadrate fixed. A parietal foramen. Neck elongated, the tail never long. Vertebrae platycoelous. Cervical ribs attached exclusively to the centrum, the dorsal ribs exclusively to the arch by a single head. A single, large coracoid on each side. Girdles stout. Pelvis with large pubo-ischiatic opening, or secondarily a thyroid foramen. No sternum. Parasternals stout.

There is still much doubt as to the derivation and genealogical relationships of this order of reptiles, chiefly because of the structure of the temporal region. The general characters of the skeleton are more or less modified by aquatic adaptations. The boundaries of the temporal region seem to be those of the upper opening of the diapsid reptiles; and there are many who believe that it really is the upper one, and that the order is nearest related to the Proganosauria. The opening, it is seen, is bounded quite like that of some members of the Therapsida, especially the Cynodontia; and these reptiles are confidently believed to have descended from theromorphous reptiles with a typical lower opening. The more general opinion is that the Sauropterygia are related to the anomodont-like reptiles. Some, however, would trace their descent directly from the Cotylosauria; others from the Diapsida, by the loss of the lower arch. The author believes that the first of these views is the correct one, but in the present uncertainty they may be left in an independent group.

Whatever has been their origin, we must await the discovery of their more terrestrial ancestors in the early Trias. The modifications of structure in adaptation to aquatic life are very pronounced, even in the Nothosauria. The order is clearly divisible into two chief groups, the Nothosauria and the Plesiosauria.

A. SUBORDER NOTHOSAURIA

Crawling or swimming reptiles from three to seven feet in length, of exclusively Triassic age. Skull depressed, more or less elongate, the orbits situated far forward, looking upward. Nares about midway between the orbits and extremity. Lacrimals possibly absent. Palate without openings, except the large internal nares, the vomers and pterygoids meeting in the middle line throughout. From twenty to twenty-five cervical, twenty-five to thirty dorsal, two to five sacral, vertebrae, and a moderately long tail. Clavicles stout, the interclavicle vestigial. The elongated coracoids meet in the middle line. Epipodials much shorter than propodials. Phalangeal formula primitive, or with the loss of one phalanx in the fourth finger. Digits probably webbed in life.

The Nothosauria were all aquatic in habit, but not exclusively so like the plesiosaurs, the feet still retaining terrestrial characters, with but minor aquatic adaptations. The parasternals, like those of the Plesiosauria, are very stout, apparently also an aquatic adaptation. The body was never slender, though less broad than that of the plesiosaurs, and it is not probable that they were rapid swimmers. They doubtless lived in the shallow waters, as do the crocodiles, coming frequently to land, and subsisted chiefly upon fishes and invertebrates, for the capture of which their slender, curved teeth were well fitted. A peculiar parallel adaptation to that of the contemporary aquatic Labyrinthodontia is seen in the forward position of the eyes in the flat skull, and also in the unusually stout clavicular girdle of both.

Several families have been proposed, based upon minor characters of the skull chiefly. For the present they may all be placed in a single family, the Nothosauridae.

FAMILY NOTHOSAURIDAE. Upper and Middle Trias. *Anarosaurus* Dames, *Cymatosaurus* Fritsch, *Dactylosaurus* Gürich, *Doliovertebra* Huene, *Lamprosaurus* Meyer, *Lariosaurus* Curioni, *Microleptosaurus* Scuphos, *Neusticosaurus* Seeley, *Nothosaurus* Münster, *Parthanosaurus* Scuphos, *Pistosaurus* Meyer, *Proneusticosaurus* Volz, *Simosaurus* Meyer.

B. SUBORDER PLESIOSAURIA

Marine reptiles from eight to about fifty feet in length, with paddle-like, hyperphalangic limbs. Skull moderately broad to very slender. Nares small, situated remote from the extremity and near the orbits. Orbits with sclerotic plates. No distinct nasals. Internal nares small, situated in front of the external. A pair of posterior interpterygoidal openings divided by the parasphenoid always present; other openings variable on the palate. The squamosals meet in the middle line posteriorly. Coracoids very large, contiguous in midline; clavicles and interclavicle small, sometimes vestigial. Ilium rod-like, articulating below with ischium only, above with a well-developed sacrum of three or four vertebrae.

An extensive and long-lived group of purely marine reptiles, widely distributed over the earth; as a whole clearly defined, but with many minor modifications. The neck was extremely variable in length, with from thirteen to seventy-six cervical vertebrae. The body was broad, though not nearly so broad as represented in most modern restorations. The most perfect specimen known — and the author has seen most of them in the collections of the world — is that of *Thaumatosaurus victor*, in the Stuttgart museum, of which a figure copied from a photograph is reproduced here. The body, it is seen, is broadly oval, but not flat, protected below by the extraordinary developments of the pectoral and pelvic girdles and intervening parasternal ribs. Their phylogenetic relationships with the Nothosauria are incontestable, though the closed palate of the latter indicates that no known form could have been actually ancestral to them.

FAMILY PLESIOSAURIDAE. Skull moderately long. From thirty-five to [seventy-six] cervical vertebrae, the cervical ribs double-headed. Scapulae not contiguous in the middle; no interclavicular foramen; epipodials much longer than broad, no accessory epipodials. Coracoids contiguous throughout.

Jurassic. *Plesiosaurus* Conybeare, *Thaumatosaurus* Meyer, Europe.

FAMILY PLIOSAURIDAE. Skull long, neck short, composed of about nineteen vertebrae. Cervical ribs double-headed; five pectoral and about twenty dorsal vertebrae. Premaxillae continuous to parietals in middle. Scapulae closely approximate in midline; coracoids con-

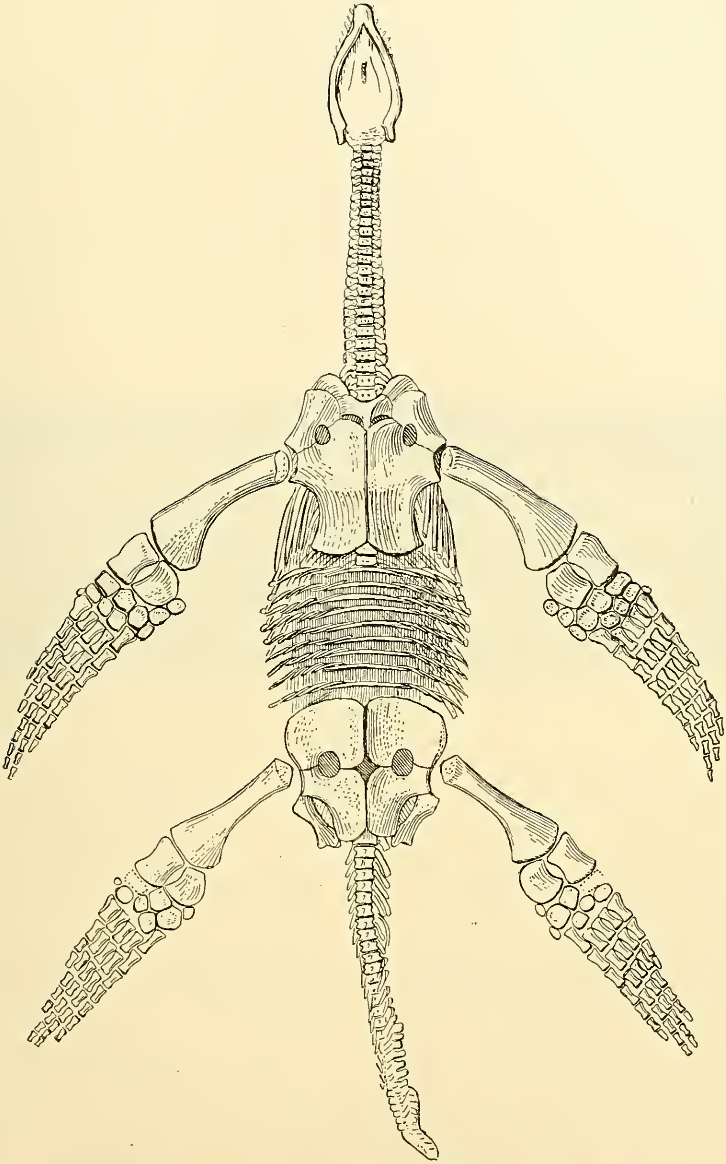

FIG. 173. Skeleton of *Thaumatosaurus* (Plesiosauria). After Fraas. One twentieth natural size.

tiguous throughout. Two or three epipodials, as broad as long or broader. Ischia long. Large or very large.

Jurassic. *Pliosaurus* Owen, *Peloneustes* Lydekker, Europe.

Family Cryptocleididae. Very much like the following family, but the neck is shorter, with from thirty-two to forty-four vertebrae; and the coracoids are contiguous throughout. From two to four epipodials, all short. Cervical ribs single-headed. Skull short.

Jurassic. *Cryptocleidus* Seeley, *Muraenosaurus* Seeley, *Tricleidus* Andrews, *Picrocleidus* Andrews, *Microcleidus* Watson, *Sthenarosaurus* Watson, Europe.

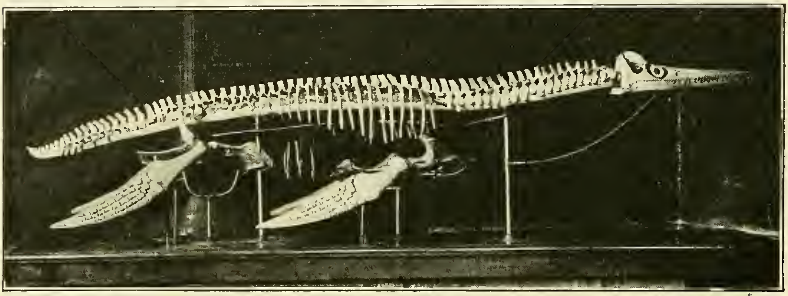

Fig. 174. Skeleton of *Trinacromerum osborni*, a Cretaceous plesiosaur, as mounted in the University of Kansas Museum.

Family Elasmosauridae. Head short, neck very long, with from more than fifty to seventy-six vertebrae; ribs single-headed. The scapulae meet in midline; no interclavicular foramen. Coracoids broadly separated on their posterior half. Ischia short. Two epipodials only, short.

Upper Cretaceous. *Elasmosaurus* Cope, *Ogmodeirus* Williston and Moodie, *Leurospondylus* Brown, North America.

Family Polycotylidae. Skull very slender. Premaxillae articulating with parietals. Neck not longer than head, with from twenty-three to twenty-six vertebrae; ribs single-headed. The precoracoidal process separates the scapulae in the midline; an interclavicular foramen; coracoids contiguous throughout. Ischia elongate. Three or four epipodials, all short.

Upper Cretaceous. *Polycotylus* Cope, *Trinacromerum* Cragin, ? *Piratosaurus* Leidy, North America.

Family Brachauchenidae. Skull long, neck very short, with but thirteen vertebrae, shorter than skull. Cervical ribs singleheaded. Pterygoids not reaching to vomers. Paddles imperfectly known.

Upper Cretaceous. *Brachauchenius* Williston, North America.

Genera incertae sedis

Triassic. "*Plesiosaurus*" Conybeare, Europe.

Jurassic. *Eretmosaurus* Seeley, *Colymbosaurus* Seeley, *Ischyrodon* Meyer, *Liopleurodon* Sauvage, *Spondylosaurus* Fischer, *Simolestes* Andrews, Europe. *Megalneusaurus* Knight, *Pantosaurus* Marsh, "*Muraenosaurus*" Seeley, North America.

Lower Cretaceous. "*Plesiosaurus*" Conybeare, North America.

Upper Cretaceous. *Mauisaurus* Hector, New Zealand. *Polyptychodon* Owen, Europe. *Cimoliosaurus* Leidy, *Oligosimus* Leidy, *Brimosaurus* Leidy, *Piptomerus* Cope, *Orophosaurus* Cope, *Embaphias* Cope, *Taphrosaurus* Cope, *Uronautes* Cope, "*Plesiosaurus*" Conybeare, North America.

7. ORDER PLACODONTIA

Temporal opening bounded by parietal, postfrontal, postorbital, and squamosal. Jaws and palatines with few, very large, flat crushing teeth. A parietal opening. Vertebrae amphicoelous, with hyposphene, hypantrum. Ribs double-headed. Remainder of skeleton unknown.

This singular group of littoral, shell-eating reptiles has long been a problem, because of our ignorance of the skeleton. Some would include them among the Sauropterygia as a separate suborder; others would give to them the same rank among the Therapsida. If the supratemporal and interparietal are really present, as believed by Huene, they would certainly find no place among the Sauropterygia. But their presence has been denied. On the other hand, if there should prove to be but a single coracoid on each side in the pectoral girdle, their location among the Therapsida would be improper. *Placochelys* has a carapace of bony plates, both above and below, with isolated ones upon the skull, all of which seem to be wanting in *Placodus*. Their presence or absence, however, is of no more importance than in the Dinosauria, or Squamata, as examples.

As might be suspected in such forms, the number of presacral vertebrae is reduced.

The temporal vacuity is bounded as in the plesiosaurs, and also in some theriodonts. The maxillae are large, the nares situated rather far back, perhaps an adaptation for grubbing in the mud after invertebrates. Possibly there was a moderate adaptation in *Placodus* for life in shallow water.

The placodonts were reptiles of considerable size, perhaps eight or ten feet in length, undoubtedly slow in movement, and with a heavy skull, as have all shell-eating reptiles.

Until more is known of the skeleton, the group may remain in an independent position, though there is little in the structure of the skull that would entitle them to an ordinal rank; shell-eating animals with crushing teeth occur in various orders.

FAMILY PLACODONTIDAE. Upper Triassic. *Placodus* Agassiz (*Anomosaurus* Huene), *Placochelys* Jaekel, *Cyamodus* Meyer, Europe.

