# MEMOIRS

OF THE

# American Museum of Natural History.

VOLUME I, PART VIII.

The Reptilian Subclasses Diapsida and Synapsida and the Early History of the Diaptosauria.

By HENRY FAIRFIELD OSBORN.

WITH CONTENTS AND INDEX TO VOLUME I.

November, 1903.

The Knickerbocker Press, Rew York

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#### INTRODUCTION.

In the course of a series of annual lectures in Columbia University upon the Evolution of the Vertebrates, which I am now collecting for publication in condensed book form, the ideas which are developed in this memoir have been gradually forming. I enjoyed several discussions on reptilian descent with the

late Professor George Baur, who always seemed to me to be nearer the truth and more logical in his theories than the late Professor Edward D. Cope whose classifications were based too largely on single characters. The comprehensive treatise of Professor Carl von Zittel has been of the greatest service in the study of the reptiles, as well as the more recent and more condensed treatise of another friend, Dr. Arthur Smith Woodward. After this memoir had been practically completed I fortunately learned through Franz Baron Nopcsa of the important recent papers of Dr. R. Broom, and I received some of these papers from the author in time to incorporate part of his work in the present memoir; especially that on the homologies of the vomer and prevomer, which tends to confirm rather than disprove the theory of the division of the Reptilia into subclasses; also his surprising demonstration of the actual affinity of *Procolophon* to the Rhynchocephalia rather than to the Cotylosauria. I am greatly indebted to Dr. J. H. McGregor and Mr. W. K. Gregory for assistance in the preparation of this memoir.

# PART I.—THE PRIMARY DIVISION OF THE REPTILIA INTO TWO SUBCLASSES, SYNAPSIDA AND DIAPSIDA.

The classification and phylogeny of the Reptilia is at present in very great confusion. It appears that Cope was less logical in his arrangement of the reptilian orders than in that of any other group of vertebrates: his 'Archosauria' will have to be abandoned; his 'Theromorpha,' as Baur showed, was founded upon a misconception and must be totally eliminated from classification. The impression left by the masterly writings of Baur was that the Reptilia all traced their origin back through a primitive *Sphenodon*-like form or 'Proganosaurian,' to the Cotylosauria. This is certainly an error, because many reptiles never passed through a 'proganosaur' or rhynchocephalian stage.

None the less, Cope and Baur have been, more or less unconsciously, among the leading contributors toward a movement or tendency which appears to result in the separation of the Reptilia into two great groups phylogenetically distinct. The steps in this movement may now be briefly outlined.

#### I. OUTLINE OF RECENT HISTORY OF CLASSIFICATION.

(1) In 1867 there began a tendency to classify the Reptilia by the structure of the temporal region of the skull. In that year Günther showed that the Rhynchocephalia differ from the Squamata (Lacertilia, Mosasauria, Ophidia) in the possession of both upper and lower temporal arches, the Squamata retaining only the upper arch.

<sup>&</sup>lt;sup>1</sup> Günther, A. C. Contribution to the Anatomy of *Hatteria* (*Rhynchocephalus* Owen). Philos. Trans. Roy. Soc., London, CLVII, pp. 595-629, 1867.

- (2) The Term Archosauria Invalid.—In 1869 Cope 1 originally defined Archosauria to correspond with the Monimostylica of Müller exclusive of the Testudinata, to include reptiles in which there was a close sutural attachment of the quadrate, typified and defined by the condition in Nothosaurus, a primitive Sauropterygian, but including also the Crocodilia, Thecodontia, Dinosauria, Anomodontia, Rhynchocephalia,—a totally unnatural grouping based upon a single primitive character, the fixed quadrate, with no mention whatever of the temporal arches. The fixed quadrate is obviously the primitive condition, streptostyly being dependent on the reduction of one or both temporal arcades.<sup>2</sup> The Plesiosaurs and Anomodonts are, as we now know, distinguished by a single infratemporal arch composed of the two arches closely conjoined or not yet separated. Cope was, therefore, not at liberty afterward <sup>8</sup> to exclude the typical Plesiosaurs and the Anomodonts and redefine the term "Archosauria" to include the fundamentally distinct open or two-arched types, Rhynchocephalia, Dinosauria, Phytosauria, and Crocodilia.
- (3) The Term Theromorpha Invalid.—In 1878 Cope 4 proposed to include the Anomodontia Owen and Pelycosauria Cope in a new superorder THERO-MORPHA, a term which still exerts a baneful influence in classification, for, as Baur and Case have shown, the Pelycosauria are specialized Sphenodon-like animals totally unrelated to the Anomodontia.

The only proper term for the mammal-like reptiles is Anomodontia

- (4) In 1880 and subsequently Cope proposed and defined the order Coty-LOSAURIA as distinct from the Anomodontia and all other reptiles, and as alone resembling the Stegocephala in the solid or closed condition of the skull in the temporal region. Although in his first description of the order he did not appreciate that this solid condition was the most important feature of the skull, he mentioned it distinctly, and this term Cotylosauria anticipates and must replace the term Pareiasauria Seeley.
- (5) In 1892-94 Cope<sup>7</sup> and Baur<sup>8</sup> developed the theory of fenestration, namely: the secondary evolution from a primitively closed (Stegocephalian or Cotylosaurian) temporal region, first, of a supratemporal fenestra or fossa, in Sauropterygia, Chelonia, Anomodontia, and, second, of both supra- and laterotemporal fenestræ in a two-arched condition, in the reptiles grouped as Archosauria.

<sup>&</sup>lt;sup>1</sup> Cope, E. D. The Extinct Batrachia, Reptilia and Aves of North America. Trans. Amer. Philos. Soc., XIV, No. 1, p. 30, 1869.

<sup>&</sup>lt;sup>9</sup> See especially the recent embryological work of Broom. Journ. Anat. and Phys., Vol. XXXVII.

<sup>Cope, E. D. The Primary Factors of Organic Evolution, 1896, p. 114.
Cope, E. D. The Theromorphous Reptilia. Amer. Naturalist, XII, pp. 829-830, 1878.</sup> 

<sup>&</sup>lt;sup>5</sup> Cope, E. D. The Skull of Empedocles. Amer. Nat., Vol. XIV (1880), pp. 382-383.

<sup>&</sup>lt;sup>6</sup> Cope, E. D. Third Contribution to the History of the Vertebrata of the Permian formation of Texas. Proc. Amer. Philos. Soc., XX (1882), pp. 447-461.

<sup>&</sup>lt;sup>7</sup> Cope, E. D. On the Homologies of the Posterior Cranial Arches in the Reptilia. Trans. Amer. Philos. Soc., XVII, Apr. 27, 1892.

<sup>8</sup> Baur, G. Bemerkungen über die Osteologie der Schläfengegend der höheren Wirbeltiere. Anat. Anz., Bd. X, Nr. 10, 1894.

- (6) Smith Woodward,<sup>1</sup> in 1898, was the first to publish an arrangement of the reptiles in two great groups, the first with a supratemporal fenestra only, comprising the Anomodontia, Plesiosauria, Chelonia, Ichthyosauria. "From the earliest members of this prime division of reptiles," he observed, "Palæontology seems to demonstrate that the Mammalia (with one robust zygomatic arch) arose.

  . . . In a second group, comprising the Rhynchocephalia, Dinosauria, Crocodilia, and Ornithosauria . . ." the two-arched condition appears, and this group by the loss of the lower arch gives rise to "the Squamata (Lacertilia + Ophidia) in comparatively late geological times; while some of its early divisions are generally believed to be related in an undetermined way to the ancestry of the class Aves, which never possesses the upper, though always the lower bar in question."
- (7) Following Smith Woodward, Broom<sup>2</sup> in 1901, went so far as to assign a distinct phylogenetic value to these groups, but placed the Ichthyosauria (in which, following Baur, he recognized strong Rhynchocephalian relationships) in a neutral position or intermediate between these two groups. Smith Woodward and Broom thus anticipated me in the separation of the reptilia into two groups; though Broom was uncertain in which group to place the Ichthyosaurs. My conclusions were, however, reached independently of Broom since I had no knowledge of his important paper until recently.
- (8) The next step was taken by McGregor,<sup>8</sup> in 1902, who showed that the Phytosauria or Belodontia are related to the Ichthyosauria rather than to the Crocodilia, and that the Ichthyosaurs possibly originated in two-arched forms, in which the laterotemporal fenestra became secondarily closed by the encroachment of the greatly enlarged orbit upon the temporal region. This ingenious hypothesis, which is supported by many structural resemblances in the two groups, opened the way for the removal of the Ichthyosauria from the single-arched group, in which they had been placed by Smith Woodward, to the division with (primitively) two temporal arches.
- (9) In the meantime Parker,<sup>4</sup> Cope,<sup>5</sup> Baur,<sup>6</sup> and Lydekker<sup>7</sup> had pointed out many resemblances between the Plesiosauria and the Testudinata, in addition to the possession of a compound laterotemporal arch. Other authors (Andrews<sup>8</sup>) again directed attention to the analogous evolution of the shoulder girdle in these orders, which, in fact, had been originally observed by Owen.<sup>9</sup> The Testu-

<sup>&</sup>lt;sup>1</sup> Woodward, A. S. Outlines of Vertebrate Palæontology, 1898, p. 142.

<sup>&</sup>lt;sup>2</sup> Broom, R. On the Structure and Affinities of Udenodon. Proc. Zool. Soc. Lond., 1901.

<sup>&</sup>lt;sup>8</sup> McGregor, J. H. The Ancestry of the Ichthyosauria. Science, N. S., Vol. XVI, No. 392, p. 27, July 4, 1902.
<sup>4</sup> Parker, W. K., A Monograph on the Structure and Development of the Shoulder Girdle and Sternum in the Vertebrata. Roy. Society. 1868.

<sup>&</sup>lt;sup>5</sup> Cope, E. D. On the Homologies of some of the Cranial Bones of the Reptilia, and on the Systematic Arrangement of the Class. Proc. A. A. A. S., XIX. B., p. 233.

<sup>&</sup>lt;sup>6</sup> Baur, G. On the Phylogenetic Arrangement of the Sauropsida. Jour. Morph., I, 1887, pp. 93-104.

<sup>&</sup>lt;sup>7</sup> Lydekker, R. Catalogue of the Fossil Reptilia and Amphibia in the British Museum, Part II. London, 1889. <sup>8</sup> Andrews, C. W. On the Development of the Shoulder Girdle of a Plesiosaur, etc. Ann. and Mag. Nat. Hist., Ser. 6, Vol. XV, April, 1895, p. 345.

<sup>&</sup>lt;sup>9</sup> Owen, R. On the Orders of the Fossil Reptilia and their Distribution in Time. Rep. Brit. Assoc. Adv. Sci., 29th meeting, Aberdeen, 1895, p. 161.

dinata were then shown to exhibit analogies with the Placodontia by Jaekel<sup>1</sup>; the Placodonts in turn exhibit closer resemblances to the Anomodontia than to any other order of Reptiles; their affinities to the Testudinata are, however, apparently not genetic (E. Fraas).

Thus the closer study of the structure of the temporal arches gradually led the way to the conception of the fundamental division of the reptiles into two large groups, analogous to the larger subdivisions or subclasses, (a) Prototheria and (b) Eutheria, of the Mammalia. This division if really existent must have been very ancient, because in the earliest known reptiles from the Permian we find three widely separated types, namely: (1) the solid skull of the Cotylosauria or Pareiasauria, which I regard as surviving from Stegocephalian ancestors; (2) the single- or compound-arched skull of the Anomodontia; (3) the twoarched, lightly constructed skull of Palæohatteria and its allies.

(10) Division into two Subclasses.—Classifications, as well as phylogenetic speculations, based on single characters, have so often proved futile and shortlived, that the crucial problem to my mind appeared to be to ascertain how far this temporal-arch character was associated with other distinctive characters in different parts of the skeleton; to determine, in fact, what supplementary and confirmatory evidence could be adduced for a natural subdivision of the class Reptilia into two groups. This was examined with the valuable aid of Dr. J. H. McGregor. Every part of the skeleton-skull, vertebral column, girdles and limbs-was carefully compared. In the autumn of 1902, I reached the conclusion that the Reptilia actually divide into two subclasses,2 namely the subclass Synapsida,8 primarily with single or undivided temporal arches, and the subclass Diapsida,4 primarily with double or separate temporal arches.

One obstacle to this diphyletic arrangement of the Reptilia still remained, namely, the supposed derivation of the Sauropterygia (Nothosauria and Plesiosauria) from the Proganosauria or Mesosauria, represented by the lower Triassic aquatic types Stereosternum and Mesosaurus, of undoubted Rhynchocephalian affinity; in the present review this supposition will be shown to be untenable. The remote common stock uniting the two subclasses is not the Proganosauria but the Cotylosauria with a solid skull roof.

I propose then the following diphyletic classification:

<sup>&</sup>lt;sup>1</sup> Jackel, O. Ueber Placochelys n. g. und ihre Bedeutung für die Stammesgeschichte der Schildkröten. Neues Jahrb. f. Mineralogie, etc., Jahrg. 1902, Bd. I, pp. 127-144.

<sup>&</sup>lt;sup>9</sup> Osborn, H. F. On the Primary Division of the Reptilia into two Subclasses, Synapsida and Diapsida. Science, N. S., XVII, pp. 275-276, Feb. 13, 1903. Read before the American Association for the Advancement of Science, Dec., 1902, as a joint paper with Dr. J. H. McGregor.

<sup>&</sup>lt;sup>8</sup> δύν, together, αψίς, an arch.

 $<sup>^4\</sup>delta\iota$ -, double,  $\alpha\psi\iota$ s, an arch.

Subclass SYNAPSIDA.

Primarily with single or undivided temporal arches.

- I. Cotylosauria.
- II. Anomodontia (superorder).
  - Theriodontia.
     Cynodontia.
     Gomphodontia.
  - 2. Dicynodontia.
  - 3. Placodontia.
- III. Testudinata.
- IV. Sauropterygia.
  - 1. Nothosauria.
  - 2. Plesiosauria.

Subclass DIAPSIDA.

Primarily with double or divided temporal arches.

- I. Diaptosauria (superorder).
  - 1. Protorosauria.
  - 2. Pelycosauria.
  - 3. Rhynchosauria.
  - 4. Procolophonia.
  - 5. Proganosauria.
  - 6. Choristodera.
  - 7. Rhynchocephalia.
- II. Phytosauria (including the Belodonts and Aëtosaurs).
- III. Ichthyosauria.
- IV. Crocodilia.
- V. Dinosauria (superorder).
  - 1. Theropoda.
  - 2. Cetiosauria.
  - 3. Orthopoda.
- VI. Squamata (superorder).
  - 1. Lacertilia.
  - 3. Mosasauria.
  - 3. Ophidia.

VII. Pterosauria.

Giving rise to the Mammals through some unknown member of the Anomodontia.

Giving rise to the Birds through some unknown type transitional between Protorosauria and Dinosauria.

#### II. Cotylosauria, the stem Reptilia.1

These animals were first regarded as stem Reptilia by Cope and Baur. By many palæontologists they are still regarded as a subdivision of the Anomodontia. The order Cotylosauria Cope (Pareiasauria Seeley) presents in many respects a transition between the Stegocephalian and Reptilian types. Four distinctively Stegocephalian characters persist in the Cotylosaurs, which are not found in higher reptiles, namely: (1) the broadly depressed form of the cranium, with only five openings as seen from above (two narial, two orbital and a median, pineal opening); (2) a superior opening of the auditory or tympanic depression in certain forms; (3) the apparent persistence in certain forms (? Pariotichus) of the epiotic or os tabulare just internal to these openings; (4) separate epiclavicles or cleithra—a vestige of the ichthyopsidan attachment of the shoulder girdle to the skull. The prevomers, palatines and pterygoids may be dentigerous.

Certain of the Cotylosauria (Diadectes) show rudimentary supratemporal

<sup>&</sup>lt;sup>1</sup> Baur fully recognized the Cotylosauria as stem Reptilia, but he placed the Proganosauria, including *Mesosaurus* and *Palæohatteria*, as an intermediate stage to all higher Reptilia.

openings; according to the recent observations of Case these are variable in the Permian Cotylosaurs of Texas, in certain cases being present on one side and not on the other. These rudimentary openings support the theory of fenestration as well as the theory that the Cotylosauria are the source of both the Diapsida and Synapsida.

The Cotylosauria are, however, readily distinguished from the Stegocephala in the palatal view of the skull by: (1) The prominent basioccipital element in the condyle, which is either wholly basioccipital or includes more or less of the exoccipitals, thus embracing the tripartite type; (2) the reduction of the parasphenoid (vomer). Characteristic features of the Cotylosauria are the following: (1) The pterygoids unite with the prevomers; (2) the prevomers separate the internal nares, which are anterior in position; (3) the palatines are relatively short and transverse; (4) unlike the Stegocephala, there is an ectopterygoid; (5) the supratemporal fenestræ are either wanting or rudimentary; (6) vertebræ amphicælous, perforated by the notochord; (7) hypocentra are present; (8) the shoulder girdle embraces large suturally connected coracoids and procoracoids, interclavicles, clavicles, and epiclavicles; (9) the pelvic girdle includes an expanded and continuous or plate-like ischium and pubis, the latter with an obturator foramen, but no puboischiadic opening or thyroid foramen.

Morphologically the Cotylosauria pass so directly into the Anomodontia and other Synapsida that English anatomists actually embrace the order within the Anomodontia. Theoretically, however, they constitute a far more primitive group, which will undoubtedly be found to include some of the Carboniferous animals which are now placed with the Stegocephala. The passage from the Stegocephala to the Cotylosauria, so far as the skull is concerned, is theoretically a simple one, involving only the reduction of the parasphenoid, the corresponding ossification of the basioccipitals, the substitution of a median basioccipital or tripartite (basi- and exoccipital) condyle for the widely separated and exclusively exoccipital condyles of the Stegocephala. Similarly in the vertebral column the hypocentra are reduced, the paired pleurocentra are united into a single centrum, etc.

Theoretically also the Cotylosauria gave rise by the lateral compression of the skull and the precocious formation of superior and lateral temporal fenestræ, through such a type as Procolophon, to the Diapsida, but there is no further evidence that such a transition took place except by inference from the possession of a number of primitive characters in common by the Synapsida and Diapsida.

These are as follows:

#### III.—CHARACTERS COMMON TO SYNAPSIDA AND DIAPSIDA.

(1) Both groups possess the bony elements which constitute the supra- and laterotemporal arches, namely: squamosals, prosquamosals, postfrontals, postforbitals, quadratojugals and jugals; the only difference is that in the Synapsida

these arches are still undivided, whereas in the Diapsida they are widely separated by the laterotemporal fenestra.

- (2) In the occipital view both groups have preserved the parietosquamosal bar which occasionally is elevated to form the posttemporal fenestra.
  - (3) The occipital condyle is either exclusively basioccipital or tripartite.
- (4) The palate in both groups is in primitive forms (*Procolophon*, *Ptychognathus*) precisely like that of the Cotylosauria as above described, namely, pterygoids uniting anteriorly with prevomers and leaving an interpterygoid space, into which the parasphenoid (vomer, Broom) projects.
- (5) The vertebræ in the most primitive forms are also Cotylosaurian, namely, amphicælous, perforated by the notochord, with hypocentra.
- (6) In all the Synapsida and in some of the more primitive Diapsida (Pelycosauria, Procolophonia, and Rhynchosauria) the coracoid and procoracoid are distinct elements more or less united by suture.

It is the common inheritance of these primitive characters from Cotylosaurian or Stegocephalian ancestors, in the Permian and lower Triassic members of the two subclasses which has formed the deceptive basis of the monophyletic theory, namely, that such orders as the Sauropterygia and Testudinata sprang from Protorosaurian, Proganosaurian, or primitive Rhynchocephalian ancestors.

This monophyletic theory is rendered untenable by a consideration of the divergent characters which clearly distinguish the earliest known members of these two subclasses. These are of two kinds: (1) fundamental divergences, such as the structures which show that the Testudinata, Sauropterygia, Anomodontia and Mammalia never passed through a Diapsidan stage; (2) progressive divergences, illustrated in the different trend of structural modification and development in the two subclasses,—in the coracoid region for example.

#### IV.—DIVERGENT CHARACTERS OF SYNAPSIDA AND DIAPSIDA.

	Synapsida.	Diapsida.
Temporal arches:	A single large supratemporal fenestra; laterotemporal fenestra rudimentary or wanting. Bony elements of upper and lower temporal arches not separated, upper arch tending to degenerate first.	Large supra- and laterotemporal fenestræ. Laterotemporal fenestra sometimes secondarily closed. Bony elements of arches widely separate. Lower arch tending to degenerate first.
Squamosals and prosquamosals:	These elements large, expanded, early coalesced, forming a portion of the occiput, suturally covering the quadrate, secondarily entering the glenoid fossa.	Often reduced, more generally separate, partially covering or withdrawn from the quadrate, not suturally united with it.
Opisthotics:	Tending to remain distinct.	Tending to unite with exoccipitals.
Quadrate:	Reduced, frequently covered and suturally united with the squamosal.  Monimostylic, never movable.	Large, loosely united with squamo- sals; frequently movable, strepto- stylic.