CHAPTER XI

THE SUBCLASS PARAPSIDA

8. ORDER PROGANOSAURIA

Primitive, aquatic reptiles with long neck, body, and tail, two or three feet in length. Structure of skull imperfectly known, probably with a single, upper temporal opening on each side. Face long and slender, the nostril near orbits, the premaxillae elongated. Teeth numerous, long and slender; small teeth on vomers, probably also on other palatal bones. Vertebrae deeply amphicoelous; intercentra unknown; eleven or twelve cervicals, eighteen to twenty-two dorsals, two sacrals and sixty or more caudals. Free ribs on all presacrals except atlas; dorsal ribs stout, single-headed, articulating with centra. Numerous parasternal ribs. Scapula fan-shaped; a single coracoid; clavicular girdle primitive; pelvis with small pubo-ischiatic vacuity. Humerus with entepicondylar foramen. Propodials long; epipodials short, carpus and tarsus primitive; phalangeal formula of pes (in *Mesosaurus* and *Noteosaurus* at least) 2, 3, 4, 5, 6, the fifth toe elongate.

These small reptiles, the first known in geological history with marked aquatic adaptations, retain many primitive characters, though highly specialized in the scapular girdle with its single coracoid, the earliest known. Aside from the Dolichosauria and certain dinosaurs they are the only known aquatic reptiles with both neck and tail elongated. Until the skull is better known, however, doubt remains as to their relationships with other reptiles. By some they have been placed with the double-arched reptiles; by others among the Sauropterygia. Because of the articulation of the single-headed ribs especially, and the probable possession of but a single, upper temporal opening, their natural association seems to be near the ichthyosaurs and lizards.[1]

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[1] [Much further evidence for this view is given by von Huene in his memoir *Die Ichthyosaurier des Lias und ihre Zusammenhänge*, 1922, 4to, Berlin.—Ed.]

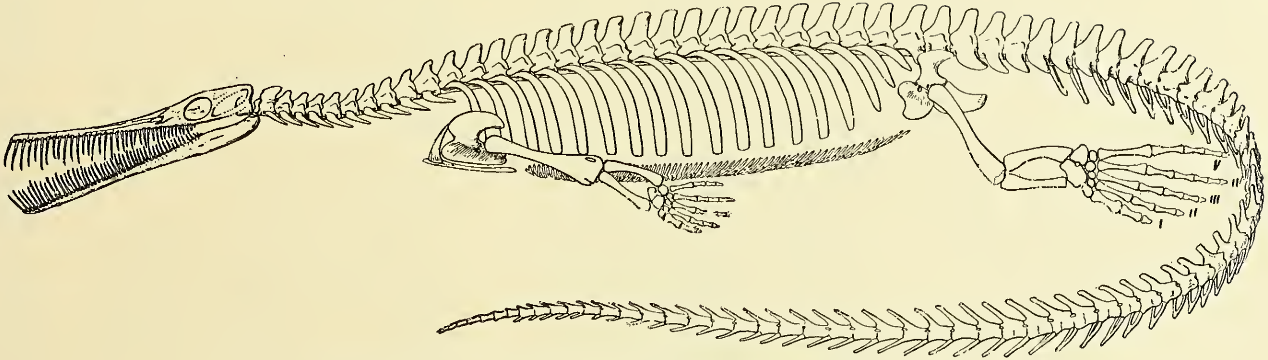

Fig. 175. Skeleton of *Mesosaurus* (Proganosauria). After McGregor. About four tenths natural size.

FAMILY MESOSAURIDAE. Lower Permian. *Stereosternum* Cope (*Notosaurus* Marsh), *Mesosaurus* Gervais, Brazil. *Mesosaurus* Gervais (*Ditrichosaurus* Gurich), ? *Noteosaurus* Broom, South Africa.

FIG. 176. Restoration of *Mesosaurus*. After McGregor. The posture of the hind leg is slightly modified.

9. ORDER ICHTHYOSAURIA

Marine reptiles with all aquatic adaptations of the tail-propelling type: elongated face; posterior nares, sclerotic plates, short neck, elongated body, no sacrum, long, flattened or dilated tail, short propodial and epipodial bones, hyperphalangy, and often hyperdactyly. Premaxillae long; maxillae short. A parietal foramen; free paroccipitals, large stapes; no ectopterygoids or dermosupraoccipitals. Teeth inserted in sockets or grooves, labyrinthine in structure; none on palatal bones. The large upper temporal vacuity is bounded by parietal, postfrontal, and tabular (supratemporal). No lateral opening. Vertebrae short, deeply amphicoelous, without persistent dorsal intercentra. Scapulae small; a single coracoid; clavicles and interclavicle present. No sternum, but numerous parasternals. Pelvis more or less plate-like with small pubo-ischiatic vacuity. Prearticular bone of mandible distinct.

The ichthyosaurs were exclusively marine reptiles, more perfectly adapted to aquatic life than any other known ones unless it be the plesiosaurs. They varied from about two to about thirty feet in length.

Family Mixosauridae. Cervical ribs for the most part holocephalous. Tail with a preterminal dilatation, slightly decurved. Chevrons Y-shaped. Epipodials relatively long; feet pentedactylate. Face less elongate. Teeth more or less anisodont, inserted in sockets.

Middle and Upper Triassic. *Mixosaurus* Baur, Spitzbergen, Switzerland, Germany.

Family Shastosauridae. Body more elongate. Cervical ribs dichocephalous. Tail distinctly expanded and decurved distally. Chevrons Y-shaped. Epipodials relatively long. Feet tetra- or tridactylate.

Both the Mixosauridae and Shastosauridae, which Merriam gives only sub-family values under the Mixosauridae, are more primitive, with less perfect aquatic adaptations than the later forms of the Ichthyosauridae, and especially the Ophthalmosauridae.

Middle or Upper Triassic. *Cymbospondylus* Leidy, *Toretocnemus* Merriam, *Merriamia* Boulenger, *Delphinosaurus* Merriam, *Shastosaurus* Merriam, *Phalaradon* Merriam, California, Nevada. *Pessosaurus* Wiman, Spitzbergen.

Family Ichthyosauridae. Fewer presacral vertebrae; pelvis more reduced; tail with a broad terminal fin; epipodials shorter; dorsal ribs dichocephalous; chevrons separate or fused; hind limbs

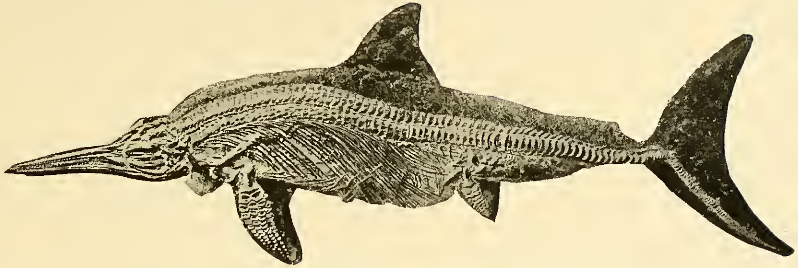

Fig. 177. Skeleton of *Ichthyosaurus*. After Dreverman.

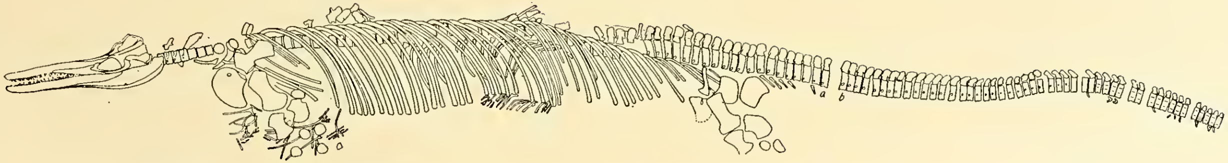

Fig. 178. Skeleton of *Cymbospondylus*, a Triassic ichthyosaur. After Merriam. One sixty-second natural size.

usually more reduced; frequently hyperdactylate. Teeth inserted in grooves. Face longer.

Upper Triassic to Upper Cretaceous. *Ichthyosaurus* Koenig (*Proteosaurus* Howe), Europe, Asia, Africa, Australia, New Zealand, South and ? North America.

A widely distributed genus as it is ordinarily accepted. It presents, however, numerous minor modifications that might justify its division.[1]

Family Ophthalmosauridae. Differs from the more typical Ichthyosauria in the more reduced teeth, the presence of three epipodial bones in the front paddles, the more reduced hind paddle, the fusion of the ischium and ilium, in the apparent entire absence of chevrons, and in the more discoidal form of the phalanges.

Upper Jurassic. *Ophthalmosaurus* Seeley (? *Baptanodon* Marsh), Europe and North America.

Cretaceous (Upper Greensand). ? *Ophthalmosaurus* Seeley.

? ORDER OMPHALOSAURIA[2]

Family Omphalosauridae. Marine reptiles with a short, shell-crushing skull. Mandibles short, the dentaries united in a strong symphysis, their broad, convex, superior surface beset with several rows of low-crowned, button-like crushing teeth, the largest about fifteen millimeters in diameter. Vertebrae amphicoelous. "Palate plesiosaur-like." Skeleton otherwise unknown.

The incompletely known remains of these reptiles, described by Merriam, are very suggestive of a new type of shell-eating aquatic reptiles, but until more is known they are merely suggestive, the ordinal rank and relationships provisional or conjectural. In themselves the characters are not of ordinal rank, but their associations and their age make it not at all improbable that when fully known they will justify the rank provisionally given to them. From essentially the same horizon in Spitzbergen similar teeth have been described by Wiman, which seem to pertain to the same kind of

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[1] [Von Huene (1922) divides the old genus *Ichthyosaurus* into several phyletic lines, the evolution of which he traces from the Triassic to the Upper Cretaceous.—Ed.]

[2] [Recent authors (von Huene, Nopcsa) class the Omphalosauria with the Ichthyosauria.—Ed.]

reptiles. Somewhat doubtfully associated with those remains are others of ichthyosaur-like bones that the describer provisionally associated with the Ichthyosauria, bearing possibly a like relation to the known Ichthyosauria that *Globidens* does to the typical Pythonomorpha.

Middle Triassic. *Omphalosaurus* Merriam, Nevada. *Pessopteryx* Wiman, Spitzbergen.

10. ORDER PROTOROSAURIA

Quadrupedal, arboreal, terrestrial, or subaquatic reptiles one to six feet in length, with a single, upper temporal opening between the parietal and the temporal arch, the quadrate fixed. Ribs in part or all single-headed, articulating with centra — a single coracoid, an interclavicle, and clavicles.

This order, as here limited, is a provisional one, including several reptiles, some of them imperfectly known, which cannot be placed in any other known order. Most of them have hitherto been classified with the Rhynchocephalia, from which they are distinguished by the absence of a lateral temporal opening, so far as known. Perhaps when finally known they will be found to be incoherent. For the present they may be defined as families.

Family Araeoscelidae. Very slender, arboreal or leaping, hollow-boned reptiles of less than eighteen inches in length, with long legs and long tail. The broad lateral temporal region is formed apparently of a single bone, here identified as the squamosal, the quadratojugal absent. The dermosupraoccipital is apparently large. Lacrimal vestigial or absent. A parietal foramen. All cranial bones paired. Palatal bones with teeth. At least seven cervical vertebrae, twenty dorsal, two sacral, and a long, slender tail. Vertebrae amphicoelous with persistent intercentra. Cervical ribs, at least, single-headed, the dorsal more or less dichocephalous. Coracoid and scapula closely fused. Humerus with both entepicondylar and ectepicondylar foramina. Pelvis primitive. Phalangeal formula primitive. Calcaneum produced.

Araeoscelis, the type of the family, is the earliest definitely known reptile with a single, upper temporal vacuity, bounded as in the lizards, and a fixed quadrate. It was a very slender, leaping or

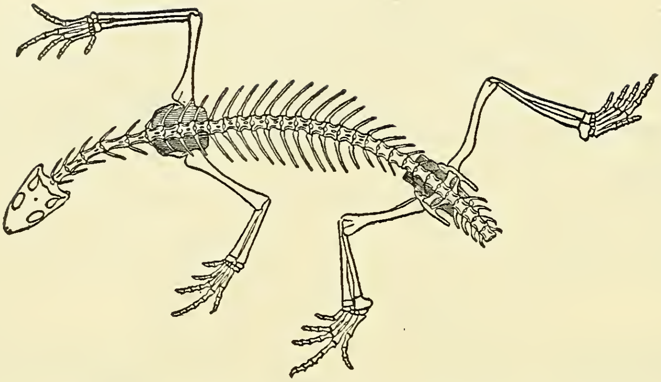

Fig. 179. Skeleton of *Araeoscelis* (Protorosauria). About one fourth natural size.

Fig. 180. Restoration of *Araeoscelis*.

arboricolous, insectivorous, lizard-like reptile from the Lower Permian of Texas. Of *Kadaliosaurus*, unfortunately, the skull is unknown. Its slender bones were less hollow, and it has also numerous parasternal ribs, unknown in *Araeoscelis*.

Lower Permian. *Araeoscelis* Williston, Texas. *Kadaliosaurus* Credner, Germany.

Family Protorosauridae. Elongate reptiles with long neck and hind legs and hollow bones, from three to five feet in length. Skull imperfectly known, probably with an upper temporal opening only. Sclerotic plates in orbits. Prevomers, palatines, and pterygoid with small teeth. Vertebrae amphicoelous, with persistent intercentra. Seven cervicals, sixteen to eighteen dorsals, two or three sacrals, and a long tail. A single coracoid. Pelvis more or less plate-like, with probably a small pubo-ischiatic vacuity. Ribs single-headed, articulating with centrum, those of the cervical region very slender. Epipodials about as long as propodials, the hind legs much longer than the front. Humeri with ectepicondylar (?) foramen; nine or ten carpals, seven tarsals; phalangeal formula primitive, the digits long. Numerous abdominal ribs.