Prevomers and vomers:	Prevomers and vomers equal, or prevomers reduced and vomers enlarged (Broom).	Prevomers large or reduced (certain Lacertilia), vomers small or vestigial (Broom).
Skull proportion:	{ Cranium typically elongate,¹ face primitively abbreviate.	Cranium typically abbreviate, face primitively elongate.
Occipital condyle:	Often tripartite, basioccipitals sometimes reduced, producing the dicondylic condition.	Basioccipitals always extensive, ex- occipitals sometimes prominent, producing the tripartite but never a dicondylic condition.
Palate:	Secondary palate when formed composed of horizontal plates of maxillaries and palatines (Anomodonts and Testudinata).	Secondary palate when formed composed of palatines and pterygoids.
Anterior cervical vertebræ:	Hypocentra reduced, anterior cervicals less distinctly temnospondylous.	Free pleuro- and hypocentra; pro- nounced temnospondylous condi- tion in anterior cervicals.
Shoulder girdle:	Coracoid and procoracoid large, suturally united, or tending to separate.	Procoracoid early forming close union with coracoid, tending to reduction.
Pelvic girdle:	{ Ventral elements expanded.	Ventral elements tending to become more contracted, slender.
Phalangeal formula:	2, 3, 3, 3 in most primitive forms (Cotylosauria, Anomodontia, Testudinata).	Manus 2, 3, 4, 5, 3, pes 2, 3, 4, 5, 4 in most primitive forms (Diaptosauria.)

The above table deals chiefly with structures in which the two groups either actually diverge or show strongly divergent tendencies. Certain of the most primitive members of the two subclasses, the Pelycosauria and *Procolophon*, for example, exhibit the persistent Cotylosaurian separation of coracoid and procoracoid. Others, such as the typical Proganosauria (*Mesosaurus*, *Stereosternum*), show the progressive obliteration of the suture between coracoid and procoracoid.

The two subclasses may, therefore, be defined as follows:

#### Subclass Synapsida.

#### Subclass Diapsida.

(1) Roof of cranium solid (Cotylosauria) or with a single large supratemporal fenestra, the laterotemporal fenestra rudimentary or wanting. (2) Squamosal large, early coalescing with prosquamosal, suturally uniting with and more or less covering the quadrate, entering into glenoid fossa. (3) Quadrate more or less reduced, never movable. (4) Coracoid and procoracoid separate or united by suture. (5) Phalangeal formula primitively 2, 3, 3, 3, or less than 2, 3, 4, 5, 3.

(1) Roof of cranium open with two distinct temporal arches, which may secondarily, one or both, disappear. (2) Squamosal relatively small, frequently separate from prosquamosal, not entering into articulation with the lower jaw. (3) Quadrate relatively large, uncovered and sometimes secondarily movable. (4) Coracoid and procoracoid early coalesced into a single bone, or procoracoid degenerate. (5) Phalangeal formula primitively 2, 3, 4, 5, 3-4.

<sup>&</sup>lt;sup>1</sup> Lystrosaurus frontosus Cope, a Dicynodont, exhibits an extraordinarily abbreviate cranial and facial region.

#### Temporal Arches and Skull Proportion.

The contrast between the elongate cranium and large supratemporal fenestra and the abbreviate cranium and short supratemporal fenestra, is one of the most striking distinctions between the Synapsida and Diapsida. Comparison of the superior view of the skull of an Anomodont (Dicynodon, Fig. 1), of a primitive Plesiosaur (Nothosaurus, Fig. 2), of one of the Testudinata (Trionyx, Fig. 2a), and of a primitive mammal (Pantolambda, Fig. 3) reveals a striking similarity which appears to be due to common origin. The elongation of the cranium exposes the proötic in certain Plesiosaurs (Williston) and in the Testudinata. On the other hand, in all the Diapsidan types without exception the supratemporal fenestra is relatively small. (See Rhynchocephalia, Phytosauria, Ichthyosauria, Dinosauria, etc.).

#### Squamosals, Prosquamosals, Quadrates and Opisthotics.

In all Synapsidan types above the Cotylosauria the squamosals and prosquamosals early coalesce (Fig. 4); they are peculiarly arched in certain of the Anomodonts, but the dominant feature is that they form a firm lateral attachment to the quadrate, more or less covering this element and invading the glenoid facet (Fig. 5). Correlated with this firm outer support may be the fact that in Testudinata and Plesiosauria the opisthotics tend to remain suturally distinct from the exoccipitals. In the Diapsida, on the other hand, the quadrates are never so firmly supported externally; the degeneration of the lower arch leads into the streptostylic condition and the opisthotics firmly unite with the exoccipitals.

In the above characters we have very strong evidence of independent derivation from Cotylosaurian ancestors; neither the Synapsidan nor Diapsidan types being derivable from each other.

#### Occipital Condyles.

This region does not so sharply distinguish the two groups because the strictly monocondylic condition in which the condyles are wholly basioccipital is independently evolved in both Synapsida and Diapsida (Plesiosauria and Crocodilia for example). The tripartite condition is also seen in both groups (Chelonia and Lacertilia). Actual reduction of the basioccipitals, however, producing the dicondylic, exoccipital condylar condition, is found only in the Anomodontia and Mammalia.<sup>1</sup>

#### Vomer and Prevomers.

Vomer.—According to Dr. R. Broom<sup>2</sup> the mammalian vomer "is a median element developed in connection with that part of the basicranial axis which is

<sup>&</sup>lt;sup>1</sup> Osborn, H. F. The Origin of the Mammalia. III. Occipital Condyles of Reptilian Tripartite Type. Amer. Nat., Vol. XXXIV, 1900, pp. 943-947.

Gadow, H. The Origin of the Mammalia. Zeitschr. f. Morph. u. Anthrop., 1902, Bd. IV, Hest II, pp. 345-364.

On the Mammalian and Reptilian Vomerine Bones. Proc. Linn. Soc. N. S. Wales, 1902, part 4, Oct. 29, pp. 545-560, pll. xxiv-xxvi.

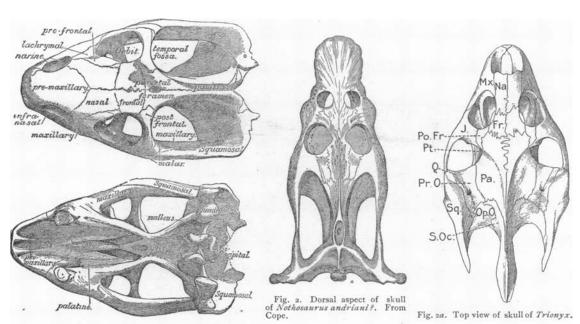


Fig. 1. Palatal and superior views of the skull of *Dicynodon*, showing the elements as interpreted by Professor Seeley. Note especially the exposure of the prevomer, the large extension of the squamosal, the pre- and postfrontals, the single squamosomaxillary bar. After Seeley.

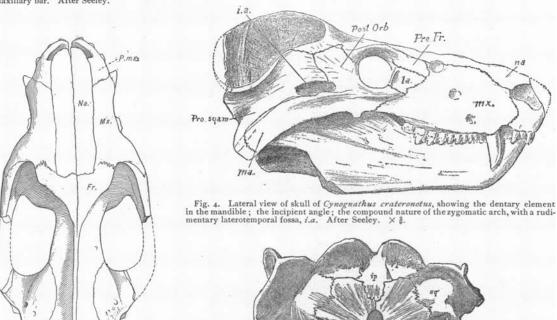


Fig. 3. Top view of the skull of a primitive Amblypodous Ungulate, Pantolamb-× 1.

Fig. 5. Posterior view, occiput of *Ptychosiagum declive*. A Dicynodont, showing the tripartite structure of the occipital condyle, the large interparietal, and the extension of the squamosal upon the occiput. The bones lettered  $\not pa$  correspond in position with the epiotics in the Stegocephala. After Lydekker.

THX.

formed from the united trabeculæ"; this is homologous with the large median membrane bone in the Amphibia, named "parasphenoid" by Huxley, which, according to Parker, "first appears in the frog as a parostosis beneath the intertrabecular space." In the Dicynodonts this median or true vomer is greatly developed and in the Theriodonts it is also strongly developed as a support of the secondary palate. In the Chelonia, the median vomer is also developed as the support of the palate, a condition somewhat resembling that of the Dicynodonts. In the Plesiosauria, however, the vomer (parasphenoid) is reduced. Thus in all the specialized Synapsida except the Plesiosauria a large true vomer is present. In the known ancestral Synapsida or Cotylosauria, however, the vomer is characterized by Broom as small.

Prevomers.—The bones in the Lizard and Sphenodon, which have usually been regarded as homologous with the mammalian vomers, are really entirely distinct paired elements, which are formed in connection with the nasal capsules and are termed by Broom "prevomers." These are well represented in the palate of the following Diapsidan types and orders: Rhynchocephalia, Pelycosauria, Ichthyosauria, Dinosauria. They are also large in the Cotylosauria, and in the supposed Synapsidan Plesiosauria. In all other specialized Synapsidan types, namely, Anomodontia, Theriodontia, Testudinata, Mammalia, the prevomers are small, vestigial, or wanting. In the Monotremata the prevomers are represented by the dumbbell bones of Ornithorhynchus. In the Marsupialia they are replaced by backward projections of the premaxillæ. In the higher Mammalia they are probably present in the embryos of Edentata and Chiroptera (Miniopterus).

In general, therefore, if Broom is correct, it may be said that a large median vomer is characteristic of the Synapsida (Chelonia, Anomodontia, Mammalia), with the exception of the Plesiosauria, in which this element is present or reduced, and of the known Cotylosauria, in which it is small. The prevomers are small in most Synapsida, but are large in the Cotylosauria, and present in the Plesiosauria. The prevomers, on the other hand, are specially large and characteristic of the Diapsidan orders; whereas the vomers are small or vestigial in these orders.

#### Hypocentra.

In Diapsida the compound or separate condition of the atlas and axis, the presence of hypocentra throughout the entire vertebral column or in a number of the cervicals and caudals is a characteristic condition. In the Testudinata and Plesiosauria the anterior cervicals are less distinctly temnospondylous, but it is clear that the Mammalia, in which free hypocentra occur, are derived from Anomodontia and Cotylosauria in which these elements are persistent.

#### Coracoid and Procoracoid.

This seems to be one of the most characteristic of all the lines of division. In the Diapsida (Fig. 6) only comparatively few forms (certain Pelycosauria, Fig.

12, Rhynchosauria, *Procolophon*) are known in which the procoracoid is suturally distinct from the coracoid; and generally there is certainly a strong tendency toward the early union of these elements into a single bone, the suture entirely disappearing; this is followed in many forms by a marked reduction. In the

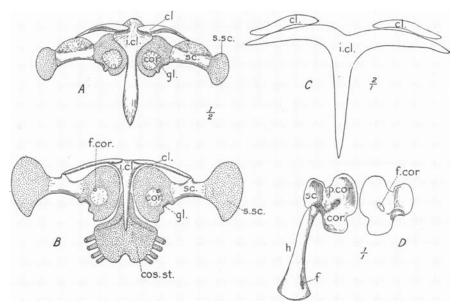


Fig. 6. Diapsidan types of shoulder girdle. A, Palwohatteria. After Credner. The cartilaginous areas are entirely restored. Restoration by J. H. McGregor. × ½. B, Sphenodon juv. (15 cm.). Modified from Howes. By J. H. McGregor. × ½. C, Pleurosaurus. Cartilaginous elements omitted. After Dames. × ½. D, Mesosaurus tenuidens. Modified from Gervais. × ½.

Cl, clavicle; i.cl, interclavicle; sc, scapula; s. sc, suprascapula; cor, coracoid; p.cor, procoracoid; f.cor, coracoid foramen; ½, humerus; f, entepicondylar (ulnocondylar) foramen.

Synapsida (Fig. 7) on the other hand we have the anomalous condition presented, in the Testudinata and Plesiosauria, of a broadly transverse coracoid with procoracoid suturally separate, entirely separate or wanting. The persistent sutural separation of these two large equal-sized elements is one of the most distinctive features of resemblance of the Cotylosauria, Anomodontia and primitive Mammalia (Monotremata, Fig. 7, E). Even in the higher mammalia Howes has shown that the coracoid and procoracoid tend to remain suturally separate (Fig. 7, F).

#### Phalangeal Formula.

It is surprising that so little attention has been paid to the phalangeal formula in discussions of the phylogeny of the Reptilia. In the Diapsida certainly the most striking character is the extremely early occurrence, in the Permian forms, of the formula 2, 3, 4, 5, 3-4, which characterizes all of the higher Diapsida excepting only those in which hyperphalangy has occurred. In the Synapsida, on the other hand, the most primitive forms (Cotylosauria, Anomodontia,

<sup>&</sup>lt;sup>1</sup> Howes, G. B. The Morphology of the Mammalian Coracoid. Jour. Anat. and Phys., XXI, Jan., 1887, pp. 100-108.

Testudinata) are singularly constant in the exhibition of the formula 2, 3, 3, 3, which is very little removed from that of the Stegocephala, and is identical with that of mammals. In certain aquatic Testudinata (Trionychoidea) the formula secondarily rises nearly to that of the Diapsida. In the earliest Plesiosauria the

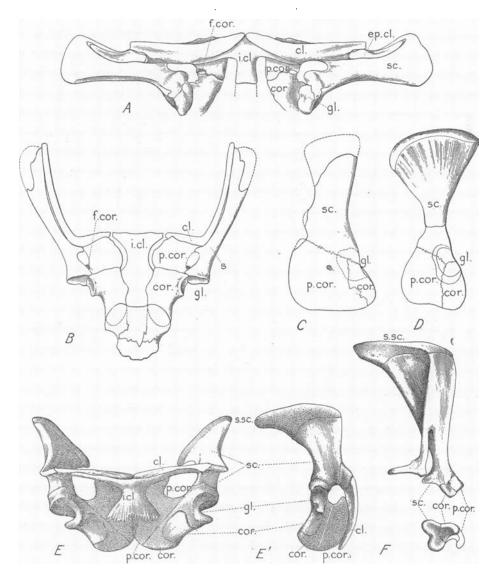


Fig. 7. Synapsidan and mammalian types of shoulder girdle. A-D, after Seeley; E-F, after Howes. A, Pareia-saurus bainii. B, Keirognathus cordylus. C, Deuterosaurus. D, Rhopaiodon. E, ventral; E', lateral views of Ornithorhynchus. F, Lepus.

formula of the manus is not definitely known; it is recorded as 2, 3, 4, 4, 3 (Lario-saurus, Boulenger) but may be higher; the formula of the pes, as recorded, is truly Diapsidan, namely 2, 3, 4, 5, 4 in Lariosaurus. We must therefore await the discovery of the ancestors of the Sauropterygia before this group can be positively considered of Synapsidan origin in respect to this character.

#### Epiphyses.

A fact which may prove to be of some importance is the reported presence of the characteristically Mammalian elements, rudimentary epiphyses, in certain Plesiosauria (Kükenthal) and Testudinata (v. Zittel).

#### V.—Subclass Synapsida.

Next to the Cotylosauria, which have already been characterized, the Anomodontia are to be regarded as the stem forms of Synapsida. They apparently bear the same general ancestral relation to the Chelonia, Plesiosauria, and Mammalia that the Diaptosauria bear to the higher Diapsida.

These remarkable Permian and Lower Triassic reptiles should be clearly separated from the Cotylosauria or Pareiasauria, with which they are by some authors confused. The Anomodont forms known at present, through the researches of Owen, Seeley, and Broom, exhibit an adaptive radiation of terrestrial, ambulatory, carnivorous, herbivorous, and possibly aquatic (Placodontia) forms analogous to that of the Creodont Mammalia. When we discover the, as yet unknown, smaller, short-limbed, littoral and amphibious members of the Anomodontia we shall probably be not far from the ancestry of the Sauropterygia and Testudinata, which is at present unknown. Similarly, in my opinion as expressed several years ago, the discovery of small unspecialized insectivorous Anomodonts will bring us near the ancestry of the Mammalia. In other words, the adaptive radiation of the Anomodonts will furnish us with the ancestry of all the Synapsidan orders.

The Coracoid and Procoracoid in Sauropterygia and Chelonia.—In this connection the question of the homologies of the bones composing the shoulder girdle of the Plesiosaurs and Testudinata becomes of very great importance. There has been a strong tendency recently to compare and homologize these elements very closely; but there is danger of mistaking analogies for homologies. We have as yet received no final palæontological demonstration of the bone representing the procoracoid in the earliest Plesiosaurs. It may be said that such high authorities as Gegenbaur and his successor, Fürbringer, both regard the anterior ventral process of the scapula in the Testudinata as a modified procoracoid. On the other hand, Baur, Howes, and other equally reliable authorities regard this process as a development from the scapula, in other words, as a proscapular process. If the latter view be correct we must await further knowledge of the Lower Triassic Testudinata to show the fate of the procoracoid element in the Chelonia. Whatever the homology of the anterior ventral element of the shoulder girdle of these orders proves to be, a separation of the procoracoid from the coracoid is an unquestionable characteristic. The known Permian and Lower

<sup>&</sup>lt;sup>1</sup> The Origin of the Mammalia. Amer. Nat., Vol. XXXII, May, 1898, p. 333. Also Amer. Journ. Sci., Vol. VII, Feb., 1899, p. 95.

Triassic *Diapsidan* shoulder girdles, on the contrary, uniformly exhibit a broad coraco-procoracoid plate tending to coalesce into a single bone, and invariably perforated by the coracoid foramen.

#### VI.—Subclass Diapsida.

The mode of origin of the Diapsida is still doubtful. Whereas the transition from the Cotylosauria to the higher Synapsida is a gradual one, the Diapsida appear full-fledged, so to speak, in the Permian Protorosauria, which are strikingly modified in type. However, so many Cotylosaurian characters persist in the most primitive Diapsida that there can be little doubt that the Diapsida sprang, independently of the higher Synapsida, from the Cotylosauria; in support of this theory are the transitional, Cotylosaurian to Diapsidan characters observed in *Procolophon* (see p. 497).

#### PART II.—THE DIAPTOSAURIA, THE MOST PRIMITIVE SUPER-ORDER OF TWO-ARCHED REPTILES.

As shown below, the different groups more or less related to *Sphenodon* are variously known as Protorosauria, Proganosauria, Mesosauria, Pelycosauria, Choristodera or Simædosauria (*Champsosaurus*), Homæosauria, Rhynchosauria, etc., or, more simply, as Rhynchocephalia and Rhynchocephalia vera (Boulenger). I propose to unite all these primitive or stem Diapsida in a new superorder which may be called Diaptosauria, in reference to the common possession of two separate temporal arches. This superordinal grouping expresses two facts: *First*, that a primitive genetic relationship existed between the many known and doubtless still larger number of unknown forms, of the same grade as that whereby the Lacertilia, Mosasauria and Ophidia are united into the superorder Squamata, or the Theropoda, Cetiosauria, and Orthopoda (Predentata) are united into the superorder Dinosauria.

The reason I do not follow Boulenger and v. Zittel in placing all these animals as families or suborders within the single order Rhynchocephalia lies in the second fact, that, apart from the awkwardness and technical impropriety of the term Rhynchocephalia vera, we have no precedent for such procedure; no existing or extinct order of reptiles embraces such widely diverse forms as Palæohatteria, Rhynchosaurus, Champsosaurus, Dimetrodon, and Stereosternum; the characters which separate these animals are of superordinal value; they indicate fundamental separation and radiation. In other words, we must conceive of a great adaptive radiation of the Diaptosauria as occurring all over the world in pre-Permian, Permian and post-Permian times, the only surviving spur of which is the order Rhynchocephalia; other spurs extended only as far as the Jurassic and Cretaceous; still others gave rise to the subsequent radiation of the Squa-

mata, Dinosauria, and the other Diapsidan Reptilia, namely, the Phytosauria, Ichthyosauria, Crocodilia, and Pterosauria.

This conclusion was reached only after I had reëxamined and analyzed all the accessible evidence and literature relating to these animals, as shown in the following pages, in which the anatomy, adaptive radiation and phylogenetic relations of each of the separate orders of Diaptosauria are briefly discussed. The chief grounds for the more conservative view of Boulenger will also be brought out. They consist, first, in our very limited knowledge of these animals; second, in the fact that the divergence or separation has progressed in many cases only to that point where it is extremely difficult to decide whether it should be given family, superfamily, subordinal or ordinal rank. We are perfectly clear that the Pelycosauria and Rhynchocephalia should be ranked as distinct suborders or orders; we are not so clear as to the Protorosauria, Proganosauria, Choristodera, etc.

#### Diaptosauria, superordo nov.

Including the "Rhynchocephalia" of Zittel, the Rhynchocephalia (i. e., Protorosauria + Rhynchocephalia vera) of Boulenger, the Pelycosauria of Cope, the Procolophonia of Seeley, and the unmodified ancestors of all Diapsidan orders.

Primitive or stem Diapsida. Skull with two temporal arches. Vertebræ typically amphicœlous, perforate or imperforate by notochordal canal; hypocentra present throughout column or reduced in dorsal region. Ribs originally on all vertebræ anterior to the 8th to 10th caudals, mainly single-headed; capitular attachments, hypocentral, pleurocentral, or neurocentral. Abdominal ribs or plastron always present. Coracoid and procoracoid separate in primitive forms but early uniting into a single bone. Pubis and ischium in continuous contact, or secondarily separated by pubo-ischiadic fenestra.