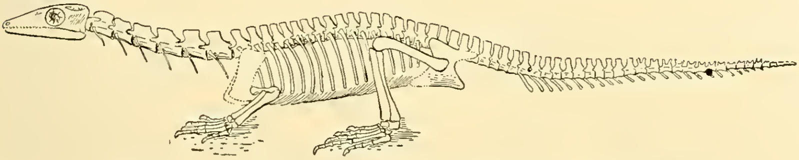

Fig. 181. Skeleton of *Protorosaurus* (Protorosauria), modified from Seeley. About one tenth natural size.

Although the first-described fossil reptiles, the protorosaurs are still imperfectly known in the details of their structure, especially of the skull, pectoral, and pelvic girdles. In the elongation of the neck and the slender legs *Protorosaurus* very much resembles *Araeoscelis*, and doubtless had similar habits, whether or not the structure of the skull was the same. The numerous known specimens of *Protorosaurus* differ so much from each other that it is not at all improbable that they represent different genera.

Aphelosaurus is still more problematical, inasmuch as all that is known of it are the trunk and limbs. The limbs resemble those of

Protorosaurus in size, slenderness, and proportions. The single-headed ribs are described by Thevenin as articulating intercentrally.

Lower Permian. ?*Aphelosaurus* Gervais, France.

Upper Permian. *Protorosaurus* v. Meyer, Germany.

The nares were described by Seeley as immediately in front of the orbits — an error. There may be a small antorbital foramen, but it is doubtful.

FAMILY SAPHAEOSAURIDAE. Slender, terrestrial or subaquatic reptiles about two feet in length. Skull with a single temporal opening, the quadrate fixed and the lateral temporal region moderately broad. No postfrontals; postorbitals large. No parietal foramen. Maxillae and dentaries edentulous, with cutting edges. Vertebrae procoelous without intercentra; twenty-three presacrals, two sacrals, and fifty or more caudals. Caudal vertebrae with splitting point (?). Ribs single-headed, articulating with anterior part of centrum. Coracoid with two median emarginations. Interclavicle T-shaped, the clavicles slender. Parasternals numerous, composed of a median unpaired pices and a lateral splint on each side. Pubes and ischia broadly separated by pubo-ischiatic opening, the ischia with a stout posterior tuberosity. An ectepicondylar foramen in humerus. Manus and pes pentedactylate, with primitive phalangeal formula.

Saphaeosaurus, usually called *Sauranodon*, has long been classed as a representative of a distinct family of the Rhynchocephalia. The skull, as described by both von Meyer and Lortet, has but a single temporal opening on each side, bounded externally by the postorbital and squamosal (tabular?). There is no lower temporal opening. The structure of the temporal region as described is doubtful. In much probability the tabular, squamosal, and quadratojugal are all present. In all its essential characters it is a Lacertilian with a primitively fixed quadrate. The vertebrae, as figured and described by Lortet, are procoelous, perhaps the first known evidence of such in geological history.

Upper Jurassic. *Saphaeosaurus* v. Meyer (*Sauranodon* Jourdan), France.

FAMILY PLEUROSAURIDAE. Very slender, snake-like, aquatic reptiles, with short neck, long body, very long flattened tail, and small pentedactylate legs; attaining a length of nearly five feet. Skull

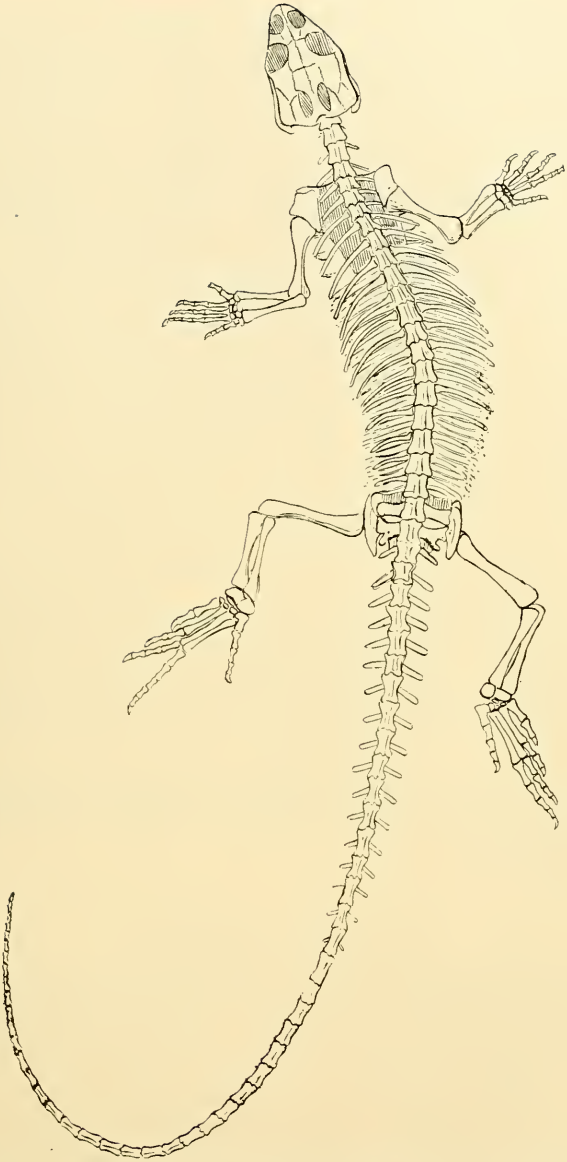

Fig. 182. Skeleton of *Saphaeosaurus* (Protorosauria). After Lortet. One fourth natural size.

elongate, pointed, the nares remote from end. No postfrontals. A parietal foramen. The single temporal opening is bounded within by the parietal, without by the postorbital and (?) squamosal. A small quadratojugal. Teeth pointed and recurved. Acrodont. Palatal teeth unknown. Five cervicals, forty or forty-one dorsals, two sacrals, and more than seventy caudals. Vertebrae amphicoelous, cervical intercentra hypapophysial. Ribs single-headed, articulating as in the Squamata. Numerous slender, parasternal ribs.

Pleurosaurus, the only certainly known genus of the family, was long supposed to be a member of the Rhynchocephalia, though it has also long been known to have but a single upper temporal opening. Its remarkable adaptation to aquatic life is shown in the elongated head, posterior nares, short neck, very slender trunk, very small legs, and enormously elongated tail, with its long chevrons and spines, which in life was surmounted by a thin crest of scales.

Acrosaurus is probably only the young of *Pleurosaurus*, as the author convinced himself by examination of specimens in the Munich museum. In consequence, the ordinal name once proposed for these reptiles, Acrosauria, is inappropriate. The structure of the temporal region still needs confirmation. If there is but a single bone bounding the temporal opening posteriorly, it is in much probability the real squamosal.

Uppermost Jurassic. *Pleurosaurus* v. Meyer (*Anguisaurus* Münster, *Saurophidium* Jourdan), Germany, France. ? *Acrosaurus* v. Meyer. Germany.

11. ORDER SQUAMATA

With a single temporal vacuity on each side, bounded by parietal, tabular, squamosal, and postorbital, secondarily sometimes roofed over or the arcade obsolete. No lower temporal opening or bar. Quadrate movably articulated, streptostylic, secondarily sometimes fixed. No supratemporals, dermosupraoccipitals, or quadratojugals. The pterygoids articulate in front with the palatines, never with the prevomers. Paroccipitals fused with exoccipitals. Interorbital septum not ossified. Teeth acrodont or pleurodont, often attached to palatine and pterygoid. Prearticular fused with articular. Ribs single-headed, articulating with centrum.

A. SUBORDER LACERTILIA (SAURIA)[1]

Subvolant, arboreal, terrestrial, burrowing, subaquatic, or marine reptiles from a few inches to about forty feet in length; quadrupedal, bipedal, or limbless; herbivorous, insectivorous, or carnivorous. Brain-case in front of proötics more or less membranous. Lacrimals small or vestigial. Posterior arcade sometimes absent. Mandibles usually united by suture. Vertebrae procoelous, except in the Geckonidae and Uroplatidae; not more than two sacral vertebrae. Clavicles and interclavicle rarely absent. No entepicondylar, but usually an ectepicondylar foramen in humerus.

This group is often given an ordinal rank, equivalent to the Ophidia or even to the Pythonomorpha, but the ultimate distinctions between them are almost trivial, as will be seen, and in many legless burrowing lizards the skull structure mimics that of the snakes. More than eighteen hundred species are known, distributed widely throughout the world, usually classed in about twenty families and numerous genera.

Because of their predominantly terrestrial habits, but few remains of lizards are found in the rocks, aside from the more aquatic or marine types. Only about fifty genera of extinct forms have been described and less than one hundred species, and the greater majority of those are for the most part fragmentary and incomplete, so much so that their systematic positions are very often uncertain and provisional. Doubtless they have had a long and abundant geological history from very remote times, but of the true land lizards almost nothing is known throughout the Mesozoic. But few positive characters are distinctive of the group, though many negative ones are. The mandibles are usually suturally united in the middle, but a few forms have them ligamentously attached. The presence of legs is not distinctive, though at least a vestige of the pectoral girdle remains. The more or less open brain-case in front is perhaps the most diagnostic, only partially enclosed by the more or less vestigial postoptics ("alisphenoids," "postorbitals"). However, in the Amphisbaenia even this character is doubtful, and in the mosasaurs a distinct descending plate from the parietals resembles that of the snakes,

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[1] [For a very comprehensive morphological and taxonomic revision of the Lacertilia, see C. L. Camp, "Classification of the Lizards," *Bulletin*, Amer. Mus. Nat. Hist., 1923, XLVIII. — ED.]

but does not reach the basisphenoid. The jugals, squamosals, and tabulars may be more or less vestigial, and even the quadrate may be secondarily fixed and immovable.

TRIBE KIONOCRANIA

Terrestrial, burrowing, subaquatic, or subvolant. A slender epipterygoid articulates with parietal and pterygoid; no descending plates of the parietals. Palate with large openings, usually with teeth on palatines or pterygoids or both. Feet when present usually pentedactyl, with the primitive phalangeal formula, the fifth metatarsal more or less hook-shaped proximally. Eight cervical vertebrae.

FAMILY GECKONIDAE. Vertebrae amphicoelous,[1] notochordal, with persistent intercentra. Quadrupedal. Jugal vestigial. No temporal arcade. Parietals paired. Clavicles perforated near mesial end.

A family of small lizards widely scattered over the earth, comprising nearly three hundred species and about fifty genera. They are of interest because of the persistently primitive condition of the vertebrae. They must have had a long independent history from early Mesozoic times, but no species are known as fossils.

FAMILY EUPOSAURIDAE. Small lizards, from two to four inches in length, of doubtful position; referred to the Anguinidae by Boulenger. Head relatively large and broad, orbits very large, the temporal openings said to be closed. Structure poorly known, twenty-three presacrals.

Upper Jurassic. *Euposaurus* Lortet, France.

FAMILY AGAMIDAE. Temporal and postorbital arches complete. A parietal foramen.[2] No dermal ossicles [on back]. Teeth acrodont. Quadrupedal.

This exclusively Old-World family includes about two hundred known species of about thirty genera, some of them attaining a length of three feet. Perhaps the most noted members are the Flying Dragons (*Draco*), small lizards with an extraordinary development of the ribs to support a parachute membrane. *Chlamydosaurus*, one of the largest of the family, has an extraordinary frill about the neck

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[1] [Rarely procoelous. See G. K. Noble, 1921, Amer. Mus. *Novitates,* No. 4.—ED.]

[2] [Except *Liolepis.*—G. K. N.]

supported by the elongated hyoid bones. Some are subaquatic in habit. The Moloch lizard, much like a "Horned Toad" in appearance, has long dermal spines.

Oligocene. France [*Agama*].

Pleistocene. *Chlamydosaurus*, Australia.

Family Iguanidae. Arboreal, terrestrial, burrowing, or subaquatic, reaching a length of six feet. Teeth pleurodont. No dermal ossifications. Temporal and orbital arches complete. Spines of vertebrae sometimes elongate. A parietal foramen. Zygosphenes sometimes present. Herbivorous and insectivorous.

About three hundred species and fifty genera are known of this family, almost exclusively American in distribution, including our largest and some of our most common lizards, — the Basilisc lizards, Iguanas, "Horned Toads," etc. The large Galapagos lizard, *Amblyrhynchus*, is a noteworthy herbivorous, aquatic form that seeks its food in shallow water, returning to the land for safety when pressed by enemies; perhaps one of the ways in which terrestrial reptiles acquired water habits.

Eocene. *Iguanavus* Marsh, North America. *Proiguana* Filhol, France.

Family Anguinidae. With well-developed, pentadactyl limbs, or limbs vestigial. Body covered with dermal ossicles beneath corneous scales. Temporal opening roofed over by dermal bones. Teeth pleurodont. A parietal foramen.

This family, common to Europe and America, comprises about fifty species. Most noteworthy are the "Glass Snakes" and the "Slow Worms," with vestigial limbs or wholly without them.

Miocene. *Anguis*, *Diploglossus*, France.

Family Helodermatidae. Poisonous, terrestrial lizards with grooved, slender, pleurodont teeth. A postorbital but no temporal arch, the squamosal absent; prefrontal and postfronto-orbital in contact over orbits. Parietals and frontals fused. No parietal foramen. Upper surface of body and skull more or less covered by dermal ossicles. An ossified, subfrontal, rhinencephalic chamber. Quadrupedal.

But one genus and two species of this family are known, the famous "Gila Monsters" of Arizona. They are thickset, slow lizards with a club-like tail, reaching a length of about two feet, the only known poisonous members of the suborder.

Eocene. *Glyptosaurus* Marsh, *Thinosaurus* Marsh, North America. *Placosaurus* Gervais, France.

Oligocene. *Helodermatoides* Douglass, North America.

Family Lacertidae. Quadrupedal, terrestrial lizards. Upper surface of skull with numerous dermal bones. Temporal opening roofed over by the postfrontal extending back between parietal and squamosal, the arches complete. A parietal foramen. Teeth pleurodont.

The family of Lacertidae comprises about one hundred species restricted in distribution to Europe, Asia, and Africa. None is large and some are common throughout England; one, *Lacerta vivipara*, is the only reptile known to occur in Ireland.

Miocene. *Lacerta*, France.

Family Tejidae. Arboreal, terrestrial, or subaquatic lizards attaining a length of three feet. No postorbito-squamosal arch.[1] A parietal foramen. No dermal ossicles. Zygosphenes sometimes present.

A family of American lizards including about one hundred species, some, like the *Cnemidophorus*, common throughout the United States. The teeth of *Dracaena* are large oval, crushing organs.

Uppermost Cretaceous. ? *Chamops* Marsh, North America. Oligocene, *Tejus*.

Family Scincidae. Temporal arch complete. Temporal openings roofed over by dermal bones. Body also covered by dermal ossicles beneath the corneous scales. Quadrupedal, bipedal, or limbless; terrestrial, subaquatic, or burrowing. Pleurodont.

The large family of skinks comprises about four hundred living species, cosmopolitan in its distribution. Some attain a length of about two feet. *Trachysaurus* of Australia is peculiar in its stumpy tail and very large scales of the body. *Cyclodus* has spherical crushing teeth.

Lower Cretaceous (Neocomian). *Ardeosaurus* Meyer.

Eocene. *Cadurcosaurus* Filhol, France.

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[1] [A postorbital arch is present.—G. K. N.]

Oligocene. *Dracaenosaurus* Gervais, *Protrachysaurus* Stefano, France.

Pliocene. *Didosaurus* Günther.

TRIBE PLATYNOTA

Terrestrial or subaquatic lizards from two or three feet to about thirty in length. Epipterygoid and parietal foramen present. Feet pentadactylate, with the primitive phalangeal formula. Sacrals present.

FAMILY VARANIDAE. Terrestrial or subaquatic, reaching a length of about thirty feet (*Megalania*). Skull more or less elongate, the nostrils rather far back, broadly open. Premaxillae, nasals, and parietals unpaired. Postorbital arch incomplete. Descending plates from the frontals enclose a rhinencephalic chamber. An imperfect joint between angular and splenial. Large palatal openings. Nine cervical, twenty dorsal, vertebrae. Girdles complete. No dermal bones.

This family, exclusively [Australian], African, and Asiatic, includes but one genus, *Varanus*, with about thirty living species, none more than seven feet in length.[1] Some are subaquatic in habit, seeking the water, in which they swim with freedom by aid of the long flattened tail, to escape their enemies. Their structure is so like that of the following forms of the Dolichosauridae, and especially the Aigialosauridae, that it would seem very probable they all had a common origin in early Cretaceous times. *Megalania*, from the Pliocene of India [and Pleistocene of Australia], is the largest of all known terrestrial lizards. Unlike most lizards, they have a long protrusible tongue.

Eocene. *Saniva* Leidy, North America. *Paleovaranus* Filhol, *Proganosaurus* Portis, France.

Pliocene. *Megalania* Owen, India.

Pleistocene. *Varanus*, India. [*Megalania*, Australia.]

FAMILY DOLICHOSAURIDAE. Slender aquatic lizards, two or three feet in length, with a relatively small skull, long neck of thirteen

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[1] [*Varanus komodoensis* Owens, of the Dutch East Indies, reaches a length of thirteen feet.—H. C. Raven.]

vertebrae, slender cylindrical body of twenty-six or twenty-seven vertebrae, two sacrals, and a long flattened tail. Zygosphenes present. Legs relatively small, the front ones smaller than the hind. Pleurodont.

The dolichosaurs, with their greatly elongated neck and body, have been thought by some to be ancestrally related to the snakes but this is very doubtful, since their flattened tail shows a distinct adaptation to water life and it is improbable that the snakes ever passed through an aquatic stage in their evolution. Aside from the Proganosauria, they are the only known swimming reptiles with both neck and tail elongated. Just what habits were subserved by this structure is a problem. Because of the snake-like sinuosity of the neck, body, and tail, the small legs must have been of no propelling, and but little other, use in the water. *Pleurosaurus*, an allied reptile of similar form, has a short neck. In all probability the dolichosaurs were a side branch from the common varanoid ancestral stock of the aigialosaurs and mosasaurs, but not directly ancestral to any later forms.

Lower Cretaceous (Neocomion). *Acteosaurus* Meyer, *Adriosaurus* Seeley, *Pontosaurus* Kramberger, Europe (Dalmatia).

Upper Cretaceous. *Dolichosaurus* Owen, England.

Family Aigialosauridae. Subaquatic lizards from three to six feet in length. Skull large, mosasauroid. Neck of seven vertebrae; body of twenty-one vertebrae; tail long, flattened. Two sacrals. Legs of nearly equal size, the propodials somewhat shortened. Feet not hyperphalangic, probably webbed.

The skull of the aigialosaurs is almost identical in structure with that of the mosasaurs, including the remarkable joint in the mandible between the angular and splenial, and their ligamentous union in front. The neck is shortened, the body elongated, with the same number of vertebrae found in some mosasaurs. The limbs, however, were terrestrial, with only slight aquatic adaptations. Doubtless the reptiles were amphibious in habit, frequenting the shallow waters for food.

Lower Cretaceous (Neocomion). *Aigialosaurus* Kramberger, *Carsosaurus* Kornhuber, *Opetiosaurus* Kornhuber, ? *Mesoleptos* Cornalia, Europe (Dalmatia).

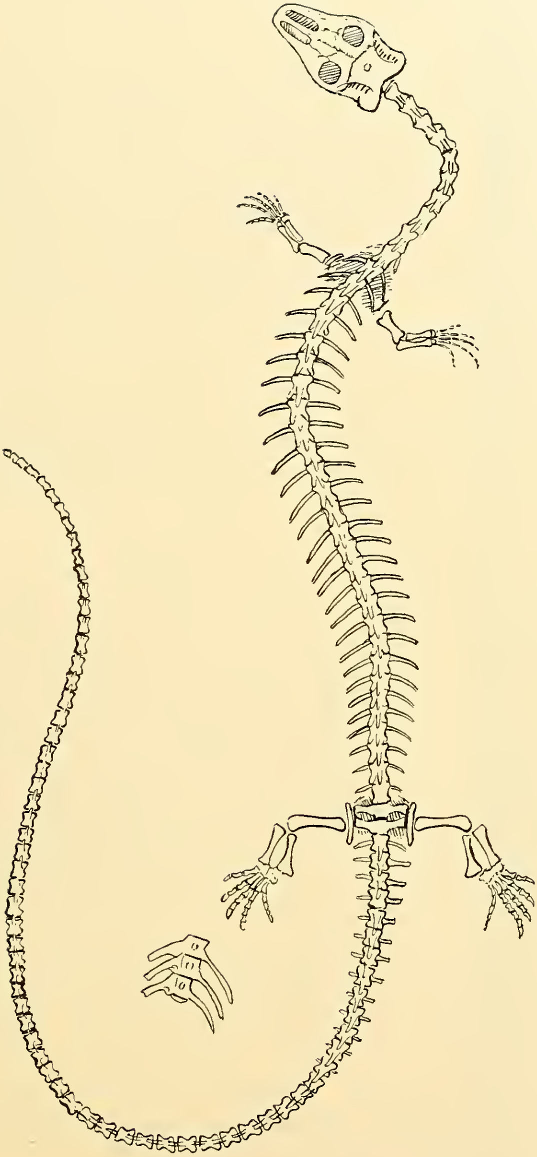

Fig. 183. Skeleton of *Adriosaurus* (Lacertilia). After Seeley. Three fourths natural size.

Tribe Pythonomorpha (Mosasauria)

Large marine lizards with more or less elongated head, shortened neck, elongated body, a long, flattened tail with a more or less subterminal dilatation, and paddle-like extremities. From six to about forty feet in length. Temporal and postorbital arches complete, the tabular with a long process wedged in between paroccipital and proötic. Parietal and frontal unpaired; a parietal foramen. Palate with large openings. Teeth with osseous base inserted in shallow pits in premaxillae, maxillae, dentaries, and pterygoids. Nasals and premaxillae fused into a single bone. A true joint between angular and splenial; rami of mandibles united by ligaments. Vertebrae procoelous. Sclerotic plates present sometimes with zygosphenes. Seven cervicals. No clavicles; sometimes a slender interclavicle. A calcified sternum. No sacrum. Legs paddle-like, short, webbed, without claws, hyperphalangic, pentadactylate.

The mosasaurs are a group of large marine lizards, of world-wide distribution during Upper Cretaceous times. In all probability they were descended from subaquatic lizards like the aigialosaurs in late Lower Cretaceous times, differing from them chiefly in the loss of the sacrum and the adaptation of their limbs to purely aquatic uses.

Three types of mosasaurs are recognized: the surface-swimming type with elongated trunk composed of as many as thirty-five dorsals, the tail with a pronounced subterminal dilatation, zygosphenes, a well-ossified carpus, and only slight hyperphalangy, of which *Mosasaurus* and *Clidastes* are types; a deeper-sea type with proportionally shorter neck, less elongated trunk with but twenty-two vertebrae, a more uniformly flattened tail, less well-ossified carpus and tarsus, and greater hyperphalangy, with *Platecarpus* as a type; a diving type, with more elongated head, heavy cartilaginous protections for the ears, a relatively short neck, body with but twenty-two vertebrae, a longer and much flattened tail, the almost entirely cartilaginous mesopodials and highly developed hyperphalangy, and greater size, of which *Tylosaurus* is the best-known type. And these three groups have been, perhaps rightly, recognized as distinct families. The mosasaurs were clothed with small *Varanus*-like scales, of which impressions have been often found. The bones, especially of the deep-diving forms, were soft, doubtless impregnated in life with fat.

Family Mosasauridae. Teeth conical, pointed.

Upper Cretaceous. *Mosasaurus* Conybeare, *Clidastes* Cope, *Platecarpus* Cope, ?*Sironectes* Cope, *Macrosaurus* Owen, *Brachysaurus* Williston, *Baptosaurus* Marsh, North America. *Plioplatecarpus* Dollo, *Prognathosaurus* Dollo, *Hainosaurus* Dollo, *Mosasaurus* Conybeare, Europe (England, France, Belgium, Russia). *Taniwhasaurus* Hector, New Zealand.

Family Globidentidae. Teeth spheroidal, rugose. Imperfectly known.

Upper Cretaceous. *Globidens*, Gilmore, Europe and North America.

Tribe Amphisbaenia

Worm-like or snake-like, burrowing lizards, reaching a length of about one and one-half feet, either legless or with short tetradactyl front limbs immediately back of the skull. Body with numerous rings and without scales, the tail very short and blunt. Eyes minute. No postorbital or temporal arch, the quadrates fixed by the pterygoids; squamosals and tabulars indistinguishable; no postorbitals, lacrimals, or jugals; the nasals large. No parietal foramen. Brain-case in front partly enclosed by plates from frontals. Palate without openings back of the nares. Stapes short and stout. Vertebrae procoelous.

A curious group of burrowing lizards, moving by vertical rather than lateral undulations. The solid skull with the palate firmly fixed, the immovable quadrates, and entire absence of arches, together with the vestigial or absent limbs, are characters almost as far removed from the typical lacertilian structure as are those of the snakes,

Fig. 184. Skeleton of *Platecarpus* as mounted in the Palaeontological Exhibit, Walker Geological Museum.

and seem to be as important in classification as those distinguishing the much more typically lizard-like mosasaurs.

No extinct lizards are certainly referable to this tribe, though it is probable that some referred to it will eventually be found to have all the essential characters of the group.

FAMILY AMPHISBAENIDAE. With the characters of the group.

Oligocene. *Rhineura* Cope, *Aciprion* Cope, *Diacium* Cope, *Hyporhina* Baur (a postorbital arch). *Cremastosaurus* Cope, *Platyrhachis* Cope, North America.

TRIBE RHIPTOGLOSSA

Small, arboreal, perching lizards. Arches complete, the quadrate slender. Postfrontals indistinguishable; premaxillae small or vestigial; no septomaxillae; parietals and frontals unpaired; no parietal foramen; epipterygoids absent or vestigial; palate with openings. Vertebrae procoelous; five cervicals, from eleven to fifteen dorsals, two sacrals, and slender, prehensile tail, the spines sometimes elongated. Clavicles absent or vestigial. Mesopodials much reduced, digital formula 2, 3, 4, 4, 3, the digits in opposable groups of two and three. Abdominal ribs present.

A group composed of about fifty living species confined to Madagascar, Africa, and India. A curious group of insectivorous tree lizards, long famous for their power to change color, and for their peculiar grasping digits. Our paleontological knowledge of them is vague.

FAMILY CHAMELEONTIDAE. With the characters of the group.

Eocene. *Chameleo* (Leidy), North America. *Prochameleo* de Stefano, France.

GENERA INCERTAE SEDIS

Triassic. ? *Paliguana* Broom. South Africa.

Jurassic. ? *Saurillus* Owen. Jura, England.

Eocene. *Enigmatosaurus* Nopcsa (de Stefano), Europe. *Naocephalus* Cope, North America.

Upper Cretaceous. *Coniosaurus* Owen, *Saurospondylus* Seeley, England. ? *Tylosteus* Cope, North America.

Pleistocene. *Notiosaurus* Owen, ? *Patricosaurus* Seeley, England.