The prevailing differences of opinion as to the classification of these animals are in part illustrated in the subjoined table, which includes most of the known Diaptosauria.

	Permian.	Triassic.	Jurassic.	Cretaceous.	Eocene.	Recent.
Order Protorosauria Seeley.						
Protorosauridæ.						
Protorosaurus v. Meyer	X					
Aphelosaurus <i>Gervais</i>	×	٠				
Palæohatteria Credner	×					
Kadaliosaurus Credner	×					
Order Proganosauria <i>Baur</i> . (Mesosauria <i>Seeley</i> ). Mesosauridæ.						
Mesosaurus Gervais	×					
Stereosternum Cope						

<sup>&</sup>lt;sup>1</sup> Text-Book of Palæontology, translated and edited by Charles R. Eastman. 8vo. London, 1902, pp. 145-152.

<sup>&</sup>lt;sup>2</sup> On British Remains of *Homwosaurus*, with Remarks on the Classification of the Rhynchocephalia. Proc. Zool. Soc., 1891, p 1.

	Permian.	Triassic.	Jurassic.	Cretaceous.	Eocene.	Recent.
Order Procolophonia Seeley. Procolophon Seeley.	×					
Group Sphenodontina Huxley, in part. Rhynchosauridæ Huxley. Rhynchosaurus Owen. Hyperodapedon Huxley		××				-
Order Pelycosauria Cope.¹ Clepsydropidæ Cope. Clepsydrops Cope. Dimetrodon Naosaurus Edaphosaurus Embolophorus Archæobelus Lysorophus Theropleura Ophiacodon Marsh Sphenacodon Bolosauridæ Cope. Bolosaurus Metamosaurus	× × × × × ×					
Order RHYNCHOCEPHALIA Günther. Group Sphenodontina Huxley, in part. (Rhynchocephalia vera Boulenger, in part) Sphenodontidæ. Sphenodon Gray	ļ					×
Suborder Choristodera Cope. (Order Simædosauria Dollo). Champsosauridæ. Champsosaurus Cope				××	×	
Suborder HOMŒOSAURIA Lydekker. Homœosauridæ. Homœosaurus v. Meyer			×			
INCERTÆ SEDIS. Telerpeton Mantell	×	×	•			

In the present memoir, which is based chiefly on original observations of Stereosternum and Champsosaurus and upon the invaluable papers of v. Meyer, Credner, Seeley, Boulenger, Dames, Dollo and Broom, it will appear that there are substantial grounds for separating these animals into at least three and possibly into five orders. But as already stated, this degree of separation is a baffling question owing to our limited knowledge; let us, therefore, for the sake

<sup>&</sup>lt;sup>1</sup> The horizon is partly Permian, partly Triassic.

of clearness, provisionally adopt seven 'orders' at their face value, clearly remarking that some of them may from fuller information be lowered to subordinal or superfamily rank.

These are:

#### ORDERS AND SUBORDERS.

- I. PROTOROSAURIA Seeley.
- II. PELYCOSAURIA Cope.
- III. RHYNCHOSAURIA ord. nov.
- IV. PROCOLOPHONIA Seeley.
- V. PROGANOSAURIA Baur.
- VI. CHORISTODERA Cope.
- VII. RYNCHOCEPHALIA Günther.

#### EXAMPLES.

Protorosaurus, Palæohatteria.
Naosaurus, Dimetrodon.
Rhynchosaurus, Hyperodapedon.
Procolophon.
Mesosaurus, Stereosternum.
Champsosaurus, Simædosaurus.
Homæosaurus, Sphenodon.

#### I. — ORDER PROTOROSAURIA SEELEY.

"I conclude," says Seeley in his memoir on *Protorosaurus speneri*, "that von Meyer was fully justified in regarding *Protorosaurus* as the type of a distinct order of reptiles, for which the name Protorosauria may be conveniently used."

Definition of Protorosauria. — This Permian order, which has been confused with the Proganosauria of Baur (Mesosauria, Seeley), has never been defined. Typified by the genera Protorosaurus, Palæohatteria and Kadaliosaurus, it may now be defined as follows:

Ambulatory; probably carnivorous Diaptosauria; neck short, 6-7 cervicals; vertebræ mostly amphicælous; hypocentra; strong pelvic attachment of dorsally expanded ilium and 3-2 sacral vertebræ; ischium and pubis more or less continuous; 2 proximal and 5-4 distal tarsalia; interclavicle rhombic anteriorly; humerus with ectepicondylar (radiocondylar) foramen.

These characters distinguish this order from the Dinosauria (group Megalosauria or Theropoda) to which it is most nearly allied and possibly ancestral, and from the Rhynchocephalia to which it is more remotely allied and certainly not ancestral.<sup>2</sup>

#### Genus Protorosaurus v. Meyer.

These large reptiles are known from twenty-one or more specimens, which belong certainly to two or more genera and several species, found in the Kupferschiefer Zechsteinformation (Permian) of Germany. Our knowledge is based upon the fine memoir of von Meyer,<sup>3</sup> and upon Seeley's more recent memoir in which he confirms von Meyer in most points, but adds some evidence for a dermal skeleton, and questions the socketed condition of the teeth.

<sup>&</sup>lt;sup>1</sup> On Protorosaurus Speneri (von Meyer). Phil. Trans. Roy. Soc. Lond., Vol. CLXXVIII B (1887), pp. 187-213, pll. xiv-xvi.

<sup>&</sup>lt;sup>2</sup> For the probable structure of the primitive Dinosaur see the writer's article 'Reconsideration of the Evidence for a Common Dinosaur avian Stem in the Permian' (Amer. Nat., Vol. XXXIV, No. 406, October, 1900).

<sup>&</sup>lt;sup>3</sup> Fauna der Vorwelt : Saurier aus dem Kupferschiefer der Zechsteinformation, 1856, pp. 1-28, pll. i-ix.

These are large, raptorial animals, attaining 1.5 metres in length, proportioned like the Monitor Lizard; with elongate, pointed skull, hind limbs considerably longer than fore limbs, long and powerful teeth, vertebræ amphicælous, and probably with hypocentra throughout. The most primitive feature is the platelike structure of the pubes and ischia. The most progressive features are the walking or ambulatory structure of the hind limb, and the straight femur, correlated with which the arrangement of tibia, fibula, calcaneum and astragalus is strikingly similar to that of the primitive bipedal Dinosaurs.

SKULL. — Triangular, with pointed snout, composed of large separate nasals, expanding premaxillæ, separate prefrontals and lachrymals (Seeley). Note especially the small antorbital fenestra as a dinosaurian character. The supratemporal fenestræ are large; the parietals small, with short, deep sagittal crest. The quadrate is large. The palate exhibits pterygoids uniting with the prevomers, and a small interpterygoid space. The premaxillaries, maxillaries and dentaries are armed with pointed, conical teeth, firmly implanted in a single, close-set series of sockets (existence of sockets is doubtful.—Seeley). Eighteen to 16 lower teeth. Palatines, prevomers and pterygoids also covered with small, pointed teeth. Jaws composed of dentary, angular, surangular, splenial and articular.

VERTEBRÆ. — Vertebræ amphicælous or slightly biconcave, fully osseous, neurocentra completely coalesced with centra, neural spines strong and broad. Both Seeley and Boulenger speak



Fig. 8. Protorosaurus speneri. Two dorsal vertebræ with hypocentrum. From Etzold. X 1.

of the cervicals as opisthocœlous (a characteristic of Carnivorous Dinosaurs). In some specimens referred to this genus, hypocentra are absent behind the atlas and axis; in others, as described by Etzold, there are dorsal hypocentra (Fig. 8). Paired cervical elements, apparently hypocentra, are figured by v. Meyer (Tab. i). Seven cervicals, 16 dorsals, or 23 presacrals in type of P. speneri; 18 dorsals, 3 sacrals in P. linkii (Seeley). Cervicals remarkably elongate, dorsals shorter. Three sacrals, and sacral ribs also, closely coalesced in P. linkii (v. Meyer, Tab. vi), forming a powerful sacral arch which unites with ilium. Forty caudals with large hæmapophyses or hypocentra.

Ribs. — Single-headed ribs on all the presacrals. Cervical ribs delicately pointed, hypocentral in position. Dorsal ribs carried on high and

short neurocentral diapophyses (v. Meyer, Tab. v, Tab. vii), opposite middle of vertebræ; 3 to 4 sacral ribs attached to sides of pleurocentra, *i. e., not* between the vertebræ or hypocentral (v. Meyer, Tab. vii).

ABDOMINAL RIBS, or plastron, composed of one or two slender lateral bars (Seeley), with single, angulate median pieces (v. Meyer, Tab. ii).

GIRDLES. — The scapula is rather short. The coracoid is large, single, indented on the anterior border, unlike that of any Nothosaur, more comparable to that of lizards and Dinosaurs (Seeley); interclavicle consisting of a rhombic anterior plate (as in Stegocephala), with a long posterior rod. The pelvic girdle consists of an elongate, arched ilium, which unites with three sacral ribs, with large, flat, expanded pubes and ischia, forming contiguous ventral plates, which von Meyer rightly compared with those of the Stegocephala, e. g., *Archegosaurus*. An obturator (puboischiadic) foramen is described by Seeley, and clearly appears in von Meyer's figure (Tab. iii, fig. 2).

LIMBS. — The fore limb is decidedly shorter than the hind limb, and includes a humerus, with prominent deltoid crest, compressed in the centre, expanded at the extremities, ectepicondylar foramen. The ulna and



Fig. 9. Protorosaurus speneri. Left manus, palmar view. After von Meyer.  $\times \frac{1}{5}$ . The radial digit (I) is to the right.

radius, of nearly equal size, are shorter than the humerus. From comparison of the large number of specimens figured by v. Meyer (Tab. v, figs. 2, 3, Tab. vii, fig. 5) it is seen that the carpus (Fig. 9)

includes ten elements, namely, 3 proximal carpalia (radiale, intermedium, ulnare) equal in size, 2 centralia, 5 distal carpalia,—a very primitive condition; unlike the Proganosaurian (Stereosternum and Mesosaurus) carpus the intermedium does not separate the radius and ulna distally. The metacarpals are moderately elongate. The phalangeal formula is typically Diapsidan, 2, 3, 4, 5, 3, the digits terminating in large compressed claws. In both manus and pes the fourth digit is the longest.

The limb bones contain large medullary cavities, with thin walls. The femur is Dinosaurian in shape, long and straight, with the head directed laterally, a broad trochanter, with thin walls and hollow interior. Equally Dinosaurian is the proximally massive tibia with a prominent median crest; the fibula barely enters into the knee joint, and is attached on the lower outer side of the tibia. The tarsus is composed of at least 7 elements, namely, a large astragalus (tibiale) with possibly an ascending process (Seeley, v. Meyer, Tab. viii), a compressed calcaneum (fibulare) and rounded centrale, and four distal tarsalia (tarsalia 1, 2, 3, and 4 + 5 conjoined). According to Baur, who does not recognize a separate centrale, the proximal elements are: astragalus (tibiale + centrale?) intermedium, fibulare. The metatarsals are decidedly longer than the metacarpals, the three median digits being especially enlarged (as in Megalosaurian Dinosaurs). The phalangeal formula is 2, 3, 4, 5, 4² (von Meyer, Tab. viii).

AFFINITIES. — As pointed out above, this animal, with all its primitive characters, is strikingly suggestive of the most primitive Dinosaurs such as *Anchisaurus* in the structure of: (1) the skull; (2) vertebræ, opisthocælous cervicals, three sacrals; (3) limbs; (4) ilium expanded. It differs chiefly in (1) fewer cervicals, (2) plate-like pubis and ischium. (See also under 'Conclusions.')

#### Genus Palæohatteria Credner.3

Palæohatteria, one of the most primitive Diapsida known, is represented by fine materials in the Dresden Collection, found associated with the allied genus Kadaliosaurus and with Stegocephala, and has been ably monographed by Credner.

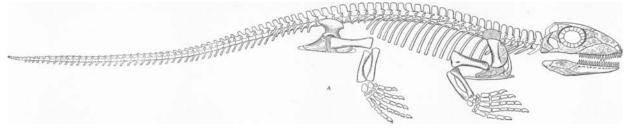


Fig. 10. Palæohatteria longicaudata. Restoration by J. H. McGregor. X 1. See also Pl. XL.

Size.—Length, 40-45 cm. with large, short limbs and long tail.

Habits.—This animal was probably ambulatory. The only possible evidence of semiaquatic habit is the distal expansion of the humerus, which is also a fossorial adaptation; the partly osseous carpus and tarsus and limb joints are interpretable either as aquatic or juvenile characters. In every respect, however, it is built

<sup>&</sup>lt;sup>1</sup> Zur Morphologie des Carpus und Tarsus der Reptilien. Zool. Anz., No. 208, Sept. 28, 1885, p. 6.

<sup>&</sup>lt;sup>5</sup> In Aphelosaurus there are said to be 4 phalanges on digit V in both manus and pes.

<sup>&</sup>lt;sup>2</sup> Die Stegocephalen und Saurier aus dem Rothliegenden Plauen'schen Grundes bei Dresden, vii Theil *Palæohatteria longicaudata*. Zeitschr. d. Deutsch. geol. Ges., Jahrg. 1888.

rather like a terrestrial type (Fig. 10): see especially the three expanded sacral vertebræ, the dorsally expanded ilium, the broad neural spines, stout pre- and postzygapophyses, digits terminating in stout ungual phalanges, with lateral grooves for claw attachment, moderate development of the caudals. As compared with *Protorosaurus* and *Kadaliosaurus*, *Palæohatteria* was certainly clumsy, heavy-limbed, and slow moving; the powerful recurved teeth are adapted to the seizure of comparatively resistant prey.

There is very considerable reason to believe that all the specimens which represent this remarkable type belong to small and immature individuals, differing in size and age, in which the ossification of the ends of the bones is still incomplete. This conjecture is confirmed by the fact that in none of the six specimens figured by Credner is the posterior cranial region ossified, and that in the development of *Sphenodon* this region long remains cartilaginous (Howes). The shoulder girdle, carpus, and tarsus are also imperfectly osseous.

SKULL.—Length, 70 mm. shaped as in *Sphenodon*, that is, apparently elevated and relatively narrow, with short temporal fenestræ; with all primitive elements separate, namely, premaxillaries, maxillaries, nasals, lachrymals, prefrontals, frontals, postfrontals, squamosals. (The

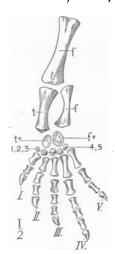


Fig. 11. Palæohatteria longicaudata. Left hind limb, restored, after Credner, by J. H. McGregor.  $\times \frac{1}{2}$ . te, tibiale; fe, fibulare. 1, 2, 3, 4, 5, distal tarsalia.

existence of separate prosquamosals is undetermined; Credner does not mention these elements.) Supra- and laterotemporal fenestræ large and of equal size. Cranium abbreviate, antorbital region more elongate than post-orbital region; nares small, terminal, separated by premaxillary septum, no preorbital opening; orbits large, with a ring of sclerotic ossicles. Premaxillaries separate, with vertical processes separating nares. Squamosal and quadrate apparently somewhat depressed. Basisphenoid perforated with two foramina as in *Sphenodon*, with a parasphenoid (vomer) process.

DENTITION.—Upper teeth, 21-22 on each side; teeth hollow, recurved, grooved at the base. Premaxillary with 3-4 teeth, maxillary with 16-18 teeth, of irregular size (as in Carnivorous Dinosaurs), large, pointed, laterally grooved near the base; also a row of palatine teeth; smaller rounded teeth on the vomers. Jaw similarly provided with 18 large teeth on each side, in the dentaries. Jaw composed of dentary, articular, angular, supraangular, and probably opercular and splenial.

VERTEBRÆ (as estimated by Credner) 6 + cervicals, 20 dorsals or 26 presacrals, 55 caudals, 3 (possibly 4) sacrals; vertebræ traversed by a large continuous notochord which expands between the centra; neurocentra separated by sutures; neurocentra of mid-dorsals and certain cervicals apparently pierced by foramina (Tab. xxiv, fig. 1); spinous processes elevated, broad prominent pre- and postzygapophyses; hypocentra through-

out column; from the sixth caudal backward modified into chevrons, which are open superiorly (closed in certain chevrons of *Sphenodon* and of *Stereosternum*). No para- or diapophyses on any vertebra. Caudal vertebræ with neurocentra placed above middle of pleurocentra (no breaking point as in Lacertilia and *Stereosternum*).

RIBS.—On all presacral, sacral, and first seven caudal vertebræ. Cervical ribs stout, elongate, with expanded heads, apparently placed on anterior part of centra. Anterior dorsal ribs, 16, elongate, chest evidently deep and narrow; posterior dorsal ribs short, recurved; 3 sacral ribs very broad, placed directly opposite centra. Proximal ends of all ribs expanded, not clearly divided into capitulum and tuberculum. Rib attachments apparently on anterior part of vertebræ except in caudals, in which ribs appear to be opposite mid-centra; 6 anterior caudal ribs curved.

ABDOMINAL RIBS.—Small, elongate, scale-like, 3 transverse series to each opposite pair of costal ribs.

GIRDLES.—Scapula large, exceptionally broad; coracoids only osseous, resembling the embry-onic coracoid of *Sphenodon* (Fig. 6), and imperforate; no procoracoid ossification in ventral plate; procoracoid cartilaginous, unless represented in Credner (Tab. xxiv, fig. 1) as an osseous element overlapping the coracoid. Interclavicle a rhombic anterior plate (as in Stegocephala) with elongate, narrow posterior bar. Large curved clavicles. Pelvic girdle composed of a continuous ventral plate, more rounded pubis with incisio-obturatoria, elongated ischia and dorsally expanded ilium, with a prominent anterior or pubic, and a broad but somewhat less prominent ischiadic peduncle.

LIMBS.—Relatively heavy and compact, the ends of all the limb bones cartilaginous. Hind limbs a little longer than fore limbs. Propodials of nearly equal size (that is, radius and ulna equal tibia and fibula). Humerus expanded distally more than proximally, with supposed radiocondylar (ectepicondylar) foramen. Femur straight, flattened; tibia and fibula equal in size. Manus longer than pes, composed of more slender elements. Carpus composed of 8 separate elements. Phalangeal formula in manus and pes 2, 3, 4, 5, 3. Phalanges stout, cylindrical; terminal phalanges laterally compressed and grooved for claw. Tarsus (Fig. 11) composed of at least seven elements, namely, a large astragalus (tibiale +? intermedium), calcaneum (fibulare) and five distal tarsalia.

RELATIONSHIPS.—Credner enumerates (op. cit., page 548) fourteen characters in which this animal resembles Sphenodon punctatus. These are without exception primitive characters and speak for the remarkably primitive, persistent nature of the New Zealand species. Palæohatteria, however, is still more primitive, in: (1) its solid pelvic plates, (2) its five distal tarsalia, (3) its simple caudal vertebræ without breaking points, (4) its rhomboidal interclavicle. It resembles Protorosaurus, and is more specialized than Sphenodon, in: (1) the presence of three sacrals, (2) the dorsal expansion of the ilium, (3) the reduction of the proximal row of tarsals to two elements.

All the progressive characters of *Palæohatteria* point toward the Dinosauria rather than toward the Rhynchocephalia.

#### Genus Kadaliosaurus Credner.1

MATERIALS.—A single specimen from the Mittel Rothliegenden (Lower Permian) associated with remains of Stegocephala (*Branchiosaurus*, *Archegosaurus*, etc.) Size.—Portion preserved, 225 mm.—about equal to the distance between the humerus and the femur.

VERTEBRÆ.—Amphicœlous perforated by large continuous notochord, hypocentra if present not exposed to view. Rudimentary diapophyses on the dorsals. Dorsal vertebræ elongate; 20 or more dorsals (15–16 only preserved); the back is certainly long; 2 sacrals. The 8 anterior caudals preserved apparently indicate that the tail was not very long.

RIBS.—The ribs indicate a deep, lightly constructed chest (longest rib 33 mm.). Ribs apparently hollow, capitulum and tuberculum not distinctly separated, capitula attached apparently to anteroinferior portion of the centrum or between centra, without union with a diapophysis. A large separate sacral rib and probably a second one concealed. Four rather strong anterior caudal ribs united with vertebræ anteriorly.

<sup>&</sup>lt;sup>1</sup> Die Stegocephalen und Saurier, etc., VIII. Theil. Zeitschr. d. Deutsch. geol. Ges., Bd. XLI, 1889.

#### 474 OSBORN, THE REPTILIAN SUBCLASSES DIAPSIDA AND SYNAPSIDA.

ABDOMINAL RIBS.<sup>1</sup>—Complex but primitive, 80 transverse series opposite twenty vertebræ, therefore 4 to 6 (Credner) attached to each costal rib; each transverse series includes 7 elements on each side (Credner, op. cit., fig. 9), and a small nodular median element, or 15 in each transverse series, the lateral elements being short and forked (Credner reconstructs, op. cit., p. 327, an angulate median costal piece, but in his plate xv the median pieces are all paired).

Pelvis.—Ischium large and plate-like, forming with pubis a solid continuous plate, which, correlated with large sacral ribs, indicates a center of motion at this point; ilium extended anteriorly and posteriorly, therefore resembling that of Dinosaurs.