B. SUBORDER OPHIDIA (SERPENTES)

Elongated, legless reptiles of from a few inches to thirty feet in length, sometimes with vestiges of hind limbs but never with front limbs or pectoral girdle. There are no temporal arches, no squamosals, jugals, epipterygoids, lacrimals, postoptics, and sometimes no ectopterygoids. The quadrate articulates loosely with the tabular only; in a few instances even the tabular is absent (Uropeltidae). The brain-case in front is enclosed by descending plates from the parietals and frontals to the sphenoid, from the latter sometimes interrupted by the coalescent optic foramina. Proötics largely visible. The pterygoids and usually the palatines have teeth. The premaxillae are small and often edentulous; maxillae rarely edentulous. Teeth acrodont. Parietals fused, no parietal foramen. The mandibles are united in front by ligaments only; the posterior bones are often fused, the coronoids sometimes absent, the dentaries loosely articulated. The vertebrae are numerous, sometimes exceeding four hundred in number, divisible into precaudal and caudal series, the first two or three without ribs, cervical. Always procoelous and always with zygosphenes and zygantra. Anterior vertebrae, sometimes to the caudals with a more or less prominent hypapophysis. No chevrons, but more or less of the caudals with a descending process on each side (lymphapophyses).

This suborder, often considered an order, includes more than eighteen hundred living species widely distributed over the earth. Like so many groups of organisms known in many related forms, there is scarcely a single positive character to distinguish them; the most decisive, as has been mentioned, is probably the complete bony closure of the brain-case; and there is never a vestige of a pectoral girdle, though several families have vestigial pelvic and hind limb bones. Probably the snakes are the latest group of equivalent rank to be evolved among the Reptilia, and of the snakes the poisonous vipers are probably among the latest. Most snakes are purely terrestrial in habit; a few are burrowing, and still others are aquatic. And chiefly because of such upland habits they are very scantily represented among fossils, not more than fifty or sixty species altogether; and of them with very few exceptions their fossil remains are few and fragmentary, and their taxonomic relations very doubtful.

FAMILY TYPHLOPIDAE. No ectopterygoids or tabulars. Maxillae vertical, toothed; maxillae and mandibles edentulous. Vestiges of pelvis present.

The Typhlopidae with but a single living genus and about one hundred species are widely distributed in the tropical regions. They are burrowing in habit. A single extinct form (*Symoleophis* Sauvage) from the Cretaceous of France (Senonian) has been referred here; the single known vertebra is more probably that of a dolichosaur lizard.

FAMILY BOIDAE (Pythonidae). Ectopterygoid and coronoid present. Maxillae horizontal, reaching premaxillae, with solid teeth, the latter with or without teeth. Tabular long, or short and closely attached to the skull (Illysiidae). Vestiges of hind limbs present.

A family of wide distribution comprising about sixty species, some of them attaining a length of nearly thirty feet. Boas, anacondas, pythons, etc.

Upper Cretaceous. *Dinilysia* Woodward, Patagonia.

Eocene. *Protagaras* Cope, *Limnophis* Marsh, *Lestophis* Marsh, *Boavus* Marsh, North America.

Oligocene. *Paleopython* Rochebrune, *Scytalophis* Rochebrune, France. *Paleryx* Owen, England.

Miocene. *Heteropython* Rochebrune, *Scatophis* Rochebrune, France. *Aphelophis* Cope, *Ogmophis* Cope, *Calamagras* Cope, North America. *Botrophis* Mercer, France.

Pliocene. *Python* Daudin, East India.

FAMILY PALEOPHIDAE. Neural spines elongate; vertebrae with an inferior ridge.

Large snakes, probably subaquatic, imperfectly known.

Eocene. *Pterosphenus* Lucas, *Paleophis* Owen, North America. *Paleophis* Owen, Europe.

FAMILY VIPERIDAE. No coronoids. Ectopterygoids present. Maxillae vertically erectile, articulating with prefrontal, excavated (Crotalinae) or not (Viperinae). Poison fangs perforated.

About one hundred living species of these poisonous snakes with erectile fangs are known, widely distributed. Pit vipers (rattlesnakes and copperheads) exclusively in America.[1]

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[1] [Occur also in Asia and Malaysia. — ED.]

Uppermost Cretaceous. ? *Coniophis* Marsh, North America.
Eocene. ? *Helagras* Cope, North America.
Oligocene. *Neurodromicus* Cope, North America.
Miocene. *Vipera* Laurenti, Germany.
Pleistocene. *Crotalus* Linné, North America.

Family Elapidae. Ectopterygoids present. Maxillae horizontal, not erectile, their anterior teeth deeply grooved or hollowed. Caudal hypophyses bifid. *Laophis*, Salonica.

This family of highly poisonous snakes, in its wider sense including the cobras, sea snakes, and the coral snakes of the southern United States, comprises nearly two hundred living species. They are practically unknown as fossils. Cobras (*Naja* Laurenti) have been reported from the Pleistocene of France, but doubtfully.

Family Colubridae. Ectopterygoid present, the coronoid absent. Maxillae horizontal, with solid teeth. Tabular present. Postorbital not produced forward.

This family of harmless snakes includes more than half of all living species, none attaining a size of more than seven or eight feet. Their distribution is world-wide.

Miocene. *Elaphis* Aldrich, *Tamnophis* Rochebrune, *Pylemophis* Rochebrune, *Periops* Wagler, Europe.

Pleistocene. *Coluber* Linné, Europe and North America [=] *Bascanion* Baird and Gerard, North America.

CHAPTER XII

THE SUBCLASS DIAPSIDA

Two temporal openings, the upper bounded by the parietal above, the postorbito-squamosal arch below; the lateral by the postorbito-squamosal arch above, the jugal, or jugal and quadratojugal, below. A single coracoid on each side; no cleithra. Pelvis with puboischiatic opening. Quadrate fixed or partly movable, never streptostylic.

The phyletic unity of this great division of reptiles and their descendants, the birds, admits of little or no doubt. In much probability they were derived from the single-arched type with the lateral opening, by the simple separation of the postorbital and squamosal from the parietal. Until recently it was confidently believed that the most primitive and oldest representative of the subclass was *Paleohatteria*, from the Lower Permian. In all probability, if not certainty, this form did not have the upper temporal opening, and must therefore be included in the more primitive group, the Theromorpha. At present the oldest known form referable to the subclass is *Youngina*, from the Upper Permian of Africa, an intermediate type peculiar in its retention of certain skull bones lost in all other members. It is, however, yet very imperfectly known. Doubtless many other forms from the Permian with these and yet other primitive characters await discovery.

12. ? ORDER PROTEROSUCHIA

Skull elongate, with palatal teeth; an antorbital vacuity. Skull only known.

[Triassic. *Proterosuchus* Broom, South Africa.]

13. ORDER "EOSUCHIA"

Family Younginidae. Skull with interparietals and tabulars (? supratemporals). Skull short; no antorbital vacuity[1]; probably with palatal teeth. Skeleton otherwise unknown.

Upper Permian. *Youngina* Broom, South Africa.

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[1] [An antorbital vacuity is present, according to Broom.—ED.]

A. SUPERORDER DIAPTOSAURIA

Teeth on some or all the palatal bones, acrodont or protacrodont. No antorbital opening; no interparietals or tabulars. Vertebrae amphicoelous. Dorsal ribs holocephalous, articulating in part or chiefly to centrum. Two or three sacral vertebrae. Fifth tarsale absent. Phalangeal formula never reduced. Parasternal ribs present.

In the absence of more complete information as to the structural details of some of the forms included under this group name, and in the differences of opinion, as usual, as to the value of the groups, the tribe or superorder Diaptosauria has a present use. Several groups formerly placed under it are now relegated to other divisions.

14. ORDER RHYNCHOCEPHALIA

Terrestrial or littoral lizard-like reptiles of small or moderate size. Palate primitive, with teeth on some or all the bones. Pectoral girdle complete. Dorsal ribs holocephalous, articulating in intercentral space and arch.

The three groups of reptiles here considered suborders are by some authors given a family rank, by others ordinal. Except the living *Sphenodon*, most of the genera are yet incompletely known. The differences between them seem hardly greater than among the Lacertilia with the inclusion of the Pythonomorpha.

A. SUBORDER RHYNCHOSAURIA

Skull more or less depressed and broad, with a strong, decurved, and edentulous beak, formed by the premaxillae. Temporal openings relatively large, their boundaries as in the Sphenodontia. No parietal foramen. Nares undivided. Palate with small interpterygoidal opening. Dorsal intercentra absent or unknown. About seven or eight cervicals and twenty-three presacrals; two sacrals. A small pubo-ischiatic vacuity. Humerus without epicondylar foramina.

A small group of terrestrial, perhaps in some cases subaquatic, shore-dwelling and shell-eating reptiles from three to six feet in length. The complete skull, tail, and mesopodials are known in none. In *Howesia* a distinct intermedium tarsus is figured; if not an error, it is the only known example among reptiles. The palatal teeth are confined to the palatines in two or three rows, save in *Howesia*, where they occur on the pterygoids only. However, the

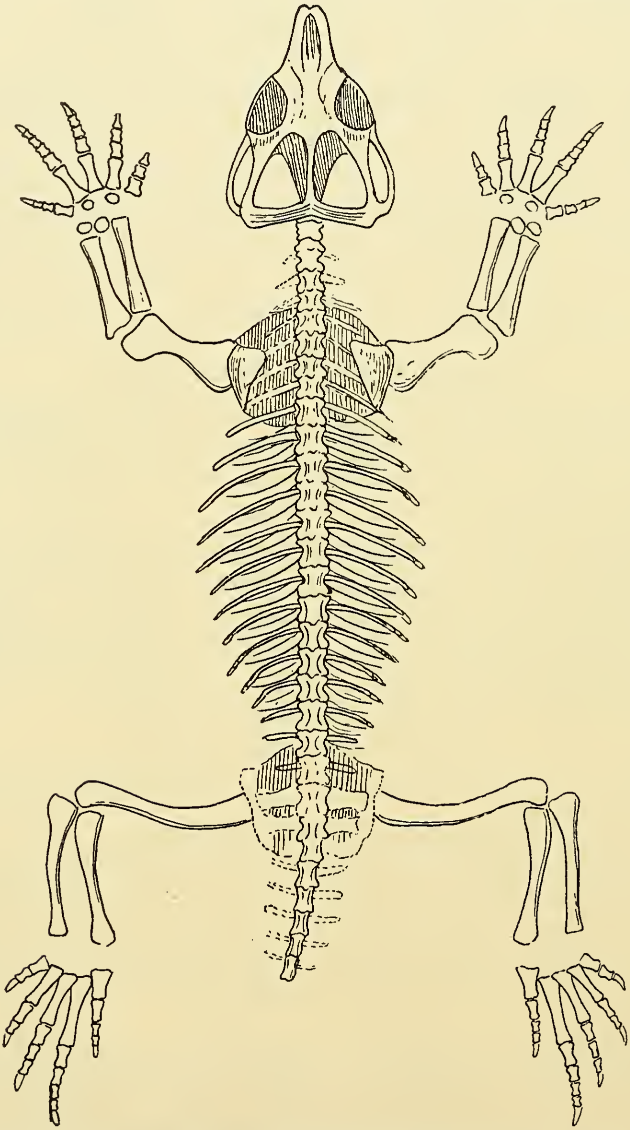

Fig. 185. Skeleton of *Rhynchosaurus* (Rhynchocephalia). After Woodward. Five sixteenths natural size.

anterior part of the skull of this genus is poorly known, and its immediate relationships with the other genera are still in doubt.

Upper Triassic. *Rhynchosaurus* Owen, England. *Hyperodapedon* Huxley, Scotland, India. *Stenometopon* Boulenger, Scotland. *Howesia* Broom, South Africa.

B. SUBORDER SPHENODONTIA (RHYNCHOCEPHALIA VERA)

Upper temporal opening bounded by parietal, squamosal, postfrontal, and postorbital. A single row of acrodont teeth on maxillae, dentaries, and palatines. Premaxillae with a decurved beak, usually with teeth. Frontals and parietals paired. No lacrimals. A parietal foramen. Humerus with an entepicondylar foramen, sometimes also with an ectepicondylar foramen. Pelvis with large pubo-ischiatic vacuity. Carpus primitive. Twenty-three to twenty-five presacral vertebrae, the neck with not more than eight. Parasternal ribs present.

Two genera only, the living *Sphenodon* and the Jurassic *Homœosaurus*, can be located with certainty in this suborder. *Sphenodon* has long enjoyed the reputation of being the most primitive of living reptiles, as evidenced by the persistent dorsal intercentra, deeply amphicoelous vertebrae, and the single-headed ribs of primitive type. So far as known *Homœosaurus* agrees closely, except that it has no uncinate process on the ribs, a character in which *Sphenodon* is almost unique among reptiles. Probably it has dorsal intercentra, but this remains to be determined. It has also no ectepicondylar foramen present in *Sphenodon*. *Palacrodon* and *Opisthias* are known only from mandibles. The former, however, is said to have teeth quite like those of *Ardeosaurus* which, according to Nopcsa, is a near relative of *Acrosaurus*. Nor is the temporal region of *Ardeosaurus* as well known as one could wish. *Brachyrhinodon* has two temporal arches, but is poorly known otherwise. Of *Eifelosaurus* the skull is wholly unknown.

Middle and Upper Triassic. ? *Eifelosaurus* Jaekel, ? *Polysphenodon* Jaekel, Germany. *Palacrodon* Broom, South Africa. *Brachyrhinodon* Huene, Scotland.

Upper Jurassic. *Homœosaurus*, v. Meyer, *Ardeosaurus* v. Meyer, Germany.[1]

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[1] [But cf. page 268 above. According to C. L. Camp (1923), *Ardeosaurus* is related to the geckos.— Ed.]

Lowermost Cretaceous. *Opisthias* Gilmore, Wyoming.
Recent. *Sphenodon* Gray, New Zealand.