SHOULDER GIRDLE.—Unknown.

LIMBS.—Fore and hind limbs equally long and slender, but metatarsals more elongate than metacarpals; limb bones solid, without cavities; ends of limb bones osseous. Humerus with a distal perforation believed to represent an ectepi- or radiocondylar foramen. Femur decidedly curved; tibia much larger than fibula, a decided indication of ambulatory and cursorial habits; astragalus and calcaneum large and solid; five distal tarsalia; distal phalanges short, bent and pointed.

AFFINITIES.—Credner calls attention to the very close resemblance of the distal end of the femur to that of *Varanus*. *Kadaliosaurus* is much more akin to *Protorosaurus* in its adaptation to rapid running, or even saltatorial life, than it is to *Palæohatteria*. In these respects it approaches the hypothetical ancestral Dinosaur, but is still far more primitive in the constitution of its vertebræ and in the presence of numerous abdominal ribs. (See also under 'Conclusions.')

#### II.—ORDER PELYCOSAURIA COPE.2

These Diapsida from the Permian of Texas and of Bohemia were unfortunately united with the Theromorpha by Cope and hence confused with the Anomodontia by more recent writers, but they have now been made completely

<sup>&</sup>lt;sup>1</sup> In other Triassic and more recent reptiles the relations of the costal and abdominal ribs are (according to Credner) as follows:

	Transverse series	Number of ab- dominal ribs to each opposite pair of costal ribs	Number in each transverse series
Kadaliosaurus	80	3–6	13–15
Palæohatteria		3	
Protorosaurus		3	3
Stereosternum		5-6	
Hyperodapedon		5-6	3
Homæosaurus \ closely resembling Sphe-			
Saphæosaurus \ nodon.			
Sphenodon	20-25	2-3	
Ichthyosauria		I	3
Pterosauria			3 (a median and two lateral)
Alligator	6-8		2
Lariosaurus		2	3 (a median and two lateral)
Plesiosaurus			3-4 " " 2-3 "

In Kadaliosaurus there being 13-15 elements in each transverse series, it follows that the number of separate abdominal ossicles is greater than that in any other known reptile, and is approached only in Palaohatteria, Protorosaurus, Stereosternum and Hyperodapedon.

<sup>&</sup>lt;sup>2</sup> Descriptions of Extinct Batrachia and Reptilia from the Permian Formation of Texas. Palæontological Bulletin, No. 28, and Proc. Amer. Philos. Soc., Vol. XVII, p. 528, 1878.

known by the researches of Baur and Case. Absolutely unrelated to the Anomodontia, they form a compact, highly specialized suborder, which rapidly developed

in the Permian and Triassic of America and Europe. As shown in Case's recent studies, the shoulder girdle (Fig. 12) is one of the most primitive known among the Diaptosauria, through the possession of large and suturally separate coracoid and procoracoid elements. On the other hand, the skull undergoes a rapid evolution from a relatively broad, flattened type (*Diopeus*)

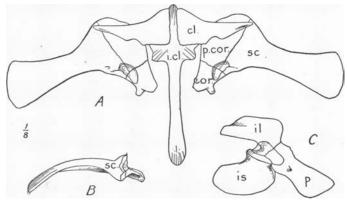


Fig. 12. A. Shoulder girdle of a Pelycosaurian (*Embolophorus*?) B. Profile view from the rear of conjoined scapula and procoracoid of same. C. Pelvis of same. After Case.  $\times \frac{1}{8}$ .

to a narrow, elevated, laterally appressed type with a depressed quadrate region (Dimetrodon).

Correlated with this was the development of the enormously elevated neural spines of the dorsal region (Fig. 13) and the abbreviation of the tail.

DEFINITION OF PELYCOSAURIA.—This order may now be defined as follows:

Raptorial, carnivorous ambulatory Diaptosauria. Skull progressively compressed, dorsal spines elongated, tail abbreviated. Vertebræ perforated by notochord, amphicælous. Ribs two-headed; capitula mainly hypocentral in attachment. Interclavicle T-shaped. Coracoid and procoracoid (in certain forms) separated by suture. A puboischiadic fenestra between pubis and ischium (Case). Humerus with entepicondylar (ulnocondylar) foramen.

Its nearest affinities are with the Protorosauria, but it is decidedly more progressive in rib, pelvic and cranial structure; it became very highly specialized and died out in the Trias.

#### PRINCIPAL CHARACTERS.

#### Primitive characters' of the Pelycosauria are:

SKULL.—(1) Acuminate, the orbits large, and paired nares near the anterior end of the snout, strikingly similar (*Theropleura*) in general outline and appearance to the skull of *Protorosaurus*. (2) Temporal arches composed of separate squamosals, prosquamosals, large quadratojugals overlapping the quadrate; quadrate of relatively small vertical extent. (3) A pineal foramen. (4) Separate prefrontals, postfrontals, postorbitals, large paroccipitals (opisthotics) separated from the quadrates by cartilage. (5) Occipital condyle, single. (6) Pterygoids tripartite. (7) Ectopterygoid not distinct so far as observed (Case). (8) Dentition: teeth conical, irregular in size, on maxillaries, premaxillaries, palatines and pterygoids. (9) Mandible typical.

(10) VERTEBRÆ. — Amphicœlous, amphiplatyan, notochordal; neurocentral sutures usually persisting; with prominent anterior facet for hypocentra in cervicals, dorsals and anterior caudals

<sup>&</sup>lt;sup>1</sup> Description based principally on the osteology of *Embolophorus* (*Dimetrodon*) dollovianus Cope, as described by Case.

(D. dollovianus); sacral vertebræ 2 (Dimetrodon) or 3, dorsal vertebræ 16, 27 + presacral vertebræ (Case, Dimetrodon dollovianus); three sacrals with separate ribs attached to sides of pleurocentra,

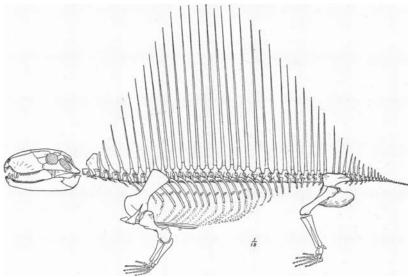


Fig. 13. Restoration of Embolophorus. About 18 nat. size. After Case.

certain of the neural arches laterally perforated at the base as in Palæohatteria; tail abbreviated, with broad hypocentra not converted into chevrons (D. dollovianus). (11) Hypocentra throughout the series (D. dollovianus) or reduced in lumbar region; hypocentra articulating with capitula of ribs by prominent lateral processes in anterior portion of vertebral column; anterior cervical vertebræ temnospondylous.1

- (12) RIBS. Two-headed (*Embolophorus*) except in first cervical or atlas, which has a single facet for the capitulum of the first rib; capitula of cervical ribs unite with hypocentra and pleurocentra in part.
- (13) GIRDLES.—Shoulder girdle with coracoid and procoracoid suturally united; coracoid remaining free from scapula, but suture between scapula and procoracoid tending to close; clavicles large, episternum T-shaped. *Pelvic girdle*, ilium, ischium and pubis entering into acetabulum, with pubic arrangement triradiate.
- (14) LIMBS. Humerus with entepicondylar foramen, ectepicondylar groove like that of *Sphenodon*, free centrale carpi as in *Palæohatteria* and *Protorosaurus*, 5 distal carpalia in *D. dollovianus* (Case) *i. e*, carpalia 4 and 5, separate. Tarsalia 4 and 5, united.

The progressive characters of the American Pelycosauria are summarized by Case from stages represented by *Diopeus*, *Edaphosaurus*, *Clepsydrops*, *Dimetrodon*, as follows:

(1) Temporal arches remaining distinct but becoming very slender. (2) Depression of the posterior angle of the skull or suspensorial region by a shortening and reduction of the quadrate. (3) Gradual elevation and transverse narrowing of the facial region by vertical growth and extension of the maxillaries and narrowing of the frontals and nasals; premaxillaries with a vertical anterior process, supporting one large and four smaller incisors. (4) Increase in size of ectopterygoid process of the pterygoids. (5) Increase of maxillary and premaxillary tusks and development of serrations on the edges of the teeth. (6) Correlated with these changes is the elevation of the neural spines from twice the length of the centrum (*Diopeus*) to twenty-eight times the length of the centrum (*Dimetrodon*); transverse processes on the spines (*Naosaurus*). (7) Coalescence of squamosal and prosquamosal, enlargement of quadratojugal, and overlapping of reduced quadrate.

<sup>&</sup>lt;sup>1</sup> A cervical complex in the Chicago Museum, originally attributed to *Dimetrodon* by Baur, shows an atlas composed of separate hypo-, pleuro-, and neurocentra, a proatlas consisting of a dorsal neurocentrum, and an axis composed of a hypocentrum, with neurocentrum and pleurocentrum conjoined.

<sup>&</sup>lt;sup>2</sup> The pelvis attributed to *Dimetrodon* by Cope proves to belong to the Stegocephalian genus *Eryops* (Case).

#### ADAPTATION.

In the development of the premaxillaries, these animals parallel the Carnivorous Dinosaurs, while in the reduction of the quadrate they take a direction the reverse of that observed in the Dinosauria and Squamata and somewhat similar to that seen in the Crocodilia. These types were adapted for seizing and holding an active prey, specializing the anterior teeth for prehensile, the posterior teeth with serrations for piercing purposes, thus progressively carnivorous, and acquiring, as observed by Case, a strictly vertical motion of the jaws. The depressed and rather weakly embraced suspensorial region was, in the opinion of Case, unadapted to resist the strain imposed by the fierce bites these animals were capable of inflicting.

The chief literature of the subject is to be found in Cope's numerous papers on the Permian Vertebrates, in the joint memoirs by Baur<sup>1</sup> and Case<sup>2</sup> and in the three recent papers by Case.<sup>2</sup>

#### III.—RHYNCHOSAURIA, ord. s. subord. nov.

These Lower Triassic animals are known from the type, Rhynchosaurus of the English Trias, and from two species of Hyperodapedon, namely, H. gordoni from the Elgin Sandstones and India, and H. minor Burckhardt from the Elgin Sandstones. They are readily distinguished by the premaxillaries and dentaries terminating in large curved beaks (which were probably sheathed with horn), by two or more rows of teeth upon the palatines, and by degeneration or absence of teeth on the maxillaries and premaxillaries. The following description is based on the contributions of Owen, Huxley and Burckhardt.

As recently pointed out by Burckhardt, whose opinion that these animals form a separate group of Rhynchocephalians with no direct affinities is here adopted, these reptiles are probably of littoral, shell-eating habits, with remarkably modified skull, beak and dentition. They are apparently as distinct from

<sup>&</sup>lt;sup>1</sup> Baur and Case. On the Morphology of the Skull in the Pelycosauria and the Origin of the Mammals. Anat. Anz., XIII, 1897, pp. 109–120.

<sup>&</sup>lt;sup>9</sup> Baur and Case. The History of the Pelycosauria with a Description of the Genus *Dimetrodon*. Trans. Amer. Philos. Soc., (2) XX, pp. 1-58, pll. i-iii, 1899.

<sup>&</sup>lt;sup>3</sup>(a) The Structure and Relationships of the American *Pelycosauria*. Amer. Nat., Vol. XXXVII, No. 434, Feb., 1903.

<sup>(</sup>b) The Osteology of *Embolophorus dollovianus* Cope. With an Attempted Restoration. Jour. of Geol., Vol. XI, No. 1, Jan.-Feb., 1903.

<sup>(</sup>c) Palæontological Notes, Lysorophus tricarinatus. Contrib. from Walker Museum, Vol. I, No. 3, Chicago, May, 1902.

<sup>&</sup>lt;sup>4</sup> Description of an Extinct Lacertian Reptile, *Rhynchosaurus articeps* . . . . Trans. Cambridge Philos. Soc., Vol. VII, part iii, 1843.

<sup>&</sup>lt;sup>5</sup> Further Observations upon *Hyperodapedon Gordoni*. Quar. Jour. Geol. Soc., London, Vol. XLIII, 1887, pp. 675-694, pll. xxvi, xxvii; reprinted in The Scientific Memoirs of Thomas Henry Huxley, Vol. IV, pp. 636-657, pll. [27], [28].

On Hyperodapedon Gordoni. Geol. Mag., Dec. IV, Vol. VII, pp. 486-492 and 529-535, Nov. and Dec., 1900.

the Proterosauria and Rhynchocephalia, the only Diaptosaurians with which they can be compared, as the Stegosauria are from the Megalosauria among Dinosaurs. The alleged resemblances to *Sphenodon* in the premaxillary region are deceptive; no real analogy even exists. It is certainly very far from the evidence to consider these animals as a family of Rhynchocephalia. At the same time it is doubtful whether they have more than subordinal rank.

DEFINITION OF RHYNCHOSAURIA.—Probably littoral, shell-eating Diaptosauria. Premaxillaries decurved, edentulous. Maxillaries edentulous. Palatines (palatopterygoids) with small tesselated teeth. A single narial opening. Vertebræ amphicælous, imperforate. Interclavicle T-shaped. Coracoid and procoracoid suturally separate (in certain forms). Pubis and ischium more or less continuous.

SKULL.—Extremely broad and short (*Hyperodapedon*) (Fig. 14); elongate (*Rhynchosaurus*—another illustration of contemporary brachycephaly and dolichocephaly in related types; face correspondingly abbreviate in *Hyperodapedon*, elongate in *Rhynchosaurus*. Skull narrow, elongate

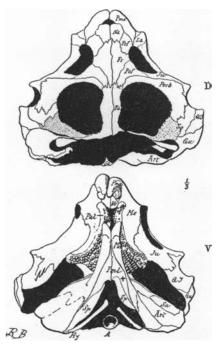


Fig. 14. Skull of Hyperodapedon gordoni. D, dorsal, V, venetral aspect,  $\times \frac{1}{3}$ . After Burckhardt. The black areas represent parts still covered by matrix.

(Rhynchosaurus); parietals with sagittal crest. Skull openings: single or median narial opening, as in Testudinata, very large orbital openings, but no pineal foramen; supratemporal fenestræ very large; laterotemporal fenestræ smaller (Huxley); probably a posttemporal fenestra (Burckhardt). Separate nasals, lachrymals, prefrontals, postfrontals, postorbitals (Burckhardt); frontals separate (Burckhardt), coalesced (Huxley); postorbitals excluded from orbits by union of postfrontals and jugals. Quadrates broad. Premaxillaries edentulous, closely compressed, decurved. Prevomers abbreviate anterior in position (Hyperodapedon), articulating posteriorly with elements determined as palatines (Burckhardt) but which may represent palatopterygoids (Osborn). Faw.—Dentaries bifurcated for united premaxillary rostrum in Rhynchosaurus, less so in Hyperodapedon. Jaw without coronoid process (Rhynchosaurus), composed of dentary, articular, angular, coronoid, splenial, presplenial (Hyperodapedon, Burckhardt). Dentition.—Premaxillaries and maxillaries edentulous in Hyperodapedon (Burckhardt). Palatines [palatopterygoids] with numerous rows, divergent posteriorly, of low conical grinding teeth (Burckhardt). In Rhynchosaurus two rows of small palatine teeth. Teeth added posteriorly. Inferior teeth on dentaries.

VERTEBRÆ.—Deeply amphicælous (Rhynchosaurus), slightly amphicælous (Hyperodapedon), "opisthocælous" (Huxley), not perforated by notochord (Rhynchosaurus); pleuro- and neurocentra firmly coalesced (Rhynchosaurus, Owen, op. cit., p. 356). No evidence of hypocentra (Rhynchosaurus, Huxley). A single hypocentrum is figured by Burckhardt. Presacrals in Hyperodapedon 23-24 (Huxley) or 22-23 (Burckhardt). Sacrals 2 (Huxley); number of sacrals doubtful (Burckhardt). Dorsal vertebræ increasing in size posteriorly, ribs expanded (Hyperodapedon, Burckhardt). Tail with large chevrons; the length of the tail is not definitely known. Cervicals short, cervical ribs large, free, pointed, articulating opposite pleurocentra (Hyperodapedon, Huxley, op. cit., pl. xxvi); cervical ribs partly attached between vertebræ, or hypocentral (Burckhardt's figure of Hyperodapedon). Dorsal ribs single-headed in Rhynchosaurus (Owen, op. cit., p. 364); heavy, broad-headed in Hyperodapedon.

ABDOMINAL RIBS.—Strongly developed (Hyperodapedon).

SHOULDER GIRDLE.—Coracoid composed of two parts: coracoid and procoracoid (Hyperodapedon, Burckhardt, op. cit., p. 3); interclavicle narrow (Hyperodapedon, Huxley). In Rhynchosaurus coracoid single and imperforate. In Rhynchosaurus, a T-shaped interclavicle (Huxley, pl. xxvii). Scapula elongate, spreading (Rhynchosaurus).

PELVIC GIRDLE.—(Huxley, Hyperodapedon, pl. xxvi, fig. 12, Rhynchosaurus, pl. xxvii, fig. 4.; Rhynchosaurus with united plate-like pubis and ischium, apparently no puboischiadic foramen. Hyperodapedon, pubis and ischium apparently separated by a puboischiadic fenestra.

LIMBS.—Short; humerus proximally expanded as in terrestrial forms, not distally as in aquatic forms; ulna and radius closely applied, podials and metapodials abbreviate, digits spreading, terminating in small claws (*Hyperodapedon*, Burckhardt), fourth digit the largest (*Hyperodapedon*), metapodials relatively long (*Rhynchosaurus*). The phalangeal formula is apparently Diapsidan (*Hyperodapedon* and *Rhynchosaurus*).

Adaptation.—Burckhardt points out the physiological parallel with the Placodontia, the food probably consisting of crustacea, molluscs, echinoderms and other hard-shelled animals, which, coupled with the strong abbreviate vertebral column, limbs, manus and pes without traces of aquatic adaptation, points to littoral marine habits. In *Hyperodapedon* the abbreviated skull, with enlarged premaxillary rostrum functioning as tusks, may have been adapted to apply considerable force to the detachment of mollusca and other forms of shell life, as in *Odobæna*. The jaws in *Hyperodapedon* could not move forward and backward as in *Sphenodon* but obliquely (Burckhardt).

The long-skulled *Rhynchosaurus* was a more ambulatory form with long and relatively slender fore and hind limbs and metapodials, the hind limbs being longer than the fore limbs.

Affinities.—Burckhardt observes that the premaxillary rostrum is not to be compared with that of *Sphenodon*; moreover, these animals lack the premaxillary and maxillary teeth observed in *Sphenodon*; he considers them an independent branch derived from the same stem as the Rhynchocephalia, paralleling in certain respects the Chelonia and Endothiodontidæ. It is certainly very far from the evidence to place these animals as a family of Rhynchocephalia vera.

#### IV.—ORDER PROCOLOPHONIA SEELEY.

Suborder Procolophonia LYDEKKER.

This order, based upon the type *Procolophon*, was originally placed by Seeley under the Rhynchocephalia and then transferred to the Anomodontia. Adopted as a suborder of the Anomodontia by Lydekker. The very large series of *Procolophon* remains in the Albany Museum examined by Dr. R. Broom led this author to the following conclusion:

"The examination of the above specimens shows that Procolophon has its

<sup>&</sup>lt;sup>1</sup> Q. J. G. S., Vol. XXIII, pp. 142-144.

<sup>&</sup>lt;sup>2</sup> Proc. Roy. Soc., Vol. XLIV, p. 383, 1888.

<sup>&</sup>lt;sup>3</sup> Cat. Foss. Rept. Amphib., Pt. IV, p. 12.

<sup>&</sup>lt;sup>4</sup> On the Remains of *Procolophon* in the Albany Museum. Records of the Albany Museum, Vol. I, No. 1, April 24, 1903.

affinities with *Palæohatteria*, and that it is not a near ally of the Theriodonts. In only one important character does it resemble the Theriodonts, viz., the possession of an ossified precoracoid; while the possession of abdominal ribs, a persistent notochord, and the presence of 3, 4, 5, and 4 phalanges in the 4 outer digits, remove it far from the Dicynodonts, the Theriodonts, and the Monotremes, and place it somewhere among the primitive Rhynchocephalians,—possibly not far from *Palæohatteria*."

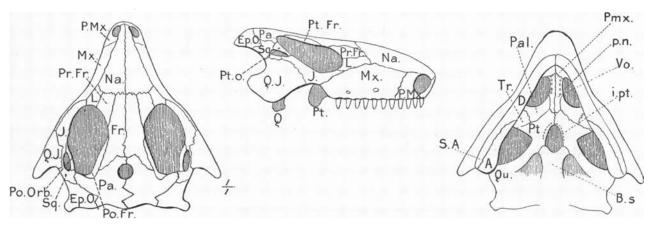


Fig. 14 a. Restoration of the skull of Procolophon trigoniceps Owen. Slightly modified from Smith Woodward. Ep.O, Epiotic; Vo, Prevomer (Broom); Tr., transversum or ectopterygoid; p.n., posterior nares; i.pt., interpterygoid space.