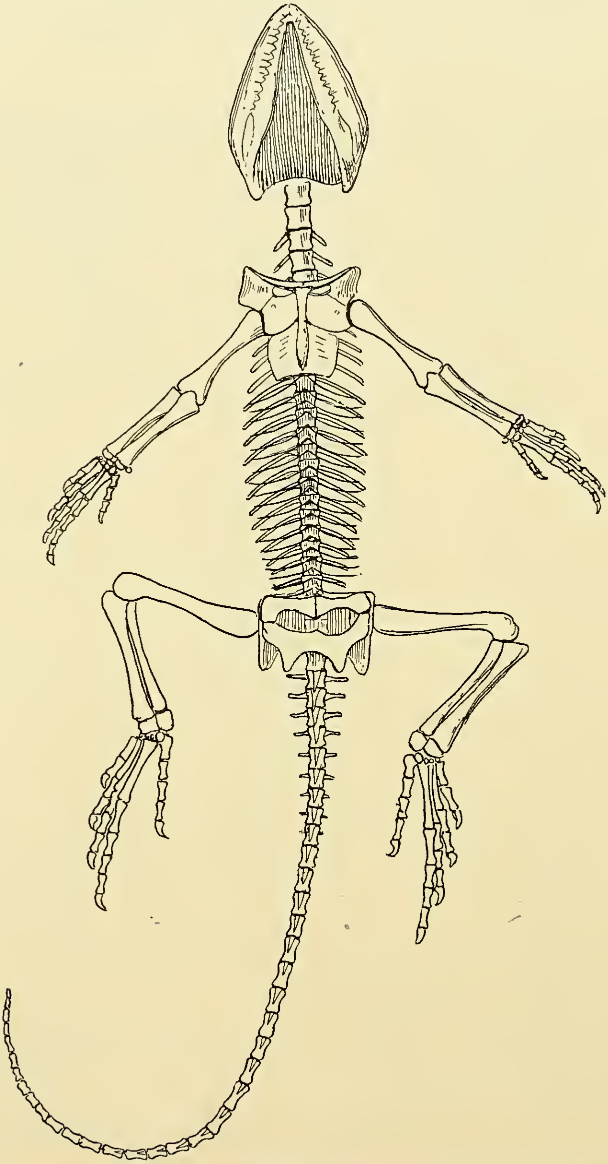

Fig. 186. Skeleton of *Homœosaurus* (Rhynchocephalia). After Lortet. Natural size.

C. SUBORDER CHORISTODERA

Elongate, subaquatic reptiles, with a very slender face, terminal undivided nares, with small teeth on all palatal bones. No parietal foramen. Internal nares posterior. Teeth labyrinthine in structure. Vertebrae shallowly amphicoelous without dorsal intercentra. Twenty-six presacral, two or three sacral, and a long, flattened tail. Dorsal ribs holocephalous, broad, and heavy. Parasternals stout. Pelvis without pubo-ischiatic opening. Humerus with ectepicondylar foramen. Mesopodials imperfectly known.

This small group of water reptiles, animals reaching a length of eight feet, is of interest because of the retention of several primitive characters, otherwise unknown in the Diapsida, especially the labyrinthine teeth and the absence of a pubo-ischiatic opening. The arrangement of the bones of the temporal region is doubtful. The legs are essentially terrestrial in structure, with but slight aquatic adaptations, but the heavy flattened ribs and the elongate flattened tail decisively indicate bottom-crawling aquatic habits. The relationships between the known genera are very close.

Uppermost Cretaceous and Paleocene. *Champsosaurus* Cope (*Nothosaurops* Leidy), North America. *Simœdosaurus* Gervais, France, Belgium.

D. ? SUBORDER THALATTOSAURIA

Marine reptiles with elongate face, posterior[ly placed external] nares, sclerotic plates, and paddle-like extremities. Premaxillary, anterior, mandibular, and pterygoidal teeth conical; those of the prevomers, and posterior part of maxillae and mandibles low-crowned. A parietal foramen. Vertebrae rather deeply biconcave; intercentra unknown. Dorsal ribs holocephalous, articulating chiefly with centra. Parasternal ribs slender. Humerus short, without foramina.

These small reptiles of but three or four feet in length are still imperfectly known; nor is it quite certain that they have two temporal openings. The upper opening occupies a peculiar position. The limbs, so far as known, resemble those of the mosasaurs. The habits of the thalattosaurs must have been similar to those of the mosasaurs; the dentition intermediate between that of the Mosasauridae and that of the Globidentidae.

Middle and Upper Triassic. *Thalattosaurus* Merriam, *Nectosaurus* Merriam, California.

AA. SUPERORDER ARCHOSAURIA

Dorsal ribs attached exclusively to the arch, at least anteriorly, by two articulations, the cervicals to arch and centrum. Usually an antorbital vacuity. The quadratojugal is well developed and usually enters the border of the lateral temporal opening. No parietal foramen, tabulars, or [dermo]supraoccipitals, and doubtfully, [if] ever, the interparietals. Teeth thecodont, confined to jaws, rarely absent. Vertebrae never notochordal, nor the dorsal intercentra persistent.

15. ORDER PARASUCHIA

From small to rather large, crawling or leaping reptiles, characterized especially by the normal pelvis, absence of a secondary palate, and a large antorbital opening. Body usually with dermal armor. Roof bones of skull always paired; postfrontals present. Vertebrae amphicoelous or platycoelous. Clavicles and interclavicle present, the corocoid not elongate. Parasternal ribs generally present. Mesopodials imperfectly known; phalanges not reduced.

The Parasuchia in the present sense were long united with the Crocodilia as two suborders, the Parasuchia, *sens. str.*, and the Pseudosuchia or Aetosauria, but the marked differences in skull and pelvis justify their ordinal separation. By some authors the three suborders here recognized are each given ordinal rank. Sclerotic plates are known in a single genus of Pseudosuchia.

A. SUBORDER PSEUDOSUCHIA

Typically a group of small, slender, climbing or leaping reptiles with more or less elongated hind legs. The external and internal nares are near the extremity of the more or less pointed skull; the lateral orbits are large, as are also the antorbital openings. The epipodials are long, the clavicles and interclavicle slender.

None of the forms referred to this suborder is completely known, and among the known forms there is a considerable diversity of structure, some departing so widely, perhaps, that their location here is provisional. Of the more typical, *Scleromochlus* has no dermal armor, and *Euparkeria* alone has sclerotic plates; the latter has been accredited with an interparietal bone.

With the inclusion of the doubtful forms there are but few constant characters to distinguish the group from the Rhynchocephalia; typically, however, the absence of palatal teeth, and the attachment of the dorsal ribs are decisive. As a whole, however, the group is one of wide genetic possibilities and [may] have had a close genealogical relationship with all the other members of the Archosauria, and especially the Saurischia. Nearly every known genus has been accredited with family rank.

FAMILY AETOSAURIDAE. Twenty-five presacrals; two sacrals. Humerus a little longer than radius and ulna; hind legs a half longer than the front. Dorsal scutes transversely elongate, covering the whole back; abdomen with small plates.

Triassic. *Aetosaurus* Fraas, *Dyoplax* Fraas, Germany. *Stegomus* Marsh, Connecticut.

FAMILY ORNITHOSUCHIDAE. Scapula slender, coracoid short and broad. Legs very slender, the epipodials a little longer than the propodials. Two rows of dermal plates, each longer than broad.

Euparkeria is accredited with an interparietal, the only member of the group.

Triassic. *Ornithosuchus* Newton, ? *Erpetosuchus* Newton, England. *Euparkeria* Broom, *Sphenosuchus* Haughton, South Africa.

FAMILY SCLEROMOCHLIDAE. Premaxillae united. Twenty-one presacrals, three sacrals. Scapulae slender, coracoid long. Pubes long and slender, expanded at extremity; calcaneum with tuberosity; feet as long as tibia, the epipodials longer than propodials. Slender parasternal ribs. No dermal armor.

Triassic. *Scleromochlus* Woodward, England.

B. SUBORDER PELYCOSIMIA

Large, heavily built, terrestrial or marsh reptiles. External and internal nares near extremity of triangular skull. Antorbital openings large, the orbits relatively small. Upper temporal opening not depressed below level of [parietals]. Palatines approximated or contiguous, without respiratory canal. Teeth compressed, curved, and sharply pointed. Legs short and rather stout.

This group, proposed as a separate order, is based almost exclusively upon *Erythrosuchus*. In the structure of the skull it is somewhat intermediate between the Pseudosuchia and the Phytosauria.

Triassic. *Erythrosuchus* Broom, South Africa. ? *Scaponyx* Woodward, South America.

C. SUBORDER PHYTOSAURIA

Large, crawling, subaquatic reptiles, reaching a length of twenty or more feet, especially characterized by the elongate face, composed chiefly of the premaxillae, the posterior nares, and the deep respiratory canal, formed by the underarching of the palatines. Skull rugose, the lateral, temporal, and antorbital openings large, the supratemporal opening small and more or less depressed below the plane of the parietals. Tip of premaxillae decurved, with two or three very long, cylindrical teeth on each. Teeth either cylindrical throughout, or the posterior ones more or less flattened and separated. Neck, body, and tail covered with four or more rows of strong dermal bones; the pectoral region and abdomen with smaller, bony scutes. Tail long and flattened, compressed. Feet probably webbed. Vertebrae platycoelous; two sacrals.

FAMILY PHYTOSAURIDAE. Ilium with postacetabular process; pubis not dilated at extremity.

Triassic. *Phytosaurus* Jaeger, *Mystriosuchus* Fraas, *Mesorhinus* Jaekel, Germany. *Parasuchus* Lydekker, India. *Paleorhinus* Williston, *Angistorhinus* Mehl, *Lophoprosopus* Mehl, Rocky Mts. *Rutiodon* Emmons (*Rhytidodon*), Carolina, New York, Connecticut.

FAMILY STAGONOLEPIDAE. A supracoracoid foramen. Ilium without postacetabular process; pubes dilated at extremity.

Triassic. *Stagonolepis* Huxley, England.

[D. SUBORDER DESMATOSUCHIA]

[Large, long-tailed reptiles reaching a length of perhaps sixteen feet, especially characterized by the probably secondary absence of the upper temporal opening. Cervical and anterior dorsal bony plates bearing long horn-like outgrowths. Skull with large antorbital opening and dorsal anterior nares, snout not greatly produced. Teeth thecodont. Distinguished from the Phytosauria especially by the absence of the upper temporal opening, which may have been secondarily lost as in the caimans. Von Huene refers *Desmatosuchus* to the Phytosauria.

Triassic. *Desmatosuchus* Case, Texas.]

16. ORDER CROCODILIA[1]

[Loricata]

Internal nares carried far back in the mouth by the union of the maxillae and palatines, and in the later forms the pterygoids also. Premaxillae never much elongate, the external nares terminal. Acetabulum formed by ilium and ischium only, the so-called pubes (? prepubes) excluded and not meeting in a median symphysis. Phalanges of fourth and fifth digits reduced; calcaneum elongate. Two sacral vertebrae.

The Crocodilia are at once distinguished from all other reptiles by the structure of the palate and pelvis. There is not a very great diversity of structure among the known forms. All are lizard-like in form, with a long, flattened tail, very predaceous, with conical thecodont teeth, and more or less water-loving in habit. In size they vary from less than one foot to about fifty feet in length. The vertebrae were platycoelous in all till about the beginning of the Lower Cretaceous; procoelous in all since the early part of the Eocene. Some have a relatively broad skull; others a more or less elongated face, sometimes very slender, as in the ancient teleosaurs and the modern gavials. In such forms the nasals do not reach the external nares, and the splenials meet in a symphysis. The upper temporal openings in the modern forms are smaller, very small in the broad-faced types. In the early types the arch between the orbit and lateral temporal opening was covered immediately by the skin; since Wealden times the bar is more cylindrical and more deeply placed. The amphibious crocodiles have a strong dermal, osseous armor along the back and tail, sometimes also on the under side. Both the carpus and tarsus are peculiarly modified, suggesting, v. Huene thinks, a primitive, more upright-walking gait.

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[1] [For recent morphological and taxonomic treatment of the Crocodilia, see numerous papers by C. C. Mook, 1921–, *Bulletin*, Amer. Mus. Nat. Hist.—Ed.]

A. SUBORDER EUSUCHIA

An antorbital opening primitively present but lost in many ancient and all modern forms. Mandible with an external vacuity posteriorly. Nine cervical vertebrae, twenty-three or twenty-four presacrals. No sclerotic plates in orbits. Body with dermal bones. Feet partly webbed, clawed, not paddle-like.

Until within recent years, and still by some authors, the Eusuchia comprised only those crocodilians with procoelous vertebrae, amphicoelian forms comprised in the suborder Mesosuchia. It is now known that the change in the form of the vertebrae was a relatively unimportant one and may have occurred in different lines of descent.

FAMILY TELEOSAURIDAE. Vertebrae platycoelous. Internal nares large, situated at posterior end of palatines. Face very long and slender. An antorbital opening sometimes present. Postorbital bar not modified. Upper temporal opening large. A nearly complete dermal armor. Front feet much smaller than hind. From two to ten feet in length.

Jurassic. *Pelagosaurus* Bronn, *Teleosaurus* Geoffroy, *Teleidosaurus* Deslongchamps, *Suchodus* Lydekker, *Aeolodon* Meyer, *Crocodilemus* Jourdan, *Gnathosaurus* Münster, Europe. *Steneosaurus* Geoffroy, Europe, Madagascar.

Cretaceous. ? *Teleorhinus* Osborn, Wyoming.