This conclusion, which is sustained by abundant evidence, is of very great importance, because *Procolophon* is not only by far the most primitive of the Diapsida, but the most nearly transitional between the Diapsida and their theoretical Cotylosaurian ancestors. Its principal characters, as enumerated by Seeley and more fully by Broom (op. cit.), are as follows:

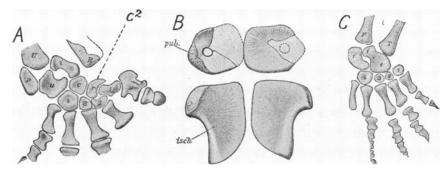


Fig. 14 b. A, manus, B, pelvis, and C, pes, of Procolophon trigoniceps Owen. After Broom.  $\times \frac{1}{2}$ .

SKULL.—Short, triangular, with sinuous sutures of Cotylosaurian type, and with all the elements characteristic of the Cotylosaurian skull, separate and distinct, including the 'epiotics,' the paired prevomers, and median true vomer or parasphenoid, also the separate ectopterygoids. Separate epipterygoids (columellæ cranii). Large orbits confluent posteriorly with the supratemporal fenestræ. Posterolateral 'auditory notch' characteristic of certain Cotylosauria and Stegocephala. Large pineal opening. Small, perhaps rudimentary laterotemporal fossæ. Palate

with typical primitive reptilian arrangement, namely, pterygoids (surrounding interpterygoid space and median vomers), uniting anteriorly with the prevomers, palatines short and transverse, premaxillæ with three teeth. Molars with broad, flattened crowns, in lower jaws anchylosed to dentary, teeth also on prevomers and pterygoids.

This survival of Cotylosaurian characters, in (a) palate, (b) auditory notch, (c) epiotics, (d) sinuous sutures in the skull, together with the Cotylosaurian separation of the coracoids and procoracoids renders it not at all surprising that this animal should have been previously placed with the Anomodontia. Certain of the following characters, however, enumerated principally from Broom's paper, demonstrate that it is one of the Diapsida.

VERTEBRÆ.—Amphicœlous, traversed by persistent notochord. Hypocentra double or paired between atlas and axis, also between axis and cervical 3; large single or median hypocentra between the succeeding cervicals and dorsals; hypocentra also between anterior caudals. Atlas composed of "an arch [neurocentra] and an inferior element," also of "a distinct, well-developed pro-atlas." Caudal chevrons beginning with the fourth caudal.

Ribs.—Apparently at sides of axis and on each succeeding vertebra, including the anterior caudals.

ABDOMINAL RIBS.—"An inner bifurcated series, with at least three additional splint bones passing outward from the presumed innermost element."

GIRDLES.—Coracoid and procoracoid separate; procoracoid large, quadrate in form, but not extending in advance of scapula. Distinct clavicles, and very long interclavicle. Ischia and pubes continuous, that is, no puboischiadic (thyroid) foramen; pubis with large obturator foramen.

LIMBS.—Short, equal-sized; humerus with ulno- (entepi-) condylar foramen, no ectepicon-dylar foramen. Carpus including intermedium, ulnare, pisiforme, carpalia 1-4 only, and apparently two centralia carpi (bone figured as radiale by Broom [pl. I, fig. 4] appears to be a second centrale; the true radiale was undoubtedly present). Phalangeal formula of manus 2, 3, 4, 5, 4; the presence of 4 phalanges on D V is noteworthy (Broom, p. 23). The pes includes a tibiale uniting with intermedium, a large fibulare, and tarsalia 1-4 only; tarsalia 4 and 5 are undoubtedly represented in tarsale 4. The phalangeal formula of the pes was 2, 3, 4, 5,?

Affinities.—We must await the publication of Broom's memoir before the nearer affinities of *Procolophon* can be determined. The chief interest lies in its primitive transitional or annectant character between the Cotylosauria (compare pp. 456, 457) and Diapsida, especially in the skull and shoulder girdle. In the manus and pes it is typically Diapsidan and even somewhat specialized.

#### V.—ORDER PROGANOSAURIA BAUR.

#### Mesosauria SEELEY in part.

The type of the order Proganosauria Baur<sup>1</sup> is the genus *Stereosternum* Cope<sup>2</sup> (Figs. 15, 16a, 17, 17a, 17b, 18, 19, and Pl. XL) from the Permian of Brazil; the chief ordinal character assigned was the possession of five separate distal tarsalia. The Mesosauria Seeley<sup>3</sup> was proposed to include both the Proganosauria of Baur and the Neusticosauria (= primitive Plesiosauria) of Seeley on the supposition that these animals were related. This name has been adopted by Boulenger, Fürbringer and others, as well as the theory advanced by Seeley that these animals are ancestral to the Sauropterygia. This theory is found to

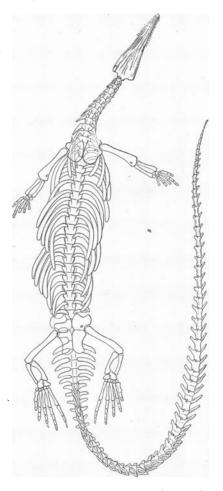
<sup>&</sup>lt;sup>1</sup>On the Phylogenetic Arrangement of the Sauropsida. Journ. Morph., Vol. I, 1887, p. 103.

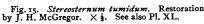
<sup>&</sup>lt;sup>2</sup> A Contribution to the Vertebrate Palæontology of Brazil. Pal. Bull. No. 40, July 30, 1885; Proc. Amer. Philos. Soc., Vol. XXIII, No. 121, 1885.

<sup>&</sup>lt;sup>8</sup> The Mesosauria of South Africa. Quar. Journ. Geol. Soc., Vol. XLVIII, 1892, pp. 586-604.

be untenable; the Proganosauria are in many respects parallel to the Neusticosauria but are not related to them.

They are probably Permian, thus being contemporaneous with the Protorosauria, the Pelycosauria, the Rhynchosauria, and the Procolophonia. They present some very marked resemblances to *Sphenodon* and some aberrant and very distinctive specializations.





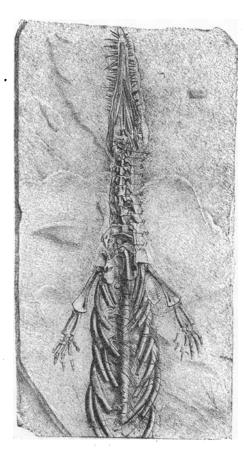


Fig. 16. Mesosaurus tenuidens. After Gervais, X 1.

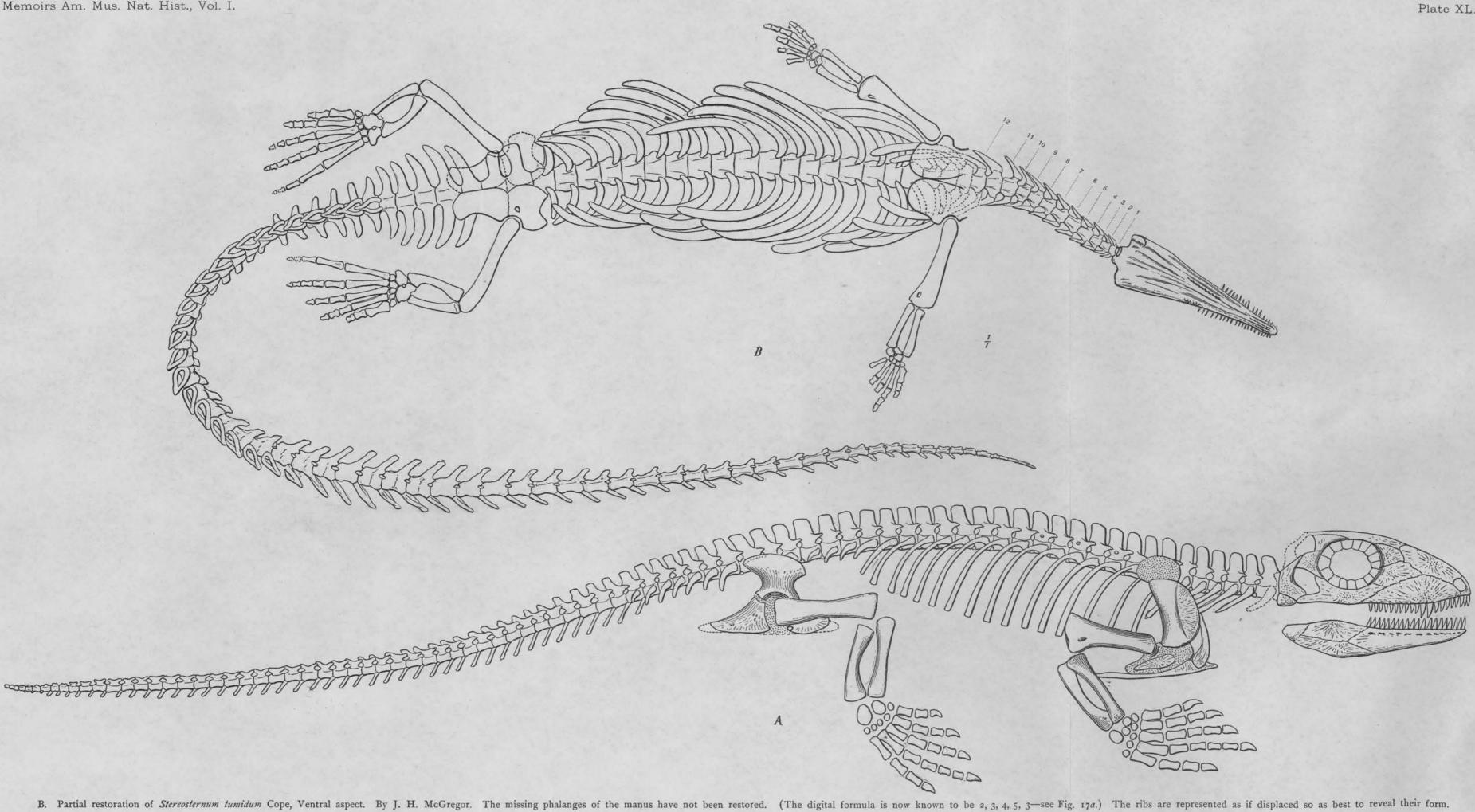
Definition of Proganosauria.—Aquatic Diaptosauria. Greatly elongated face. Slender prehensile teeth. Vertebræ expanded superiorly (i. e., neurocentra), perforated below by notochord, amphicælous; hypocentra generally wanting. Caudals with 'splitting point.' Ribs slender, proximally attached to grooves in pleurocentra, expanded distally. Pectoral girdle plate-like, without sutural division of procoracoid and coracoid. Pelvic girdle plate-like, with broad pubes perforated by obturator foramen, and more elongate ischia. Five free distal tarsalia.

This order is now known to include two genera:

Mesosaurus Gervais.

Stereosternum Cope. 12 cervicals.

9 + cervicals.



A. Restoration of Palachatteria longicaudata Credner. By J. H. McGregor. The limbs and ribs of the left side, the cartilaginous ribs and abdominal ribs are not represented as if rotated outward, bringing Digit 1 uppermost and exposing the dorsal aspect.



Materials.—The type and two other specimens of *Stereosternum tumidum* Cope were very kindly loaned to the American Museum for purposes of study by the Geological Survey of Brazil, through Dr. Orville Derby, and have been exhaustively restudied for this memoir. Many additional specimens were received from the same generous source while this memoir was in press. They add several new characters.

The material studied from plates and descriptions includes Gervais's 1 type (Fig. 16) of *Mesosaurus tenuidens* (1865) and six specimens of *Mesosaurus* (M. pleurogaster Seeley?) in the South African Museum; a more perfectly preserved specimen of *Stereosternum* in the São Paulo Museum described by A. Smith

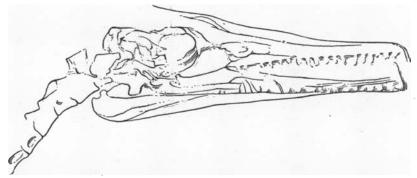


Fig. 16 a. Imperfect skull of Stereosternum tumidum Cope, showing the position of the orbits. The narial openings could not be determined. From specimen belonging to Geological Survey of Brazil.  $\times \frac{1}{2}$ .

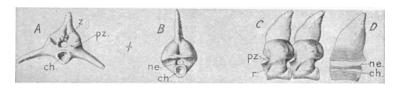


Fig. 17. Stereosternum tumidum Cope.  $\times \frac{1}{4}$ . A, First sacral vertebra, anterior view; B, Middorsal vertebra, posterior view; C, Two mid-dorsal vertebræ, lateral view; D, Imperfect dorsal vertebra. Z, Zygosphene:  $\not$ z, prezygapophysis; ch, notochordal canal; ne, neural canal; r, groove for reception of capitulum of rib.

Woodward<sup>3</sup>; finally, two specimens in the Dresden Museum described and figured by Geinitz.<sup>4</sup> The *Mesosaurus pleurogaster* material described by Seeley is from the Karoo Series of South Africa, and the *Stereosternum* material is from probably homotaxial deposits in the south of Brazil.

The following diagnosis is based upon the writer's own studies, aided by Dr. McGregor and Mr. Barnum Brown:

#### GENUS Stereosternum Cope.

SKULL.—Elongate (58.5-80 mm. in the specimens examined, exactly the length of the neck), triangular, the snout is slightly expanded anteriorly; the position of the orbits is now definitely

<sup>&</sup>lt;sup>1</sup> Zoologie et Paléontologie Générales. Ser. I, p. 223 (1867-69).

<sup>&</sup>lt;sup>3</sup> The Mesosauria of South Africa. Quart. Journ. Geol. Soc., Vol. XLVIII, 1892, pp. 586-604.

<sup>&</sup>lt;sup>8</sup>On a New Specimen of Stereosternum. Geol. Mag. (4), Vol. IV, p. 145, 1897.

<sup>&</sup>lt;sup>4</sup> Sur Stereosternum tumidum Cope du Musée royal de Minéralogie de Dresde, provenant de São-Paulo (Brésil). Ann. d. l. Soc. géol. de Belgique, Tome XXV bis (4to), pp. 35-42, pl. i. Liège, 1900.

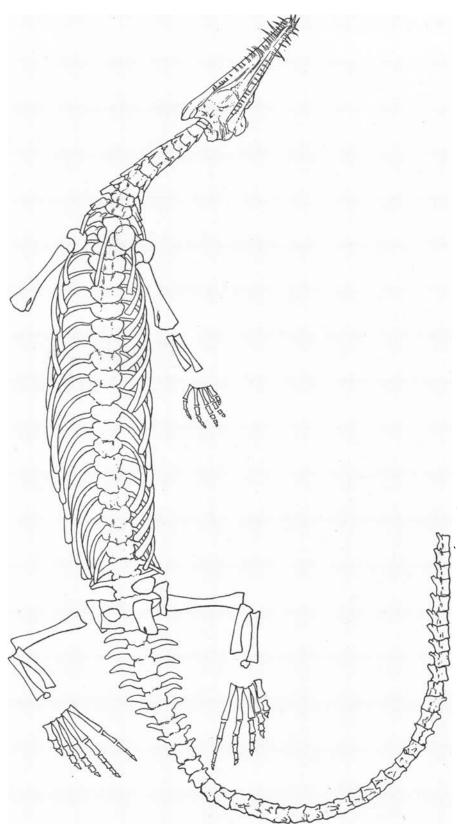


Fig. 17 a. Stereosternum tumidum Cope. Skeleton of young individual. X \(\frac{1}{2}\). In order to reveal the structure of the sacral vertebræ the right pubis and ischium are omitted. The drawing is based on a single animal represented in a slab and its counterpart. The capitula of the right side (left in drawing) are crushed out of place. Belonging to the Geological Survey of Brazil.

known, they are certainly posterior. The facial portion is therefore elongate and the cranial portion abbreviate. The palate is completely closed (*Mesosaurus*, Seeley; *Stereosternum*, Geinitz) without indication of any vacuity or interpterygoid space. Two lateral ridges, probably on the palatines, may have carried teeth in single rows. The structure of the very important temporal region has not been made out; it is therefore not known whether the skull is Diapsidan or Synapsidan.

TEETH.—Delicate, pointed, recurved, set wide apart, anterior teeth larger than posterior. Teeth on maxillaries, premaxillaries, dentaries and palatines. Teeth in sockets (Geinitz).

VERTEBRÆ (Figs. 17, 18, A).—In Mesosaurus Gervais described nine cervicals, not including the narrow ventral ring of the atlas, which makes ten. Cope's determination of the vertebræ in Stereosternum was incorrect. The vertebral formula can be clearly made out as follows:

Cervicals	I 2
Dorsals 22; or total presacrals	
Sacrals	
	60-64

In the specimen described by Smith Woodward "the tail comprises not less than sixty vertebræ of which at least the foremost seven bear robust transverse processes [caudal ribs] gradually diminishing in size backwards." In the specimens I have examined the first eleven caudals bear ribs. In Stereosternum all the vertebræ are amphicælous and the presacrals are more deeply excavated anteriorly than posteriorly. A continuous small notochordal canal pierces the upper part of each pleurocentrum, as in Pelycosauria. The neuro- and pleuro-centra are firmly coalesced, there

being no trace of a neurocentral suture. Beneath the atlas and axis are two narrow and apparently free hypocentra, but there is no trace of hypocentra beneath the other cervicals or the dorsals. The cervical vertebræ are short and tranversely extended, the total length of the neck being 58 mm.1 or exactly the length of the head. The cervical vertebræ laterally expanded into broad processes (diapophyses) which bear the ribs. The dorsal vertebræ are peculiar in the great bulbous expansion of the upper portion of the neural arches, or neurocentra, which are much larger than the inferior por-Sauropterygia of the Neustico-

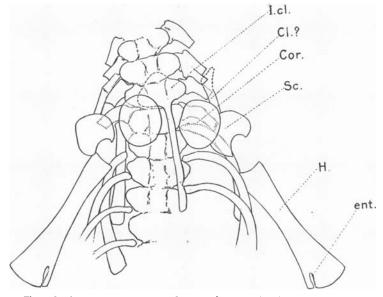


Fig. 17 b. Stereosternum tumidum Cope. X \frac{2}{3}. Pectoral region of young individual. Cervicals 9-12, and dorsals 1-4 are represented. Belonging to the Geological Survey of Brazil.

saurus type, the reverse is the case). We can distinguish pre- and postzygapophyses; also in certain vertebræ small zygosphene (Fig. 17, A, z) and zygantrum (Fig. 17, B) articulations above the neural canal. The rib attachments are unique, the slender capitulum fitting into an anterolateral groove (Fig. 17, C, r). No diapophyses for articulation with the ribs are distinguishable. The anterior and mid-dorsals exhibit broad neural spines; the anterior caudals exhibit narrow and more pointed neural spines. The two sacrals each exhibit a firmly coalesced and expanded sacral rib; eleven of the anterior caudals also exhibit ribs coalesced to the centra; each caudal exhibits an expanded

All the measurements given are from the individual figured in Plate XL.

neurocentrum, distinct pre- and post-zygapophyses, also a median vertical ridge at the side of the centrum which corresponds with the breaking or 'splitting point' of the anterior caudals of the Lacertilia, the neural spine being borne entirely upon the posterior half; the chevrons are attached to prominent posterior articular facets. The most anterior chevrons are apparently open above; but they soon pass into the form of a closed fork with a transverse proximal bar forming a triangle,

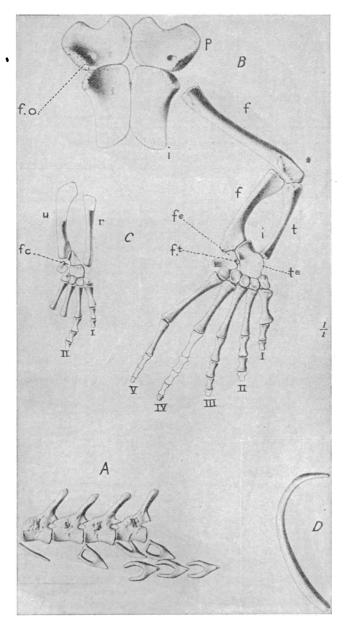


Fig. 18. Stereosternum tumidum Cope. From the type.  $\times \frac{1}{2}$ . A, Caudal verte bræ; B, Ventral view of pelvis and hind limb; C, Ventral view of fore limb; D, Dor sal rib. f.t, intratarsal foramen; f.c, intracarpal foramen; f.o, obturator foramen.

as in Sphenodon and certain Dinosaurs. The stoutness of these vertebræ and the large hæmal canal are indications of a long and powerful tail. As described by Smith Woodward, caudals 1-12 are comparatively short and stout; caudals 13-47 are more elongate, the chevrons becoming more delicate; caudals 47-60 are very slender; the tail is somewhat more than twice as long as the trunk and slightly less than three fifths the entire length of the animal. Judging from the dermal impressions, the end of the tail must have been exceedingly slender without any dermal expansion (Smith Woodward). spines persist except in the terminal vertebræ, and chevrons except in the thirteen terminal vertebræ.

Ribs.—There are 33 presacral ribs, that is, ribs can be made out on all the presacrals except the atlas. In the adult Stereosternum the cervical ribs, preserved in C2-12, are broad but single-headed, the capitula being attached to the broad lateral expansions of the pleurocentra; it is difficult to make absolutely sure whether a rudimentary tuberculum is present. The distal ends of the cervical ribs are excavated for tendinous attachments, and impressions of delicate lines of tendons can be traced along the sides of the neck. In the young Stereosternum (Fig. 17b), the posterior cervical ribs terminate very bluntly and were doubtless tipped with cartilage; they articulate with the cervical diapophyses by a broadly expanded head, which has a robust posterior and more slender anterior prolongation.