FAMILY PHOLIDOSAURIDAE. Vertebrae platycoelous. Internal nares opening in palatines and pterygoids. Face long; the nasals reach to the premaxillae. Upper temporal opening smaller than orbits. Postorbital bar modified. Front legs larger than in the Teleosauridae. Dorsal and ventral armor present.

Upper Jura and Lowermost Cretaceous. *Pholidosaurus* Meyer (*Macrorhynchus*), *Pterosuchus* Owen, Europe.

FAMILY ATOPOSAURIDAE. Vertebrae platycoelous. Posterior nares not reaching pterygoids. Head short, broad. Upper temporal openings much smaller than orbits. Dermal armor composed of two rows of quadrilateral plates, probably extending on tail. Probably no ventral scutes. Tail long. Small reptiles from eight to sixteen inches in length.

Upper Jurassic. *Atoposaurus* Meyer, *Alligatorellus* Jourdan, *Alligatorium* Lortet, Germany.

Family Goniopholidae. Vertebrae platycoelous. Internal nares bounded by pterygoids and palatines. Face rather broad, not long. Postorbital bar subdermal. A dorsal armor of two or more rows of plates.

Lowermost Cretaceous. *Goniopholis* Owen, Europe, North and South America. *Nannosuchus* Owen, *Theriosuchus* Owen, *Machimosaurus* Meyer, *Bernissartia* Dollo, Europe.

Upper Cretaceous. *Coelosuchus* Williston, *Teleorhinus* Osborn, Wyoming. *Notosuchus* Woodward, *Cynodontosuchus* Woodward, South America.

Family Dyrosauridae. Vertebrae platycoelous; internal nares between palatines and pterygoids. Face very slender. Postorbital bar subdermal. From fifteen to eighteen feet in length.

Lower Eocene. *Dyrosaurus* Pomel, Africa.

Family Hylaeochampsidae. Vertebrae probably procoelous. Internal nares surrounded by pterygoids. Palate with large foramen between ectopterygoid and maxillae. Skull short, broad.

Wealden Cretaceous. *Hylœochampsa* Owen, ?*Heterosuchus* Seeley, England.

Family Gavialidae. Vertebrae procoelous. Posterior nares surrounded by pterygoids. Face very slender. Postorbital bar subdermal. Upper temporal openings large. Nasals remote from nares. Dorsal but no ventral scutes. From ten to fifty feet in length.

Pleistocene, Recent. *Gavialis* Oppel, *Rhamphosuchus* Owen, *Paleosuchus* Falconer and Cautley, India.

Family Tomistomidae. Vertebrae procoelous. Posterior nares surrounded by pterygoids. Face less elongated, gradually merging into cranium. Postorbital bar subdermal. Nasals extend into nares. Sometimes an antorbital opening. From six to forty or more feet in length.

Upper Cretaceous. *Thoracosaurus* Leidy, *Holops* Cope, United States.

Eocene. [*Tomistoma*, Europe, Africa.] *Eosuchus* Dollo, Belgium.

Pliocene. *Tomistoma* (?) [*Gavialosuchus*], Florida.

Pleistocene. *Tomistoma*, Hungary.

Recent. *Tomistoma*, Borneo.

Tertiary. *Leptorhamphus* Ameghino, *Oxydontosaurus* Ameghino, Argentina.

FAMILY CROCODILIDAE.[1] Vertebrae procoelous. Posterior nares surrounded by pterygoids, single or divided. Upper temporal openings small. Postorbital bar subdermal. Face never slender. Teeth stout, anisodont. Dorsal plates in two or more rows, the ventral armor present or absent. The nasals usually reach the external nares. From four or five to more than forty feet in length.

Uppermost Cretaceous. *Deinosuchus* Holland, *Bottosaurus* Leidy [Agassiz], *Brachychampsa* Gilmore, *Leidyosuchus* Lambe, ? *Polydectes* Cope, North America. *Crocodilus* Laurenti, Italy.

Eocene. *Crocodilus* Laurenti, *Diplocynodon* Pomel, Europe, North America. *Limnosaurus* Marsh, North America.

Oligocene. *Caimanoidea* Mehl, South Dakota.

Miocene. "*Crocodilus*" [?], [*Alligator*], North America.

Pleistocene. *Crocodilus* Laurenti, Europe, India, Africa, North America. [*Alligator*, North America.]

[Recent. *Crocodilus*, *Osteolaemus*, *Osteoblepharon*, *Alligator*, *Caiman*, *Jacare*.]

INCERTAE SEDIS. Lower Jurassic. *Notochampsa* Broom, South Africa.

B. SUBORDER THALATTOSUCHIA

Marine crocodiles, without bony armor, and with limbs more or less modified as paddles, without claws. Vertebrae platycoelous. Face more or less elongated. Nares at posterior end of palatines. Prefrontals large, protuberant. Supratemporal openings large. Bones of skull smooth. Orbits with sclerotic plates. No antorbital or mandibular openings. Seven cervical, twenty-five presacral, vertebrae. Tail long, with distal fin-like dilatation.

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[1] [Williston here includes the genera *Alligator* and *Caiman* under the Crocodilidae, and places *Tomistoma* in a separate family, but Mook (*op. cit.*) has shown that *Alligator*, *Caiman*, and *Jacare* are more distinct from *Crocodilus* and its allies (*Osteolaemus*, *Osteoblepharon*) than is *Tomistoma*. — ED.]

FAMILY METRIORHYNCHIDAE.

Upper Jurassic. *Dacosaurus* Quenstedt, *Geosaurus* Cuvier, Europe. *Metriorhynchus* Quenstedt, Europe, Patagonia.

Lowermost Cretaceous. *Neustosaurus* Raspail, ? *Enaliosuchus* Dollo, Europe.

[DINOSAURIA]

17. ORDER SAURISCHIA

More or less upright-walking reptiles. The normal pubes and ischia meet in a ventral symphysis, the acetabulum perforated. No predentary or rostral bones. One or more antorbital openings. No dermal bones.

A. SUBORDER THEROPODA

Carnivorous or secondarily herbivorous in habit. More or less bipedal in gait, the hind feet more or less digitigrade, the front legs more or less reduced. Pubes meeting in a long ventral symphysis, with a distal dilatation.

FAMILY PLATEOSAURIDAE. Teeth less compressed, not recurved and somewhat thickened, their anterior and posterior borders denticulated. Anterior vertebrae platycoelous; twenty-three presacrals, three sacrals. Front legs a little longer than the femora, preaxonic, their phalangeal formula 2, 3, 4, 5, (?), the first claw large. Hind feet more mesaxonic, the first and fifth toes reduced. Feet digitigrade or semiplantigrade. Astragalus without ascending process.

Upper Triassic. *Plateosaurus* Meyer, *Gressylosaurus* Rütimeyer, *Pachysaurus* Huene, *Teratosaurus* Meyer, Europe. *Euskelosaurus* Huxley, *Gryponyx* Broom, South Africa.

This, the most primitive family of the Theropoda, is thought by some to have an ancestral relationship with the Sauropoda. The characters drawn chiefly from *Plateosaurus* may not and probably do not apply to all the genera listed in the family. The reptiles were clearly bipedal in gait, though of rather heavy build. Jaekel thinks that the hind feet were purely plantigrade, but this was improbable since the mesaxonic structure distinctly indicates the elevation of the ankle from the ground. *Plateosaurus* attained a length of about fifteen feet.

Family Anchisauridae. Smaller and more slender theropods. Vertebrae amphicoelous. Teeth compressed, more or less recurved. Astragalus without ascending process.

Upper Triassic. *Anchisaurus* Marsh, *Megadactylus* Hitchcock, *Ammosaurus* Marsh, Connecticut Valley. *Thecodontosaurus* Riley and Stutchbury, England, Africa, Australia. *Massospondylus* Owen, South Africa. *Zanclodon* Plieninger, *Sellosaurus* Huene, Europe.

[No MS. was found for (1) the Coelurosauria, containing several families and numerous genera of light-limbed saurischian dinosaurs, including the Ornithomimidae, (2) the Megalosauria group of the Jurassic, and (3) the Deinodont group of the Cretaceous. For group 1 see papers by Osborn 1917 (*Bulletin*, Amer. Mus. Nat. Hist., vol. XLIII), von Huene 1921 (*Acta Zoölogica*, Bd. II); for groups 2 and 3 see Matthew and Brown, 1922 (*Bulletin*, Amer. Mus. Nat. Hist., vol. XLVI). — Ed.]

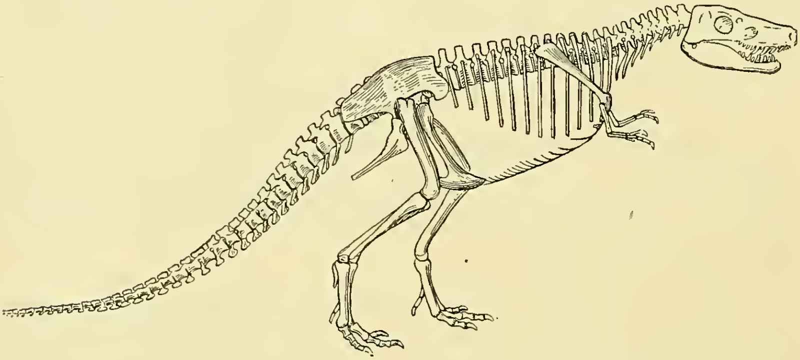

Fig. 187. Skeleton of *Gorgosaurus* (Saurischia). After Lambe. One thirty-sixth natural size.

B. Suborder Sauropoda (Opisthocoelia, Cetiosauria)

Quadrupedal, semiplantigrade, herbivorous dinosaurs, with long neck and tail and small skull. Postfrontal sometimes present. Teeth subcylindrical, with a thickened, spoon-shaped crown, in a single row, and more or less restricted to anterior part of jaws, the premaxillae with teeth; no predentary. No coronoid process to mandible. The anterior, sometimes all, presacral vertebrae opisthocoelous, with a more or less developed hyposphene-hypantrum articulation, and with hollow, lateral cavities in centra. Four or five sacrals, twenty-six or twenty-seven presacrals. The pubes are massive and meet in a large ventral symphysis. Carpals and tarsals reduced, feet preaxial. Limb bones cancellous in structure. From about fifteen to about ninety feet in length.

Family Cetiosauridae. Spines of dorsal vertebrae simple, not furcate. Front limbs as long as the hind. Scapulae dilated distally. Pubes not constricted.

Upper Jurassic. *Cetiosaurus* Owen (*Cardiodon* Owen), England.

Lower Cretaceous (Morrison). *Haplacanthosaurus* Hatcher, *Brachiosaurus* Riggs, Rocky Mts. *Gigantosaurus* Fraas (non Seeley), (? *Brachiosaurus* Riggs), South Africa. *Pelorosaurus* Mantell, Europe, Madagascar.

Family Camarasauridae. Spines of dorsal vertebrae furcate. Front limbs distinctly shorter than hind. Scapulae distally expanded. Ischia slender.

Lower Cretaceous. *Camarasaurus* Cope (*Morosaurus* Marsh), *Pleurocoelus* Marsh, North America. *Titanosaurus* Lydekker, Europe, Madagascar, India.

Upper Cretaceous. *Titanosaurus* Lydekker, France, Patagonia.

Family Atlantosauridae. Spines of presacral vertebrae furcate. Front legs much shorter than hind. Scapulae narrow distally. Ischia expanded at extremity.

Lower Cretaceous (Morrison). *Atlantosaurus* Marsh, *Apatosaurus* Marsh (*Brontosaurus* Marsh), *Amphicoelias* Cope, Rocky Mts.[1]

Family Diplodocidae. Spines of presacral vertebrae furcate. Front legs shorter than hind. Teeth slender, confined to anterior part of jaws. External nares near top of skull, remote from extremity. Ischia not expanded distally, the pubes constricted in middle. More slender sauropods.

Lower Cretaceous (Morrison). *Diplodocus* Marsh, Rocky Mts.

Genera Incertae Sedis: ? Jurassic., *Dystrophaeus* Cope, Rocky Mts.

Upper Jura and Wealden. *Bothriospondylus* Mantell, *Chondrosteus* Owen, *Chondrosteosaurus* Owen, *Eucamerotus* Hulke, *Ischyrosaurus*

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[1] [Belongs in Diplodocidae.—Osborn and Mook.]

Hulke, *Nesodon* Mousaye, *Oplosaurus* Gervais, *Ornithopsis* Seeley, Europe.

Lower Cretaceous (Morrison). *Barosaurus* Marsh,[1] *Caulodon* Cope,[2] *Elosaurus* Peterson and Gilmore, *Epanterias* Cope, *Symphyrophus* Cope, ? *Astrodon* Leidy, Rocky Mts.

Lower Cretaceous. *Dinodocus* Owen, *Hypselosaurus* Matheron, *Aepysaurus* Gervais, *Morinosaurus* Sauvage, Europe.

Algaosaurus Broom, South Africa.

Upper Cretaceous. *Argyrosaurus* Lydekker, *Microcoelus* Lydekker, South America.

18. ORDER ORNITHISCHIA

[ORTHOPODA, PREDENTATA]

Quadrupedal or bipedal dinosaurs, especially characterized by the presence of a predentary bone in the mandible and by the structure of the pelvis. Premaxillae rarely with teeth. Antorbital openings small or absent. Vertebrae amphicoelous or amphiplatyan, the anterior ones often opisthocoelous. Pubes not meeting in a median symphysis, with an anterior, more or less spatulate, *prepubis*, and a posterior, usually long, *postpubis*, underlying the ischium. Front limbs always shorter than hind, never functionally pentadactylate, rarely with as many as four phalanges in any digit. Hind limbs usually functionally tridactylate, more or less digitigrade. Ungual phalanges short and broad.

A. SUBORDER ORNITHOPODA

Bipedal in habit, digitigrade. External nares near extremity of face, divided. Postpubis complete, slender. Antorbital opening sometimes small.