The adult dorsal ribs are highly characteristic, the shafts being very stout (as in Sauropterygia and Sirenia); they increase in size to about the fifth rib, which measures 47.5 mm.; there are in all 22 pairs of thoraco-lumbar ribs; unique features are the delicate or tapering capitula (Fig. 18,

D), which are apparently loosely attached in delicate, shallow, lateral grooves below the prezygapophyses in the anterior portion of the centra; but this point cannot be positively determined in the specimens under observation; no parapophysis can be observed.

In the young Stereosternum, (Fig. 17a) the series of ribs are clearly shown, although the capitula on the right side of the chest (left in the figure) have shifted somewhat from the actual points of attachment; the first rib is blunt and is inserted intervertebrally, or on the anterior side of the centrum of D I; the 2d-22d ribs on the left side also are shifted slightly backwards to the sides of the neurocentra, which, owing to crushing, are artificially in the same plane as the pleurocentra; the supposed relation of the capitula to a rib-groove mentioned above is not shown, owing perhaps to the crushing of the specimen.

The same relations obtain in *Mesosaurus* (Seeley, pl. xviii). The ribs expand distally and arch laterally, thickening below in a stout, blunt termination; the chest cavity was therefore narrow and deep (Fig. 19, B). As stated above, the two sacral ribs are broadly expanded and coalesced with the vertebræ; and the eleven anterior caudal ribs are also coalesced with the vertebræ, but somewhat less expanded. In *Mesosaurus tenuidens* the anterior cervical ribs are apparently single-headed,

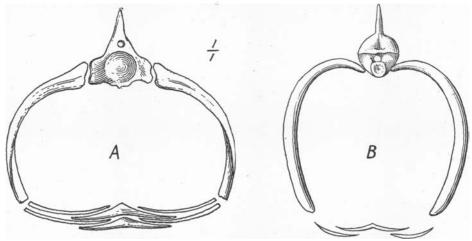


Fig. 19. A, Restored chest section of *Dactylosaurus*, a primitive Sauropterygian. After Deecke.  $\times \frac{1}{2}$ . B, Restored chest section of *Stereosternum*.  $\times \frac{1}{4}$ .

but in the 10th and 11th vertebræ, counting from the skull, the ribs are incipiently double-headed; these vertebræ, however, are usually enumerated among the dorsals, the line of demarcation between cervicals and dorsals being not so clear as in *Stereosternum*.

ABDOMINAL RIBS.—Contrasted with the heavy costal ribs, the abdominal ribs of *Stereosternum* are flattened and slender, almost filiform, placed in three transverse rows; the lateral rows partly bifurcated, the middle row overlapped and slightly angulate. In *Mesosaurus*, Seeley describes the abdominal ribs as "five or six times as numerous as the costal ribs."

GIRDLES.—In the shoulder girdle of the adult Stereosternum there is no proof of the separation of the coracoid and procoracoid; the specimen is much crushed, but no evidence of a division between these elements can be made out; the coracoid foramen is externally placed, that is, it is nearer the glenoid cavity than in Mesosaurus; the scapula and the dermal elements of the shoulder girdle cannot be made out. In the young Stereosternum (Fig. 17b), oval osseous coracoids, imperforate, are clearly shown; there is no evidence of the procoracoids which may have been represented in cartilage (compare young Sphenodon, Fig. 6). The supposed scapulæ are broadly semilunar in form. A long, slender inverclavicle with an anterior expansion is shown (Fig. 17b); there is some evidence of the presence of clavicles also. (Fig. 17b, cl.?)

<sup>&</sup>lt;sup>1</sup> Seeley describes the ribs as rising from the anterior portion of the neural arch in *Mesosaurus pleurogaster*; this observation we cannot confirm. (See notes below.)

In the *Mesosaurus tenuidens* (Fig. 6, D) type the girdle includes the scapula and a single coracoid + procoracoid element. In *M. pleurogaster* it is important to note that according to Seeley the coracoid and procoracoid are separate, or paired, on one side, and united on the opposite side (Seeley, Q. J. G. S., 1892, pl. xviii, p. 593), and that the coracoid is firmly coalesced with the scapula, there being no suture between them; together these bones form a broad plate extended anteroposteriorly. This observation as to the separation of coracoid and procoracoid in the adult appears, however, to require confirmation.

In the *pelvic* girdle (Fig. 18, B) of *Stereosternum* we can clearly make out solid ventral plates composed of the broad anterior pubes, which are perforated by the obturator foramen, and the more elongate ischia; these ischial plates are exactly similar in form to those of *Palaohatteria*, although less cartilaginous on the borders.

In the young *Stereosternum* (Fig. 17b) the borders of the pubis and ischium are less extended; the *ilium* is a small element, narrow or rod-like superiorly, resembling that of *Sphenodon* (compare Fig. 22 A), and totally different from that of *Protorosaurus* or *Palæohatteria*.

Limbs.—Before describing the limbs (Fig. 18, B, C) in detail it is important to note that both the pectoral and pelvic girdles are solid and expanded ventrally; and that although the hind limb is larger than the fore, there is a striking similarity (Fig. 15) between the pectoral girdle and fore limb and the pelvic girdle and hind limb in the following points: (1) the absence of osseous terminal facets of the limb bones, the region of the joints being flat; (2) the striking homodynamy or similarity in the disposition of the propodials, podials, and metapodials in the fore and hind limbs; (3) the articular relations of the ulna and fibula to the intermedium carpi and intermedium tarsi respectively; (4) the slender elongate digits; (5) the perforation of both carpus and tarsus by a foramen between the intermedium and the ulnare and fibulare respectively; (6) the divarication of the postaxial (5th) digit, as in Mosasaurs; (7) reduction of the claws in the phalanges, which terminate distally in flattened expansions; the last two characters apparently indicating the possession of incipient webs. The conclusion is that the fore and hind girdles and limbs were partly homodynamous.

Fore Limb.—More in detail the humerus, measuring 32 mm., is somewhat curved and exhibits distally an ulnocondylar (entepicondylar) foramen; it is somewhat more expanded distally (15 mm.) than in Mesosaurus. The ulna and radius are widely separated inferiorly by the intermedium (as in Stegocephala); the radius is smaller and nearly straight; the ulna is larger, curved, and forms the main articulation of the intermedium, and has a stout olecranon process. There were possibly nine carpalia, but only seven osseous elements are preserved, namely: (1) an intermedium articulating principally with the ulna, (2) an ulnare, (3) a large centrale carpi, (4-7) distal carpalia 1, 2, 3, 4. Of the two supposed cartilaginous elements, distal carpale 5 is probably cartilaginous or displaced; the radiale was almost certainly cartilaginous because a clear space is indicated for it. It is possible, however, that a gap existed at both these points. A foramen is left between the intermedium and ulnare which apparently transmitted a blood-vessel, as in the young Sphenodon (f. arteria perforans mesopodii, Howes). Exactly the same condition of the carpus is seen in the two specimens of the Brazilian collections, also in Mesosaurus as figured by Seeley. The phalangeal formula of the manus is 2, 3, 4, 5, 3, as ascertained in the young individual (Fig. 17a). In Mesosaurus the phalangeal formula is 2, 3, 4, 5, 3, 4, 5, 4, 5, 4, 6, 8eley).

Hind Limb.—The femur, measuring 38 mm., is slightly curved and expanded at both ends. The tibia, 21 mm, and fibula, 25 mm., are widely arched apart, especially distally; the fibula is the largest and most curved bone and unites broadly distally with both the intermedium complex and the fibulare. As in the manus, there is a well-marked foramen between the intermedium complex and the fibulare. There are 7 osseous tarsalia, namely, fibulare, complex of intermedium (intermedium + centrale tarsi + tibiale), and distal tarsalia 1, 2, 3, 4, 5. The metapodials increase regularly in size from Mts. I to Mts. V. The digits increase regularly from D. I to D. IV. In the young individual (Fig. 17a) the phalangeal formula is determined as 2, 3, 4, 5, 4. Digits IV and V are of approximately equal length. The first or radial metatarsal is somewhat thickened, which is

a distinctly aquatic adaptation. On the whole the pes, like the manus, is elongated on the postaxial side. The terminal phalanges are reduced, not pointed; a slight spreading of the digits, especially of D. V, may indicate the existence of a swimming web. In Mesosaurus pleurogaster the digits terminate in short, conical phalanges; D. V is the longest (Seeley); the claws were reduced, not pointed.

Limbs of young individual.—In the young Stereosternum (Fig. 17a) the less extensive ossification of the (a) ribs, (b) coracoids and scapulæ, (c) pubes and ischia, is correlated with (d) the entire absence of osseous carpals, and (e) the presence of but one osseous tarsal, probably the intermedium.

We note also the (1) separation or divarication between the 5th and 4th digits, as in Mosasaurs, (2) the elongation of the 4th, but especially of the 5th digit of the pes.

Notes on Seeley's Observations.—There are some points in which my observations differ from those of Professor Seeley. He defines the cervical ribs

as having a single articulation, but his figure 5, pl. xviii, appears to show a gentle bifurcation of the head of the posterior cervical ribs in M. pleurogaster. He defines the dorsal ribs as articulating with the anterior face of the neural arch; the same figure, especially in dorsals 5–8, shows that in Mesosaurus, as in Stereosternum, the capitula lodge in the extreme anterior portion of the centra. (See also his fig. 4, p. 600.) He figures Stereosternum (p. 599) as having four sacrals; in our specimen it is clear that only two are Professor Seeley present. figures the coracoids in Mesosaurus as overlapping in the median line, as in the Amphibia Arcifera; is not this overlap probably due to the accidental lateral compression of the type of M.

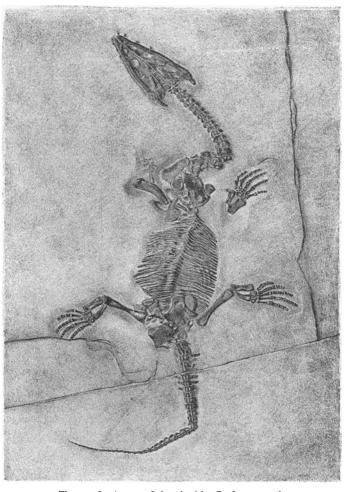


Fig. 20. Lariosaurus balsami. After Boulenger. X 1/2.

tenuidens, on which this observation was apparently based?

ADAPTATION.—On the whole this detailed study of Stereosternum demonstrates its very close affinities to Mesosaurus, but in the slightly more elongate neck and in the modification of the terminal phalanges, it may be regarded as a somewhat more progressively aquatic form and certainly as a distinct genus. The distal separation of the podials by the intermedium is probably an inherited rather than a specifically aquatic character. The same condition obtains in *Sphenodon*. The elongate head and neck and the delicate, highly prehensile teeth, the elongate and probably propulsive tail, point to the capture of small, agile prey.

The Proganosauria, Mesosaurus and Stereosternum, therefore stand adaptively very far apart from the clawed, terrestrial and raptorial Protorosauria (Palæohatteria, Kadaliosaurus, Protorosaurus). Their greatly elongate skull, specialized ribs thickened probably for gravitation purposes, slender ilium, modified limbs and feet, indicate that the teeth alone were being used in the prehension of prey, rather than the hands and feet which were apparently being modified in the direction of paddles and consequently losing the terminal claws.

NOT RELATED TO THE SAUROPTERYGIA.—The chief grounds upon which these animals might be theoretically supposed to be ancestral to the Sauropterygia (through *Neusticosaurus*) are: the thickening of the ribs, the apparently solid condition of the palate, the distally expanded humerus with ulnocondylar foramen, the similarity of the hind limbs.

Since Seeley's theory has enjoyed the able support of Boulenger, Fürbringer, v. Huene and others, it appears desirable at this point to contrast the Mesosauridæ with the earliest Sauropterygia, the Nothosauria, in some detail.

#### PROGANOSAURIA.

#### Stereosternum and Mesosaurus.

Skull.—Facial region elongate. Cranium abbreviate (Fig. 16a).

Vertebræ—Dorsal vertebræ without parapophyses, ribs placed near anterior end of centra.

Ribs.—Capitular region contracted, costal region expanded, ribs vertically extended, chest deep and narrow (Fig. 19 B).

Abdominal ribs.—Extremely delicate.

Girdles.—Broad coracoid; procoracoid not certainly separated.

Limbs.—Preaxial elements or radius and tibia reduced, postaxial elements or ulna and fibula enlarged.

#### SIMOSAURIA OF NOTHOSAURIA.

#### Lariosaurus, Pachypleura, Neusticosaurus.

Facial region abbreviate. Cranium certainly elongate (Figs. 2 and 20).

Dorsal vertebræ generally with distinct parapophyses, ribs placed opposite middle of centra.<sup>1</sup>

Ribs with distinct capitula, proximally expanded, ribs horizontally extended, chest broad and shallow (Fig. 19 A).

Strongly developed.

Narrow, transversely placed coracoid; procoracoid cartilaginous or widely separate and wanting.

Preaxial elements enlarged, postaxial elements reduced.

<sup>&</sup>lt;sup>1</sup> In Neusticosaurus (Simosaurus) pusillus the type of the order Neusticosauria Seeley, which the same author brackets with the Proganosauria to constitute the order Mesosauria, we have a small typical Triassic Sauropterygian closely related to other Simosauria in the composition of the entire skeleton. It is true that the processes for rib attachment are abbreviated or absent, but the ribs have large proximal heads or capitula, and they are given off directly opposite the pleurocentra and much expanded proximally, as shown in Professor Seeley's figures. They are thus in every respect unlike those of Mesosaurus.

PROGANOSAURIA - (Continued).

Stereosternum and Mesosaurus.

Propodials.—Separated distally by intermedium. Intermedium more or less uniting with centrale, carpus and tarsus perforated.

Proportions.—Skull elongate, neck relatively short, thoracic region elongate, tail elongate, hind limb larger than fore limb.

SIMOSAURIA or Nothosauria—(Continued).

Lariosaurus, Pachypleura, Neusticosaurus.

Same condition (a primitive character). Elements of carpus and tarsus separate and rounded.

Skull intermediate, neck elongate, thoracic region abbreviate, tail abbreviate, fore limb larger than hind limb.

This comparison shows that the Mesosauridæ are so fundamentally different from the Lariosauridæ that they present no evidence of ancestral relationship. In both families there are points of likeness due: (1) to common descent from remote Cotylosaurian ancestors, such as the separation of the propodials distally by the intermedium; (2) to analogous incipient adaptation to aquatic life; here belong (a) the thickening of the ribs, an independent or parallel character, seen also in Sirenia among mammals, (b) also the distally expanded humerus with ulnocondylar foramen, (c) the more or less amphicælous vertebræ, (d) the supposedly closed palate, etc. (Fig. 20). When studied closely, however, in all their parts, neither the primitive (inherited), nor the adaptive (progressive), structures are found to correspond as a whole. At first sight, for example, the ribs strongly suggest those of Lariosaurus, Pachypleura and other Triassic Sauropterygia, but more detailed study shows that they are fundamentally different in their proportions and relations to the vertebræ.

In other words, the relations of the Mesosauridæ and Lariosauridæ are more distinctly divergent than genetic.

In the following significant points the Proganosaura differ from the Simosauria (or Nothosauria) and approach the Rhynchocephalia:

#### Points of Resemblance of the Proganosauria to the Rhynchocephalia.

- 1. Rib articulations probably originally hypocentral as in Sphenodon, i. e., capitula intervertebral.
  - 2. Chevrons with a proximal transverse bar (as in Sphenodon, Anguisaurus, v. Meyer, Tab. xiv.).
  - 3. Splitting adaptation of caudals (as in Sphenodon).
  - 4. Delicate and very numerous abdominal ribs.
  - 5. Diapsidan phalangeal formula: probably in manus, certainly in pes.
- 6. Arterial foramen between intermedium and postaxial carpale or tarsale (as in Sphenodon embryos).

At the same time the Proganosauria are much more specialized and diverge very widely from the terrestrial and cursorial Protorosauria of Germany; the divergence is analogous in many respects, especially in its apparently aquatic tendencies, to that which separates the Mosasauria from the Lacertilia, but has not progressed equally far; curiously enough the aquatic adaptations are *sui generis* and do not lead into those of either of the subsequently developed aquatic families

of Diaptosauria, namely, the Champsosauridæ and Pleurosauridæ, which again are entirely independent of each other.

It appears best, therefore, to leave the Proganosauria incertæ sedis, with the somewhat confident expectation that when more fully known they will prove to be a separate order or suborder of the Diaptosauria more closely related to the Rhynchocephalia than to the Protorosauria.

#### VI.—ORDER CHORISTODERA COPE.1

Simædosauria Dollo.<sup>2</sup> Includes Champsosaurus Cope <sup>1</sup> and Simædosaurus Gervais.<sup>3</sup>

The genus *Champsosaurus* was separated by Cope as a suborder of Rhynchocephalia in 1876, the name Choristodera referring to the divided or temnospondylous condition of the neck vertebræ.

The known geological age is Upper Cretaceous and Lower Eocene, of North America and France. The chief references are the papers of Cope, Gervais, Lemoine and Dollo, and a forthcoming paper by Barnum Brown of this Museum.

DEFINITION OF CHORISTODERA. — This is a sharply defined division of the Diaptosauria owing to its remarkable parallelism with the Gavialoid Crocodilia. The chief characters are:

Amphibious Gavialoid Diaptosauria. Skull greatly elongated; teeth acrodont, internally folded. Vertebræ amphicælous, imperforate. Hypocentra wanting in dorsals. Dorsal ribs two-headed, attached opposite centra. Interclavicle T-shaped. Pubis and ischium continuous; no puboischiadic foramen. Humerus with ectepi (radio-) condylar foramen.

The material includes the types of Cope and of Gervais, the more complete skeleton described by Lemoine and Dollo, and especially a remarkable series of practically complete skeletons secured by the American Museum Expedition of 1902, which the writer has placed in the hands of their discoverer, Mr. Barnum Brown, for description. In the very full discussion of the characters and relations of this animal by Dollo, Simædosaurus was supposed to be very similar to if not synonymous with Champsosaurus. This is a mistake; Simædosaurus is distinguished by being more fully adapted to aquatic life, as will be seen from the following diagnosis, which refers to Champsosaurus unless otherwise specified.

<sup>&</sup>lt;sup>1</sup> On Some Extinct Reptiles and Batrachia from the Judith River and Fox Hills Beds of Montana. Palæontological Bulletin No. 23, p. 11; Proc. Acad. Nat. Sci. Phila., December, 1876.

<sup>&</sup>lt;sup>9</sup> Première Note sur le Simœdosaurien d'Erquelinnes. Bull. Mus. Roy. Hist. Nat.Belg., t. III, pp. 151-182, pll. viii, ix. Déc., 1884.

<sup>&</sup>lt;sup>8</sup> Énumération de quelques ossements d'animaux vertébrés recueillis aux environs de Reims par M. Lemoine. Journal de Zoologie, 1877, p. 75.

<sup>&</sup>lt;sup>4</sup> Communication sur les Ossements Fossiles des Terrains tertiares inférieurs des environs de Reims. Assoc. franc. p. l'Avanc. d. Sciences, Congrès de Montpellier, 1880.

The length of *Champsosaurus* is 1.5 m. It is apparently an amphibious reptile, similar in habits to the Gavials, and with many analogous adaptations. It is more primitive in some characters, more progressive in others, than *Simædosaurus* which, in its aquatic adaptation, has acquired more slender ribs, less distinct joints, more paddle-like feet.

### Genus Champsosaurus Cope.

SKULL. — Greatly elongated and Gavial-like in profile; nares terminal, separated by a septum (no septum in Simædosaurus); face greatly elongated, laterally compressed. Equal-sized supraand laterotemporal fenestræ; large posttemporal fenestræ; no pineal opening; internal nares separated by prevomers; prevomers probably articulating with pterygoids. Faw without coronoid process, splenial entering mandibular symphysis, symphysis sutural. Teeth of acrodont type, not lodged in distinct sockets in maxillaries, premaxillaries, and dentaries, pulp cavity persistent; teeth hollow, infolded internally as in Ichthyosaurus; also numerous fine palatine and pterygoid teeth firmly attached.

VERTEBRÆ. — Atlas and axis a complex composed of seven pieces, namely: 2 separate neurocentra and hypocentrum of atlas, pleurocentrum (os odontoideum) attached to axis; axis composed of united neurocentra resting upon the centrum with hypocentrum below. Vertebræ shallow amphicælous to amphiplatyan, imperforate, but faces of centra often imperfect as if retaining remains of vestigial intervertebral notochord. Five anterior cervicals with hypocentra, no hypocentra below remaining cervicals or dorsals. Vertebral formula, 26 presacrals, (9 cervicals and 17 dorsals), 2 true sacrals, 1 sacrocaudal, 21 + caudals.

RIBS.—A vestigial rib on pleurocentrum of atlas (odontoid), also a well-defined rib on axis. Cervicals 3-9 with two-headed ribs, capitulum attached opposite pleurocentrum. (Simedosaurus is described as having no ribs on atlas or axis). All succeeding cervical and dorsal ribs two-headed, arising opposite the centrum. Dorsal ribs very massive; 9 anterior caudals with suturally attached ribs, caudals 1-11 with ribs coalesced to centra, posterior caudals without ribs or transverse processes. Dorsal vertebræ with para- and diapophyses gradually uniting so that the capitula and tubercula become confluent. Chevrons beginning in third caudal vertebra.