FAMILY NANOSAURIDAE. Premaxillae edentulous. Teeth in a single row, compressed and pointed. Vertebrae amphicoelous; three sacrals. Femur shorter than tibia. Bones very hollow. Of the size of a cat.

Lower Jurassic. *Nanosaurus* Marsh, Colorado.

FAMILY HYPSILOPHODONTIDAE. Premaxillae with teeth. Teeth in a single row. Anterior vertebrae opisthocoelous. Femur longer than

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[1] [Belongs in the Diplodocidae. — Lull.]

[2] [Belongs in the Camarasauridae. — Osborn and Mook.]

tibia. Body covered with dermal ossifications. Five sacral vertebrae. Manus with five, the pes with four, digits, the fifth vestigial.

Wealden. *Hypsilophodon* Hulke, England.

FAMILY IGUANODONTIDAE. Premaxillae edentulous. Teeth in a single row. Anterior vertebrae platycoelous or opisthocoelous. No dermal ossifications. Four or five sacral vertebrae. Femur longer or shorter than tibia. Four functional fingers, three functional toes.

This family has been sometimes divided into three, the Laosauridae with platycoelous vertebrae, the Camptosauridae, and Iguanodontidae with opisthocoelous vertebrae; but the differences seem to be of minor importance.

The *Scelosaurus*, though its teeth are unknown, has been located with the Hypsilophodontidae. Its vertebrae are plano-concave or nearly amphiplatyan. It is the latest of known Ornithopoda and may eventually, perhaps, find its proper location in a distinct family.

Lower Cretaceous (Morrison, Wealden). *Camptosaurus* Marsh, *Laosaurus* Marsh, Rocky Mts. *Iguanodon* Mantell, England.

FAMILY TRACHODONTIDAE. (HADROSAURIDAE.) Teeth in many rows, forming a tessellated pavement in use. Premaxillae edentulous. Cranium often with crest. Extremity of face more or less dilated. Cervical vertebrae opisthocoelous, about fifteen in number; seven or eight sacrals. Tail flattened. Femur longer than tibia; phalanges reduced; four functional fingers and three functional toes. Subaquatic in habit; sclerotic plates in orbits.

Upper Cretaceous. *Cheneosaurus* Lambe, *Claosaurus* Marsh, *Hadrosaurus* Leidy, *Hypacrosaurus* Brown, *Kritosaurus* Brown, *Gryposaurus* Lambe, *Prosaurolophus* Brown, *Saurolophus* Brown, *Stephanosaurus* Lambe, *Corythrosaurus* Brown, *Trachodon* Leidy.

B. SUBORDER STEGOSAURIA

[Quadrupedal, with dermal armor of plates and spines; skull small; bones solid. Jurassic to close of Cretaceous. No MS.]

C. SUBORDER CERATOPSIA

Secondarily quadrupedal dinosaurs, with large skull, armed with horns and protuberances, located on nasal, postorbitals, and the margin of a greatly extended "frill" or extension of the skull over the neck. Lateral temporal openings small. Teeth with divided roots in a single functional row. No teeth on premaxillae, the upper jaws terminating in a distinct "rostral" bone. Vertebrae platycoelous, the first three or four cervicals coössified. Sacrum composed of numerous vertebrae. Ilium with long preacetabular and postacetabular process. Ischium slender, curved, the postpubis more or less vestigial. Carpus and tarsus reduced, but two carpalia. Astragalus firmly united with tibia, the calcaneum free; fifth toe vestigial.

Uppermost Cretaceous. *Anchiceratops* Brown, *Brachyceratops* Gilmore, *Ceratops* Marsh, *Chasmosaurus* Lambe, *Centrosaurus* Lambe, *Diceratops* Lull, *Eoceratops* Lambe, *Leptoceratops* Brown, *Monoclonius* Cope, *Triceratops* Marsh, *Styracosaurus* Lambe, *Torosaurus* Marsh, *Agathaumas* Cope, Western North America.

19. ORDER PTEROSAURIA

Volant reptiles with highly ossified, pneumatic skeleton. Skull elongated, more or less pointed, the external nares remote from the tip. No parietal foramen. Orbits with sclerotic plates. Neck elongate; eight or nine cervicals, ten or more dorsals, four to ten sacrals, and about twelve to forty caudals; the presacrals procoelous, the caudals amphicoelous. No supracoracoid foramen, clavicles, or interclavicle. Sternum large, well ossified; parasternals present. Humerus shorter than forearm, with large lateral process; carpus more or less reduced; a pteroid bone articulating with carpus. First three fingers small, with claws; fourth greatly elongated for support of patagium; fifth digit absent. Prepubes articulating with pelvis. Femora shorter than tibia; fibula reduced or absent; first tarsal row more or less fused with tibia; feet long, pentadactylate, the fifth toe more or less reduced.

A. SUBORDER PTERODERMATA (RHAMPHORHYNCHOIDEA)

Antorbital opening distinct. Jaws with teeth. Prevomers and internal nares distinct. Orbits large. Free cervical ribs sometimes present. Tail long, with a terminal dilatation. Metacarpals less than half the length of the forearm, articulating with carpus. Fibula present; fifth toe complete.

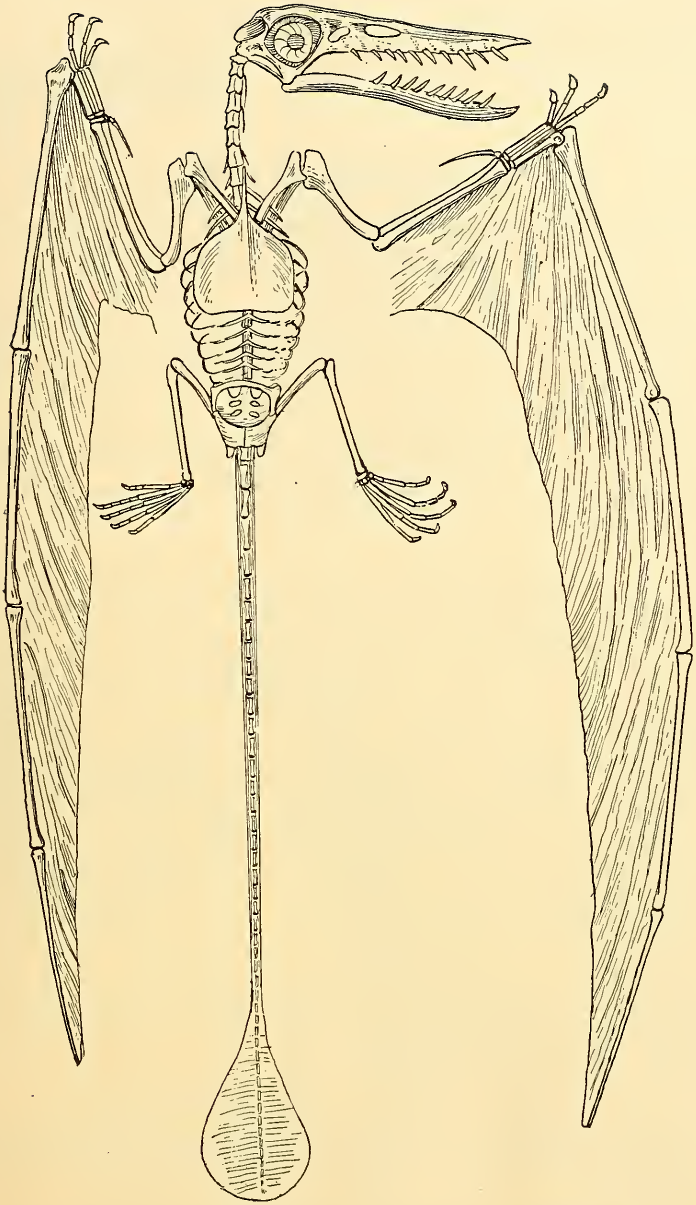

FIG. 188. Skeleton of *Rhamphorhynchus* (Pterosauria). One third natural size.

Family Rhamphorhynchidae.

Jurassic. *Rhamphorhynchus* Meyer, *Scaphognathus* Wagner, *Dimorphodon* Meyer, *Dorygnathus* Orpel, *Campylognathus* Plieninger, Europe.

B. Suborder Pterodactyloidea

Wing metacarpal, longer or but little shorter than forearm. Tail very short. No cervical ribs. Fifth toe more or less reduced.

Family Pterodactylidae. Nares and antorbital vacuity more or less coalescent. Teeth in anterior part of jaws. Anterior dorsal vertebrae not fused. All metacarpals articulating with carpus. Prepubes not band-like. Smaller.

Upper Jurassic. *Pterodactylus* Cuvier (*Ornithocephalus* Sommerring, *Diopecephalus* Seeley, *Cycnorhamphus* Seeley, *Pterodracon* Lydekker), Europe.

Family Ornithocheiridae. Skull more elongate. A supraoccipital crest. Scapula with enlarged distal end articulating with notarium. Jaws with teeth in front. Skeleton imperfectly known.

Wealden. *Ornithocheirus* Seeley, *Ornithodesmus* Seeley, England.

Family Pteranodontidae. Skull much elongated, toothless. A long supraoccipital crest. Orbits small. No antorbital opening. No fibula; fifth toe without phalanges. First three metacarpals splint-like. Upper end of scapula articulating with notarium. Prepubes band-like. From twelve to twenty-five feet in expanse of wings.

Upper Cretaceous. *Pteranodon* Marsh, North America. *Ornithostoma* (? *Pteranodon*) Seeley, England.

Family Nyctosauridae. Like the Pteranodontidae, but no occipital crest, and the upper end of scapula flat, not articulating with notarium. Eight-foot wing expanse.

Cretaceous. *Nyctosaurus* (*Nyctodactylus*) Marsh, Kansas.

Genera Incertae Sedis. *Doratorhynchus* Seeley, *Paleornis* Mantell, England.

Lower Cretaceous. *Dermodactylus* Marsh, Wyoming.

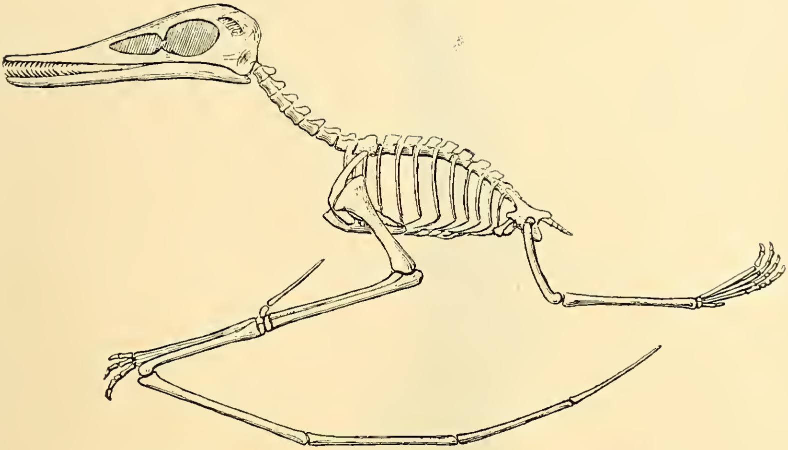

FIG. 189. Skeleton of *Pterodactylus*. Four thirds natural size.

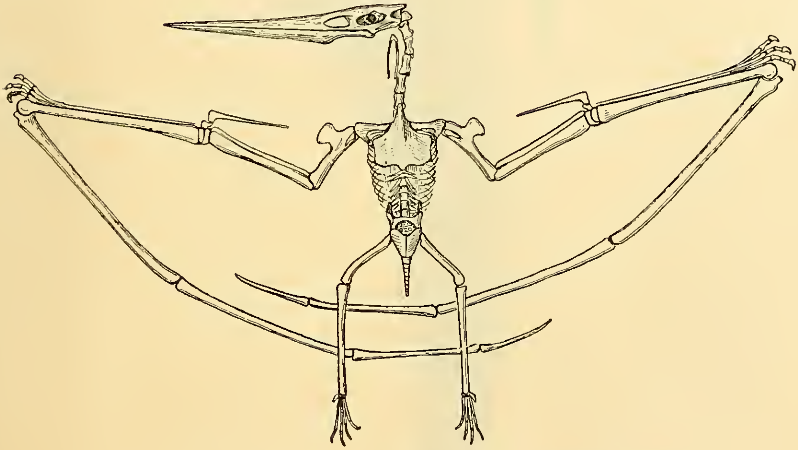

FIG. 190. Skeleton of *Nyctosaurus* (Pterosauria). One eighth natural size.

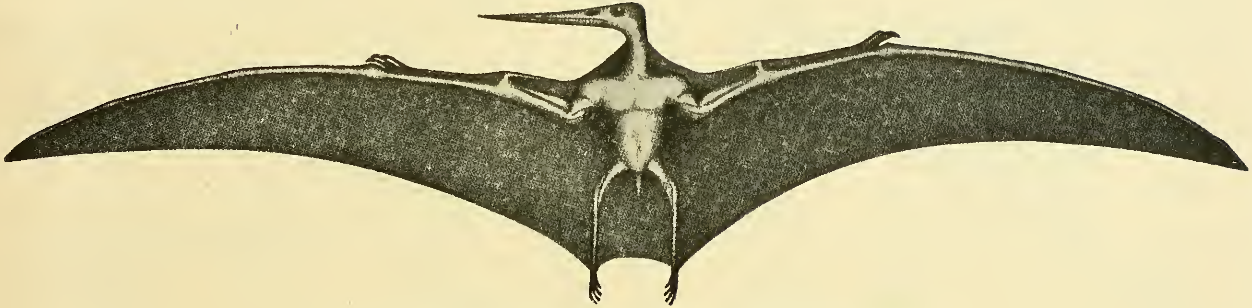

FIG. 191. Restoration of *Nyctosaurus* (Pterosauria) by Herrick E. Wilson.