ABDOMINAL RIBS. — Heavy, a central angulate and two lateral curved pieces, sometimes bifurcated.

GIRDLES. — Massive scapula and coracoid (coracoid + procoracoid) suturally united; a coracoid foramen. Scapula resembling that of *Rhynchosaurus*. Interclavicle T-shaped, with broad posterior plate; stout clavicles. In *pelvic girdle* ilia reduced, with backward extension superiorly; pubis and ischium continuous, expanded into a broad ventral plate as in *Rhynchosaurus* and Proganosauria, *i.e.*, an obturator foramen but no puboischiadic (thyroid) foramen.

LIMBS.— Humerus with radio- (ectepi-) condylar foramen or groove; no ulno- (entepi-) condylar foramen. Ulna with an obtuse olecranon. Ulna and radius of equal size, separated distally by a large intermedium; a single free centrale. Metapodials elongate, terminal phalanges pointed and clawed.

Adaptation.—These animals are progressively adapted to aquatic life.

Affinities.—The nearest resemblances are certainly to the Proganosauria (Stereosternum and Mesosaurus); how far these are due to analogous adaptation it would be premature to say. The chief differences are in the structure of the vertebræ and of the ribs, and in the modes of articulation of these parts with each other. In some respects (e. g., cervical hypocentra) Champsosaurus is more primitive; in others (e. g., two-headed ribs) more progressive.

#### VII.—ORDER RHYNCHOCEPHALIA GÜNTHER.1

Rhynchocephalia vera Boulenger.

Homæosauria Lydekker (in part).

Although represented by the still extant *Sphenodon* this order is in certain respects very primitive. The structure of the proximal part of the tarsus is more complete or primitive than that of the Protorosauria. The pelvic girdle, on the contrary, is more progressive in the development of the large thyroid foramina. As represented by the herbivorous *Sphenodon* and the carnivorous and partly aquatic Rhynchocephalia of the Jurassic, the order may be defined as follows:

Definition of Rhynchocephalia. — Maxillaries and premaxillaries with teeth (excepting Sauranodon). Vertebræ perforate or imperforate. Sacrals 2. Caudals with "splitting point." Hypocentra present or absent. Interclavicle T-shaped. Large puboischiadic (thyroid) foramina. Ilium narrow. Entepi- and ectepicondylar foramina variable. Proximal tarsalia including 3 elements (tibiale, intermedium, fibulare) partly coalesced. Distal tarsalia not exceeding 4.

The order includes a number of Jurassic types, partly terrestrial and partly adapted to aquatic life; the former are similar to *Sphenodon*, the latter are vigorously swimming animals largely propelled by the tail, with correspondingly reduced extremities and short neck; the genera are distinguished by various degrees of aquatic adaptation, in the course of which the distinctively terrestrial characters are more or less modified. Finally the body becomes narrow, elongate, with enormous development of the tail (*Pleurosaurus*).

These types include: (1) the Upper Jurassic Homæosaurus, which stands in close relation to the living Sphenodon, from which it differs however in three important points: (a) the absence of the ectepicondylar foramen in the humerus; (b) the absence of uncinate processes in the ribs; (c) the absence of hypocentra between the dorsal vertebræ; probably also in (d) the fuller ossification of the vertebral centra (Boulenger). (2) Saphæosaurus von Meyer is twice as large as Homæosaurus. (3) Sauranodon Jourdan, 77 cm. in length. (4) Pleurosaurus (synonyms, Anguisaurus?, Saurophidium) fully aquatic in habit. These animals vary in size from .15 to 1.5 m. Dames has discussed the group in his 'Beitrag zur Kenntniss der Gattung Pleurosaurus H. von Meyer.' Homæosaurus, Sauranodon, Euposaurus, Saurophidium, and Pleurosaurus are fully described and figured in Lortet's monograph of 1892. Boulenger ("On British Remains of Homæosaurus with Remarks on the Classification of the Rhynchocephalia") treats these animals in their family and ordinal relations. Lortet divides the Rhynchocephalia as follows:

<sup>&</sup>lt;sup>1</sup> Contribution to the Anatomy of Hatteria (Rhynchocephalus) Owen. Philos. Trans., Part II for 1867, pp. 1-35 pll., i-iii.

<sup>&</sup>lt;sup>2</sup> Sitzungsb. d. k. Preuss. Akad. d. Wiss. Berlin, XLIII Bd., 1896, pp. 1107-1124.

<sup>&</sup>lt;sup>8</sup> Les Reptiles Fossiles du Bassin du Rhone. Arch. d. Mus. d'Hist. nat. de Lyon, t. V, 1892.

<sup>&</sup>lt;sup>4</sup> Proc. Zoöl. Soc., Lond., 1891, pp. 167-172.

#### SPHENODONTIDÆ.

#### Including Sphenodon, Homæosaurus, Euposaurus.

Teeth on premaxillaries and maxillaries. Vertebræ amphicælous; hypocentra throughout or in cervical and caudal region only.

#### SAURANODONTIDÆ.

Including Sauranodon, Saphæosaurus.

Upper and lower jaws edentulous, deflected into a beak anteriorly, with sharp edges. Vertebræ opisthocœlous. Hypocentra reduced.

This union of Homeosaurus and Sphenodon into one group seems more logical than the separation of Homeosaurus in the separate suborder Homeosauria as suggested by Lydekker.<sup>1</sup> These animals, however, certainly belong to three and possibly four distinct families the wide adaptive radiation of which is shown in the following table:

#### Furassic Families of the RHYNCHOCEPHALIA.

A .- Short, broad skull; short tail; prehensile limbs; terrestrial. Family Homæsauridæ.

Homæosaurus, small..........v. Meyer, Tab. xi. Euposaurus, juv.....

B.—Short skull; long tail; prehensile limbs; semiaquatic. Analogous to the Varanidæ. Family Sauranodontidæ Lortet.

> Sauranodon.....Lortet, pl. iii.

C .- Long, narrow skull, and long tail; prehensile limbs; semiaquatic. Analogous to the Varanidæ. Family Pleurosauridæ.

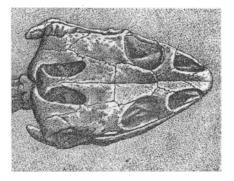
Pleurosaurus Goldfuss................v. Meyer, Tab. xiv.

D.—As above, but with natatorial limbs and tail; aquatic. Family Acrosaurida v. Meyer.

Acrosaurus, very small........................v. Meyer, Tab. xii. Anguisaurus 2 minor..... Dames, Tab. xii. Saurophidium.

The point I wish to emphasize now is that this most interesting group rep-

resents an independent adaptive radiation of true Rhynchocephalians. Striking peculiarities in addition to those mentioned are: (1) the abbreviation of the neck to 6 or 5 cervical vertebræ. (2) The absence of hypocentra in the dorsal region. (3) There is no mention known to the writer of the existence of a notochordal canal. (4) The giving off of the dorsal ribs opposite the pleurocentra (that is vertebrally). (5) The thickening of the supratemporal arch, which appears to include in Fig. 21. Sauranodon incisivus Jourdan. Top view of skull. After Lortet. × 1. some forms (Sauranodon) entirely separate



squamosal and prosquamosal elements, (Fig. 21). (6) The presence of radio-(ectepi-) condylar foramen in Saphæosaurus, of both radio- and ulnocondylar

<sup>&</sup>lt;sup>1</sup> Cat. Foss. Rept. and Amphib., Part I, p. 290.

<sup>&</sup>lt;sup>2</sup> The identification of Anguisaurus with Pleurosaurus by Dames appears very doubtful.

foramina in *Pleurosaurus minor* (Dames, op. cit., Tab. xii) or of an entepicondylar foramen in *Homæosaurus* (Boulenger). Altogether very careful morphological and systematic revision of these animals is still needed.

SKULL.—In Homæosaurus and Saphæosaurus the skull is comparatively short and wide with broad facial portion; in the aquatic forms it is elongate pointed and triangular as in Stereosternum and Mesosaurus. Pterygoids separated in the median line (Pleurosaurus, Homæosaurus) by an interpterygoid space; a pineal foramen (Homæosaurus); jaw with elevated coronoid process (Homæosaurus); superior teeth acrodont, laterally compressed (Homæosaurus); premaxillaries with a single cutting tooth (Homæosaurus), or pointed and toothless (Sauranodon, Pleurosaurus, Dames); deflected into a beak (Sauranodon).

VERTEBRÆ.—Amphicœlous, fully osseous; notochord not persistent; hypocentra wanting in dorsal region, persistent in anterior cervicals and in anterior caudals. The 'splitting point' is absent in the tail of certain genera (Anguisaurus, v. Meyer, Tab. xiv) but apparently present in others (Sauranodon, Lortet, pl. iii, fig. 1). Caudals with divided neural spines carried posteriorly (Homæosaurus). The number of dorsal and caudal vertebræ is highly adaptive to aquatic life; Pleurosaurus (Anguisaurus) minor, an extreme aquatic form, possesses, according to Dames, an abbreviated neck, which includes only 5 cervicals, and a correspondingly elongate back including 41 dorsals; there are thus 46 presacrals; sacrals 2-1; caudals 70. These aquatic forms with elongate skulls are placed in a separate family (Pleurosauridæ) by Lydekker. The smaller aquatic forms were grouped as Acrosauridæ by v. Meyer. Homæosaurus presents the other extreme, with 6 cervicals and 17 dorsolumbars, or 23 presacrals (Lydekker; there are 25 in Sphenodon), 2 sacrals.

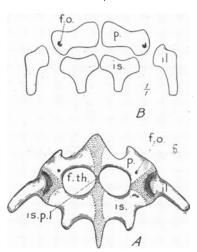


Fig. 22. A, Sphenodon punctatus. Ventral view of the pelvis of a young individual (15 cm.). After Howes. × \(\frac{3}{2}\).

B, Pleurosaurus. Ventral view of the pelvis. After Dames. × \(\frac{3}{2}\).

p, pubis; is, ischium; il, ilium; f.o, obturator foramen; f.th., thyroid or puboischiadic foramen; is.p.l. ischiopubic ligament, and gastroid cartilage.

RIBS.—Generally reduced on anterior cervicals, third and fourth cervicals with short ribs (Sauranodon); five anterior cervicals without ribs; posterior cervicals with single-headed ribs on short diapophyses (Homæosaurus); dorsal ribs single-headed (Homæosaurus, Pleurosaurus), given off directly opposite pleurocentra (Saphæosaurus, v. Meyer, Tab. xiv). Ribs coalesced to sides of 10 or more anterior caudals (Homæosaurus). No uncinate processes (Homæosaurus, Pleurosaurus).

PLASTRON.—Resembling that of *Sphenodon*; abdominal ribs including an angulate median piece, two lateral splint-like pieces (*Homæosaurus*).

GIRDLES.—Adapted to terrestrial or to aquatic life. In the terestrial *Homæosaurus*, coracoid small, without foramen, an interclavicle. In the completely aquatic *Anguisaurus minor* (Fig. 6 C and 22 B) pectoral and pelvic elements and limbs greatly reduced, separate; clavicles reduced, interclavicle large T-shaped. Unlike all the more primitive Diaptosauria a wide puboischiadic fenestra between pubes and ischia; median puboischiadic symphysis replaced by a median gastroid cartilage (Fig. 22 A).

Limbs.—More or less modified from an ambulatory to an aquatic type. Humerus with entepi-(ulno-) condylar but no

ectepi- (radio-) condylar foramen (*Homæosaurus*)<sup>1</sup>; with both ulno- and radiocondylar foramina (*Anguisaurus minor*). In *Pleurosaurus*, humerus flattened distally, a single oseous carpal, terminal phalanges without claws,—all aquatic adaptations. In *Acrosaurus* no osseous carpals. In the more terrestrial *Homæosaurus*, 10–11 carpalia.

<sup>&</sup>lt;sup>1</sup> As to the condylar foramina of *Homeosaurus* authors differ. H. v. Meyer, v. Ammon, and Baur-describe an "ectepicondylar canal"; Zittel and Boulenger an entepicondylar canal or foramen. Fürbringer (Vergl. Anat. des Brustschulter apparates . . . Jenaisch Zeitschr., 1900) suggests that it may have had both, or shown individual variation.

The aquatic adaptations in this group consist chiefly in: (1) elongation and pointing of face, (2) abbreviation of cervicals, (3) elongation of dorsals, single-headed ribs, (4) absence of uncinate processes, (5) reduction of plastron, (6) reduction of sacrals to one, (7) rod-like form of ilium, (8) cartilaginous separation of all the elements of the pelvis, (9) reduction of shoulder girdle, (10) disappearance of articular joints, (11) reduction of osseous carpals and tarsals.

Some of the above features (Nos. 1, 3, 4, 5, 10) of this adaptation are parallel with those of *Stereosternum* and *Mesosaurus*, and also of the Mosasauria, but these true Rhynchocephalians (*Pleurosaurus*, etc.) differ profoundly from all the above types in the non-elongation of the limbs and phalanges, and in the feeble development of the ventral thoracic basket; this is probably because *Pleurosaurus* was an exclusively tail-propelling animal. The digits are reduced in number from 5 to 4 and the phalanges in D. V of the pes from 4 to 3.

#### Genus Sphenodon Günther.

#### I. EMBRYOGENY.

This section is entirely founded upon the extremely important memoir by Howes and Swinnerton.<sup>1</sup>

VERTEBRÆ. — Hypocentra of two kinds: 'primary hypocentra,' "the first-formed skeletal elements" (Howes), originally paired elements and preformed in cartilage, persisting in caudal region to form the chevrons; and 'secondary hypocentra,' single transverse median elements which arise by direct ossification outside of the vertebral column, and replace the primary hypocentra in certain regions. Primary and secondary hypocentra coëxist in the anterior caudal region only.' Pleurocentra originally paired. Caudal vertebræ modified for splitting.

Ribs.—Arising in procartilage in relation to the primary hypocentra. Capitula intervertebral, tubercula vertebral; these relationships lost during later development by backward rib movement. Uncinates separate in origin.

SKULL. — Epipterygoid arising from ossification of ascending process of the pterygoquadrate cartilages; columella auris and stapedial processes derived from hyoid arch; prosquamosal not distinct at any stage; 3 pairs of upper incisor teeth. Teeth consisting of two series: an earlier developed alternating set, and a later structurally uniform set.

ABDOMINAL RIBS.—Arising by union of a number of ossifications; the median segments may be paired.

Limbs (Fig. 23). — Tarsale 5 not shown in ontogeny, basal element of digit V = mts 5. Astragalus = tibiale + centrale + intermedium. Two (possibly 3) centralia carpi. In an earlier embryo of the same stage Howes (op. cit., fig. 15) found "an intermedium and fibulare chondrified and separated by a foramen, apparently homologous with the f. arteria perforans mesopodii (f. p.), [compare Stereosternum]; the centrale and tibiale being procartilaginous, in close apposition with the intermedium and with each other."

<sup>&</sup>lt;sup>1</sup> On the development of the skeleton of the Tuatara, Sphenodon punctatus. Trans. Zool. Soc. Lond., Vol. XVI, pt. I, Feb. 1901.

<sup>&</sup>lt;sup>2</sup> Howes (p. 26) suggests that the lateral pieces of the chevrons = primary hypocentra, and that the dorsal transverse connecting pieces = secondary hypocentra. In seeking for the homology of the secondary hypocentra, the 'hypocentrum pleurale' of Fritsch, observed in certain Stegocephala, should be considered.

#### 2. OSTEOLOGY OF ADULT.

SKULL. — Paroccipitals (opisthotics) separate in young specimens (Baur); proötics separate; pterygoids uniting with prevomers, leaving an interpterygoid space. A parasphenoid (vomer) lying

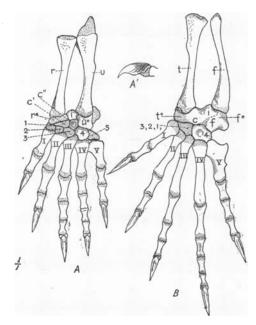


Fig. 23. Sphenodon punctatus. From Bayer, slightly modified after Howes.  $\times \frac{1}{2}$ . A' Claw; B, Left pes. A. Left manus: r, radius, f, fibula. te, tibiale. u, ulna. ue, ulnare. fe, fibulare.

i. intermedium. i, intermedium.
c, c' c', centralia.

1, 2, 3, 4, 5, distal carpalia.

in this space. Foramen between quadratojugal and quadrate. No lachrymal (Howes). Premaxillaries provided with three pairs of teeth in the young, reduced to two pairs, which are converted into the double- or single-paired tusks of the adult, sheathed with an enamel-like substance regarded as true bone by Tomes. Parallel rows of teeth on maxillaries and palatines. Mandible composed of six elements.

VERTEBRÆ. - Amphicælous; continuous notochord. Cervicals 8; a proatlas (first described by Albrecht). Pleurocentra and neurocentra suturally united in the young. Presacrals 25, including 8 cervicals, 17 dorsals (sternals 3-4, post-sternals 13-14, Howes); sacrals 2. Caudal vertebræ of splitting

Ribs. — 33, namely, presternal 5-6, sternal 3-4, post-sternal 13-14, sacral 2 (with variation), caudal 8 (Howes).

Ribs: (1) primarily intervertebral (Hofmann. Baur, Gadow), that is, lateral outgrowths from the hypocentra; (2) the hypocentral articulation is lost and finally the head of the rib disappears (Cope, Howes). Ribs of 8 anterior caudals directly opposite pleurocentrum (Howes).

Cervical Ribs. — The following clear description of the cervical ribs by Baur' is substantially confirmed by Howes. First cervical (atlas). - Singleheaded ligamentous ribs connected with distal part

of the second hypocentrum (between occipital condyle and atlas and axis). Second cervical (axis).—Two-headed ligamentous ribs. Capitulum connected with distal part of second hypocen-

trum (between atlas and axis); tuberculum connected with a small diapophysis of the vertebra. Third cervical.—First specimen, two-headed ligamentous ribs; second specimen, two-headed osseous ribs. Capitulum ligamentous, connected with small process (parapophysis) on the posterior lateral part of third hypocentrum; tuberculum connected with diapophysis. Fourth cervical.—Two-headed osseous ribs. Capitulum well developed but not entirely ossified, the proximal ligamentous part connected with the process (parapophysis) of fourth hypocentrum; tuberculum attached to the well-developed diapophysis. vical. — One-headed osseous ribs. Capitular part vestigial and ligamentous, connected with fifth hypocentrum; tuber-

c, centrale tarsi.
1, 2, 3, 4, distal tarsalia.

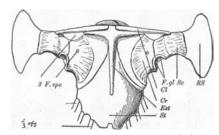


Fig. 24. Sphenodon punctatus. Ventral view of pectoral girdle of adult. After Fürbringer. X \{\bar{t}\}. Cl., clavicle; Est, interclavicle; SS, suprascapula; Sc, scapula; Cr, coracoid; St, sternum; F.spc, coracoid foramen; F.gl, glenoid fossa.

culum well developed, attached to a short but broad diapophysis. All the other cervical and dorsal vertebræ show the same condition as the fifth cervical.

Sacral Ribs. — Two sacral ribs articulating vertebrally, occasionally reinforced in part by a dorso-sacral or by a caudo-sacral (Howes).

ABDOMINAL RIBS.—22-26. Median angulate and two lateral pieces in adult.

LIMBS. — Humerus with ulno- (entepi) condylar foramen and radio- (ectepi-) condylar foramen or groove. Radius and ulna separated distally by intermedium. Femur and tibia separated distally. Tarsus: astragalus (tibiale + intermedium + centrale, Perrin, Bayer, Howes), fibulare or calcaneum and two distal tarsalia only. Carpus.—11 elements: centralia, 2 (Bayer, Baur) or ? 3 (Howes), radiale, intermedium, ulnare pisiform, five distal carpalia (Baur, Howes).

GIRDLES. — Coracoid (coracoid + procoracoid) with foramen; clavicles and narrow T-shaped interclavicle (Fig. 6, B). Pelvic girdle with large puboischiadic openings separated in the median line by ligament and gastro-cartilages (Fig. 22, A).

Our knowledge of the osteology of *Sphenodon* is chiefly due to Günther's memoir, to Baur's searching observations, and to the important memoir by Howes and Swinnerton.

#### VIII.—CONCLUSIONS.

#### I. PRIMITIVE ANATOMY OF THE DIAPTOSAURIA. A SUMMARY.

Comparison of the seven orders or suborders of Diaptosauria is of very great importance as giving us light upon the *primitive or ancestral anatomy of the Diapsida*.<sup>2</sup> It brings out two principal facts:

First, the probable community of origin of these seven groups of animals, as shown by the common possession of a large number of primitive characters.

Second, the marked adaptive specialization in which two or more of the groups partly parallel each other. The parallelism, however, is never exact or complete; for example, it is certain that the aquatic Proganosauria, Choristodera, and aquatic Rhynchocephalia have been evolved independently because they exactly parallel each other in certain sets of aquatic adaptations but widely diverge in others.

#### SKULL.

The primitive proportions of the skull with a moderately developed facial region are seen in Palæohatteria, Homæosaurus, and Sphenodon. Secondary elongation of the facial region arose independently in five groups for somewhat different functions, namely: (1) in Protorosaurus for the prehension of active prey; (2) in Hyperodapedon, as a littoral adaptation; for prehension in water (3) in Proganosauria (Mesosaurus, Stereosternum), (4) in Choristodera (Champsosaurus), (5) and in Rhynchocephalia (Pleurosaurus, Acrosaurus).

The primitive bones or elements of the skull are those inherited from the Cotylosauria; the most persistent primitive skull is that of *Procolophon* with 'epiotic' bones and a superior 'auditory notch.' Separate and paired premaxillaries, maxillaries, nasals, prefrontals, lachrymals, frontals, postfrontals, postorbitals, jugals, quadratojugals, prosquamals (supratemporals), squamosals, parietals

<sup>&</sup>lt;sup>1</sup> Über die Extremitäten einer jungen Hatteria. Sitzungsb. d. k. Akad. d. W. Math.-naturw. Cl., XC Bd., Abth., 1884, pp. 237-245.

<sup>&</sup>lt;sup>2</sup> Authority for all the points given here is cited in the previous sections.

paroccipitals (opisthotics), exoccipitals, pterygoids, ectopterygoids, epipterygoids, palatines, prevomers, are observed in one or more members of the superorder. The paroccipitals are coalesced (except in Pelycosauria and the young Sphenodon). Median basioccipital, basisphenoid, and vomer or parasphenoid are present. The fenestræ or openings are: the paired narial (secondarily confluent in Choristodera), orbital, supratemporal, laterotemporal (rudimentary in Procolophon), infratemporal, posterotemporal or parietosquamosal, pineal (large in Procolophon), interpterygoid space (into which the vomer projects), and postnarial (anterior in position and separated by the prevomers). The antorbital fenestra of Protorosaurus is an exceptional feature which points toward the Dinosaurs. Teeth are variously developed on the premaxillæ, maxillæ, prevomers, pterygoids, palatines, and dentaries.

#### VERTEBRÆ.

*Presacrals*.—The number of presacral vertebræ is primitively small, namely 23 +, and is fairly constant throughout the seven groups.

Protorosaurus Palæohatteria Pelycosauria Rhynchosauria Proganosauria	C. 7	D. 16	or 23 pr 26 27 + 22-2	"	ls (as in Dinosaurs)
(Stereosternum)	C. 12	D. 22	34	"	The neck and back secondarily elongated as an aquatic adaptation.
Choristodera	9.		26		-
(Champsosaurus)	<i>9.</i> C. <b>6</b>	D. 17	26	"	
Aquatic Rhynchocephalia		·	_		
(Pleurosaurus)	C. 5 (Second decrease	D. 41 ary (Seco se) incr	46 ondary ease)	"	Modified in aquatic adaptation.
Terrestrial Rhynchocephalia		,	,		
(Sphenodon) (Homæosaurus) (Sauranodon)	C. 8	D. 17	25	"	

Sacrals.—The primitive number of sacrals appears to be 2, as observed in Kadaliosaurus and certain Pelycosauria, in Rhynchosauria, in Stereosternum, Champsosaurus, and Sphenodon. In certain aquatic forms (Pleurosaurus) the sacrals decrease to 1. In the ambulatory, cursorial forms they increase to 3 (Dimetrodon, Protorosaurus, Palæohatteria), the same number as in primitive Dinosaurs.

Caudals. — Forty (40) in the cursorial Protorosaurus; 55 in the ambulatory Palæohatteria; greatly diminished in the quadrupedal Dimetrodon; 21 + in the aquatic Champsosaurus; 60-64 in the aquatic Stereosternum; 70 in the aquatic Pleurosaurus.

Composition of Vertebræ.— The primitive component parts of each vertebra are 6, namely: 2 hypocentra, 2 pleurocentra (centra), and 2 neurocentra (neural arches) as seen in embryos of Sphenodon. The opposite pairs of pleurocentra and neurocentra early coalesce. Pleurocentra and neurocentra, or centra and neural arches, are either suturally separate (Protorosauria, Pelycosauria, young Rhynchocephalia), or firmly coalesced (Proganosauria). The centra are primitively amphicœlous and perforated by a notochordal canal, as seen in certain Protorosauria (Palæohatteria, Kadaliosaurus), in Pelycosauria, in Proganosauria, and in certain Rhynchocephalia. In other forms they are imperforate. Another exception recorded is in the elongate cervicals of Protorosaurus, which are Hypocentra are figured as bilaterally paired in certain cervicals of Protorosaurus and are described as bilaterally paired in the three anterior cervicals of Procolophon, also as paired 'primary hypocentra' in Sphenodon em-Hypocentra are more frequently single, transversely placed or lunate elements, primitively beneath the presacrals and anterior caudals. Hypocentra secondarily disappear beneath the posterior cervicals and dorsals of certain Protorosauria, of Rhynchosauria, of Proganosauria, of Choristodera, and of certain Rhynchocephalia.

#### RIBS.

Ribs primitively single-headed on atlas and all succeeding cervical, dorsal, sacral, and anterior caudal vertebræ. On all presacrals the heads of ribs are primitively hypocentral or intervertebral in attachment. The sacral and anterior caudal ribs, however, are apparently vertebral or pleurocentral in attachment in all Diaptosauria; this would appear to render it probable that the sacrals were derived from modified anterior caudal ribs, and that the sacral and caudal ribs were, very early in the evolution of the Diaptosauria, shifted from the hypocentra to the pleurocentra; at all events, in all Diaptosauria, so far as known, the sacral and caudal ribs arise from the sides and not from between the vertebræ.

The capitula are adaptively shifted from this primitive hypocentral position to various parts of the pleurocentra (centra) and neurocentra (neural arches). For example: in *Protorosaurus*, in which all ribs are single-headed, the cervical ribs are hypocentral, the dorsal ribs are high and neurocentral as in Dinosaurs; in *Palæohatteria* and *Kadaliosaurus* the ribs are apparently attached to the anterior part of the pleurocentra; in Proganosauria the ribs are single-headed, loosely attached to the anterior part of the pleurocentra.

By the development of the tuberculum, two-headed ribs arise. In Protorosauria and Proganosauria the rudimentary separation of capitula and tubercula is observed in certain ribs; in Pelycosauria the presacral ribs are all two-headed except on the atlas; in Choristodera (*Champsosaurus*) the presacral ribs are all two-headed except on the atlas and axis. Two-headed ribs will undoubtedly be found also on the atlas, on which they are known to occur in certain higher Diapsida.

In Rhynchocephalia the ribs, primarily two-headed in embryogeny, become secondarily single-headed by the degeneration of the hypocentral articulation of the head and the development of the tubercular attachment to the pleurocentra.

The sacral ribs, 1-3 in number, single-headed, are opposite the pleurocentra. The caudal ribs vary from 6 in *Palæohatteria* to 11 in *Stereosternum*.

#### ABDOMINAL RIBS.

The principal facts regarding abdominal ribs are summarized on page 474. The presence of stout median and lateral series is highly characteristic of the Diaptosauria.

#### GIRDLES.

The primitive constitution of the shoulder girdle includes a large procoracoid suturally separate from the coracoid (Dimetrodon, Hyperodapedon, Procolophon); the secondary condition, in which these elements are reduced and the procoracoid united or wanting, is seen in the Protorosauria, Proganosauria, Choristodera, certain Rhynchosauria (Rhynchosaurus), and Rhynchocephalia. The primitive interclavicle expands into a rhombic anterior plate (Protorosaurus, Palæohatteria), suggesting that of Stegocephala; secondarily it becomes T-shaped in Pelycosauria, Hyperodapedon, Proganosauria, Choristodera, and Rhynchocephalia.

The primitive pelvic girdle similarly consists of plate-like pubes and ischia, as in the Stegocephala; puboischiadic fenestra small or wanting (Protorosauria, Rhynchosauria, Procolophonia, Choristodera); pubis perforated by an obturator foramen. Secondarily the puboischiadic or thyroid fenestra develops separating the pubis and ischium ventrally (certain Pelycosauria, all Rhynchocephalia), the obturator foramen frequently becoming confluent with the puboischiadic fenestra. The primitive ilium is probably narrow and rod-like (Rhynchocephalia, Proganosauria). In cursorial and ambulatory forms (Protorosaurus, Palæohatteria) the ilium is secondarily expanded, with an arched superior border, as in Dinosaurs. In Pelycosauria and Choristodera the dorsal expansion is asymmetrical, suggesting that of the Crocodilia.

#### LIMBS.

The primitive limbs are of a short ambulatory type (*Procolophon*, *Rhynchosaurus*) with distal phalanges curved, indicating the presence of more or less pointed, prehensile claws. In aquatic forms the terminal phalanges and claws degenerate. Elongation for cursorial habit, especially in the hind limbs (Protorosauria), and abbreviation for aquatic habit, is secondary.

Humerus.—A prominent deltoid crest is secondarily developed in Protoro-saurus. The distal or 'condylar foramina' of the humerus exhibit no fixed character and it would appear that the value of this character in phylogeny and

classification has been overrated by Baur and others. 'Radiocondylar' or 'ectepicondylar' foramina are observed in all Protorosauria (Protorosaurus, Palæohatteria, Kadaliosaurus). On the other hand, 'ulnocondylar' or 'entepicondylar' foramina develop in Proganosauria (Mesosaurus and Stereosternum), the Choristodera (Champsosaurus), and certain Rhynchocephalia (Homæosaurus). In other types both an ulnocondylar foramen and a radiocondylar foramen or groove are developed (certain Rhynchocephalia—Anguisaurus minor, Sphenodon—and certain Pelycosauria). With these striking variations of the humeral perforation in different orders and genera we cannot determine at present which is the most primitive foramen—whether the radiocondylar, the ulnocondylar, or the perforation of both condyles. The distal separation of the propodials (ulna and radius, tibia and fibula) by the intermedium, in certain Procolophonia, Proganosauria, and Rhynchocephalia is either primitive (as in Stegocephala) or a secondary adaptation; it is probably primitive.

#### PODIALS.

Carpus.—The primitive carpus undoubtedly includes ten elements, three proximal carpalia (radiale, intermedium, ulnare) equal in size, two centralia, five distal carpalia as in certain Protorosauria (Protorosaurus). In the embryo Sphenodon there are said to be eleven to twelve elements, including a pisiform and possibly a third centrale (Howes). In the secondarily reduced carpus (e. g., Stereosternum) there are but one centrale and four distal carpalia. Intracarpal and intratarsal foramina are observed in Proganosauria and young Rhynchocephalia.

Tarsus.—No ideally primitive tarsus with three distinct proximal elements (tibiale, intermedium, fibulare), free centrale or centralia, and five separate distal tarsalia, has yet been found among the Diaptosauria. More or less coalescence (astragalus = tibiale + intermedium + centrale) or degeneration of these elements has occurred in every known type. Five separate distal tarsalia are observed only in certain Protorosauria (Palæohatteria) and Proganosauria (Mesosaurus and Stereosternum), a unique feature among reptiles; in all other Diaptosauria distal tarsalia 4 and 5 are united.

#### MANUS AND PES.

Phalanges.—The primitive phalangeal formula in the manus is undoubtedly This is observed in all forms except the otherwise primitive Procolophon, in which the phalangeal formula in the manus is 2, 3, 4, 5, 4. In the pes the phalangeal formula is apparently 2, 3, 4, 5, 3 in certain Protorosauria (Palæohatteria), while in other Protorosauria (Protorosaurus) it is 2, 3, 4, 5, 4; the latter is the prevailing formula in the pes of Diaptosauria, as it is found in the Proganosauria, Rhynchosauria, Procolophonia, and Rhynchocephalia.

#### 2. CLASSIFICATION.

Before a settlement of the classification of the Diaptosauria can be reached there are two chief objects for discovery and research:

First, to determine the actual relationships of the seven groups to each other. Second, to determine the possible genetic relationships of one or more of these groups to certain of the higher Diapsida, namely: to the Dinosauria, Ichthyosauria, Phytosauria, Crocodilia, Squamata, and Pterosauria.

New materials should be especially searched for in the Permian; but it must be said with emphasis that a more exhaustive study of the materials already at hand is equally demanded. Fortunately, critical studies are now in progress: of the Pelycosauria by Case, of the Procolophonia (*Procolophon*) by Broom, of the Choristodera (*Champsosaurus*) by Brown. The rich collections of Protorosauria (*Protorosaurus*) now in various museums of Europe should be reëxamined with reference to their probable ancestry to the Carnivorous Dinosaurs. The Jurassic Rhynchocephalia require comprehensive study and critical systematic revision; the unspecialized ancestors of *Sphenodon* are still to be discovered. Among the Proganosauria (*Stereosternum* and *Mesosaurus*) our chief object is to learn the structure of the skull.

It is obvious that the superorder Diaptosauria will in the future be expanded by the discovery, in the Permian and Triassic, of additional specialized and early dying-out lines. It will be also diminished if some of the groups should prove to be ancestral to certain of the higher Diapsida, for the following reason:

In my opinion classification should directly follow, formulate, and express our progressing knowledge of phylogeny; for example, if the Protorosauria prove to be ancestral to the Dinosauria only, as I suspect, then the order Protorosauria should be transferred to the superorder Dinosauria as constituting a common stirp, a common blood relationship, a common tendency of evolution. As soon as a certain evolutionary direction is assumed by a certain group of animals toward a higher group, although the evolution may not have proceeded very far, the lower and the higher group should be united in classification, and thus segregated from groups diverging in other directions. This is in the interest of clearness of thought.

PROTOROSAURIA.—Resemblances of these animals to the primitive Dinosaurs (compare pp. 470, 471) have been remarked in part by Seeley and Credner; Osborn has suggested them as ancestral Dinosaurs; while Nopcsa has definitely placed the *Palæohatteria* skull in the morphological series leading into the Dinosaurs.<sup>1</sup>

In addition to the four Dinosaurian characters of Protorosaurus which I have

¹ In discussing the ancestry of the orders of Dinosaurs, Nopcsa\* regards the three orders as having sprung from a common stem, and in regard to the Ornithopoda he says that all other peculiarities [i. e., beyond certain specializations enumerated] which Baur found in the skull of the Ornithopoda point back partly to the Sauropoda, but chiefly directly to the Protorosauria; among the Protorosauria, Palachatteria most nearly resembles the Ornithopoda in skull and pelvis; Kadaliosaurus priscus and Protorosaurus most nearly resemble the Dinosaurs in the limbs.

<sup>\*</sup> Franz Baron Nopcsa. Dinosaurierreste aus Siebenbürgen. Schädelreste von Mochlodon mit einem Anhange zur Phylogenie der Ornithopodiden. LXXII Band, Denkschrift. Math.-Naturw. Classe, Wien, 1902.

enumerated on page 471, should be mentioned: (5) the antorbital fenestra, (6) the short, deep sagittal crest with small parietals, (7) the large quadrate, (8) the remarkably elongate cervicals, (9) the high neurocentral attachment of the dorsal ribs, (10) the relative abbreviation of the fore limb, (11) the straight femur, (12) the structure of the astragalus and calcaneum, (13) the enlargement of the three median digits of the pes, (14) the similar number, twenty-three, of presacral vertebræ, (15) the puboischiadic fenestra.

On the other hand, Protorosaurus retains a large number of primitive characters in addition to those mentioned on page 470, and some divergent characters, the weight of which should be thoroughly estimated.

Proganosauria.—As shown on pages 489-491, the theory that the Proganosauria are ancestral to the Plesiosauria does not appear to be tenable. Comparison with other long-faced, aquatic Diaptosauria is therefore desirable.

In addition to the points against their relationship to Champsosaurus mentioned on page 493, should be enumerated: (1) Champsosaurus although a geologically more recent form, has but if presacrals (C26, D 17), whereas the Permian Stereosternum has 34 presacrals (C 12, D 22). The resemblances are certainly due to parallelism rather than to genetic relationship.

Similarly the Proganosauria are too specialized to be ancestral to any of the aquatic Rhynchocephalia (Pleurosaurus, etc.).

It is therefore extremely desirable to complete our knowledge of the skull structure of these animals; especially to ascertain (1) the position of the external nares, (2) the presence or absence of a laterotemporal fenestra, (3) the structure of the The skulls I have had the opportunity of examining do not positively show the position of the nares; if these openings instead of being terminal are immediately in front of the orbits as in Phytosauria or Ichthyosauria, relationships to these orders should be taken into consideration although it does not seem at all probable.

PROCOLOPHONIA.—We await Broom's memoir for the nearer determination of the position of these animals (compare pp. 480, 481). They are certainly more primitive but there is considerable suggestion of resemblance to the Rhynchosauria: (1) in the compressed facial region; (2) in the large upwardly opening orbits; (3) in the flattening of the molar teeth, although these teeth are chiefly borne on the maxillaries and premaxillaries instead of on the palate as in Rhynchosauria; (4) in the general proportions of the body, limbs, and extremities: (5) in the separate coracoid and procoracoid; (6) in the small laterotemporal fenestræ. These resemblances again may be of no genetic significance. however, the Rhynchosauria should be found to be related to *Procolophon*, the order Procolophonia Seeley would acquire additional validity and would include the Rhynchosauria as a suborder.

RYNCHOSAURIA.—These animals (compare pp. 477-480) undoubtedly repre-Their possible descent from Procolophon-like sent an independent specialization. forms is discussed in the previous paragraph.

506 OSBORN, THE REPTILIAN SUBCLASSES DIAPSIDA AND SYNAPSIDA.

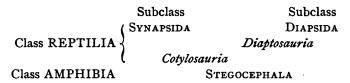
CHORISTODERA.—The Choristodera (compare pp. 492, 493) suddenly appear and leave no known descendants. The natural position of this group seems to be that of an independent order, bearing relationships to the less specialized Rhynchocephalia similar to those which the Mosasauria bear to the Lacertilia. The amount of divergence in the two cases appears to be as great or greater; that is, Champsosaurus and more especially Simædosaurus are as far or further removed from Sphenodon than Mosasaurus is from Varanus.

#### SUMMARY.

The more conservative general conclusion regarding the classification of these seven groups, therefore, is that we must await additional evidence. The Protorosauria, the Pelycosauria, the Choristodera, seem to be entitled to rank as distinct orders. Future discovery may link the Rhynchosauria and Procolophonia more closely to the Rhynchocephalia, as suborders; in which case the true Rhynchocephalians should be distinguished as the suborder Sphenodontina. The relationships of the Proganosauria are the most uncertain, and will depend upon our future knowledge of the structure of the skull.

#### 3. PHYLOGENY.

General Phylogeny.—A general phylogenetic conclusion may be expressed diagrammatically as below:



that is, the Stegocephala gave rise to the Cotylosauria or most primitive Synapsida from which sprang the higher Synapsida, also the Diaptosauria or most primitive Diapsida; from which, in turn, were partly or wholly derived the higher Diapsida.

Special Phylogeny.—The more special phylogenetic conclusion, of a very provisional and hypothetical character, may be expressed as follows:

Sphenodon				Recent
Rhynchocephalia (t. l. a.1)	Dinosauria (t.)		Choristodera (a.)	Cretaceous Jura. Trias.
Rhynchosauria (1.)  Procolophonia (t.)	Protorosauria (t.)	Pelycosauria (t.)	Proganosauria (a.)	Permian and Lower Trias.
	Primitive or Unspe	ccialized Diaptosau	ria	Carboniferous and Lower Permian

These seven groups represent the *first adaptive radiation* of the small lower forms of Diapsida, into various terrestrial, littoral, and aquatic types; its maximum development was especially characteristic of the Permian. It compares with the higher Diapsidan radiation as the Cretaceous and Lower Eocene Creodonta compare with the Eocene and Upper Tertiary Carnivora.

The second adaptive radiation of the higher and larger DIAPSIDA arose partly from spurs of the Diaptosauria, and included the radiations of the Phytosauria, Ichthyosauria, Dinosauria, Crocodilia, Squamata, and Pterosauria.

Like all speculative 'phylogenies,' this is a card castle which may serve a temporary purpose in clearly conveying some preliminary ideas based upon our present very limited knowledge.



### INDEX TO VOLUME I.

[New names of genera, species, subspecies, and of higher groups are printed in heavy-faced type. The main references to species, genera, etc., are also in heavy-faced type.]

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### ERRATA.

Page 79, line 13, for CHALICOTHERIODEA read CHALICOTHERIOIDEA.

Page 120, lines 15 and 16 from bottom, for A. bicornis read R. bicornis.

Page 228, in Synoptic Table, for Sanninoidea pacifica read Sanninoidea opalescens.

Page 229, line 17, for Sesia pictipes read Sesia albicornis.

Page 241, line 4 from bottom, for Types: . . . Coll. U. S. Nat. Mus. read Coll. H. Druce.

Page 266, lines 11 and 21, for pacifica read opalescens.

Page 292, line 4 from bottom, add: Albuna modesta Kellicott, Can. Ent., Vol. XXIV, 1892, p. 46.

Page 303, species heading, for Sesia sigmoidea (Hy. Edw.) read Sesia sigmoidea Beut.

Page 303, line 17 from bottom, for Ægeria sigmoidea read Ægeria asiliformis ROTT.



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