Reclassification of the Reptilia

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RECLASSIFICATION OF THE REPTILIA.

HENRY FAIRFIELD OSBORN.

HISTORY OF CLASSIFICATION.[1]

Philosophy of Classification.—The history of the classification of the Reptilia resembles that of the classification of other forms of vertebrates in its gradual approximation to the truth.

The general progress has been from superficial to profound characters, from purely adaptive characters to those which are phylogenetic and indicate real affinity. For a century and a half superficial resemblances and analogous adaptations have been the pitfalls out of which the final classification is slowly emerging.

Every classification, moreover, has had its underlying philosophy. The "special creation" philosophy underlays the Linnæan system, but in so far as Linnæus, Cuvier, De Blainville, Owen perceived a real order in certain profound characters, their systems will stand.

The philosophy underlying modern classification is the

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[1] Presented at the first meeting of the Society of Vertebrate Palæontologists, Philadelphia, December 29th, 1903. Abstract, in part, of a memoir entitled The Reptilian Subclasses Synapsida and Diapsida and the Early History of the Diaptosauria. *Mem. Amer. Mus. Nat. Hist.* Vol. I, Pt. VIII, Nov. 1903.

Lamarck-Darwin theory of the law of descent which involves a branching or phylogenetic scheme of relationships. Toward this we are slowly progressing. The final classification will be a formal or tabular statement of the tree of descent, in which only so much pre-Darwinian classification will survive as was based upon the perception of real phylogenetic characters.

The evolution philosophy held out a strong temptation to rapid generalization in phylogeny. It is a striking fact that the evolutionists, Huxley, Cope, Hæckel, perhaps because they attempted to generalize too rapidly, have proved less fortunate in their arrangement of the Reptilia than Owen, whose pre-Darwinian systems of 1839 and 1859 have best stood the test of time and of discovery.

Both Cope's and Huxley's systems are largely wrecks today; Huxley's because while entirely logical in method it outran the state of knowledge and discovery. Cope was less logical; his fatal error was over reliance on single characters without discriminating whether they were primitive or adaptive. Marsh was gifted with unerring taxonomic judgment as to real phylogenetic relationships; the chief defect of his system was that he partly or wholly ignored the rules of priority, renaming and redefining groups which had previously been defined with sufficient clearness to be recognized. It is with real regret that I feel compelled, as a matter of historic justice, to revive some of the older names for certain groups of which our knowledge is almost entirely due to the fundamental contributions of Marsh.

Priority.—Palæontological discovery is constantly swelling and expanding the groups of fossils discovered long ago; it is consequently necessary either to abandon these groups or to raise or lower their grade. For example, Owen's "family" Cynodontia has become a suborder, his "families" Dicynodontia and Theriodontia have become orders, his "orders" Anomodontia and Dinosauria have become superorders.

If we should confine each group to the rank or systematic position originally assigned to it by its author in a very limited state of knowledge, we should have to rename the larger number of groups, and this certainly is not advisable either in the interest of clearness or as a matter of historic justice.

The history of classification is usually presented by giving the complete schemes published successively by various anatomists.

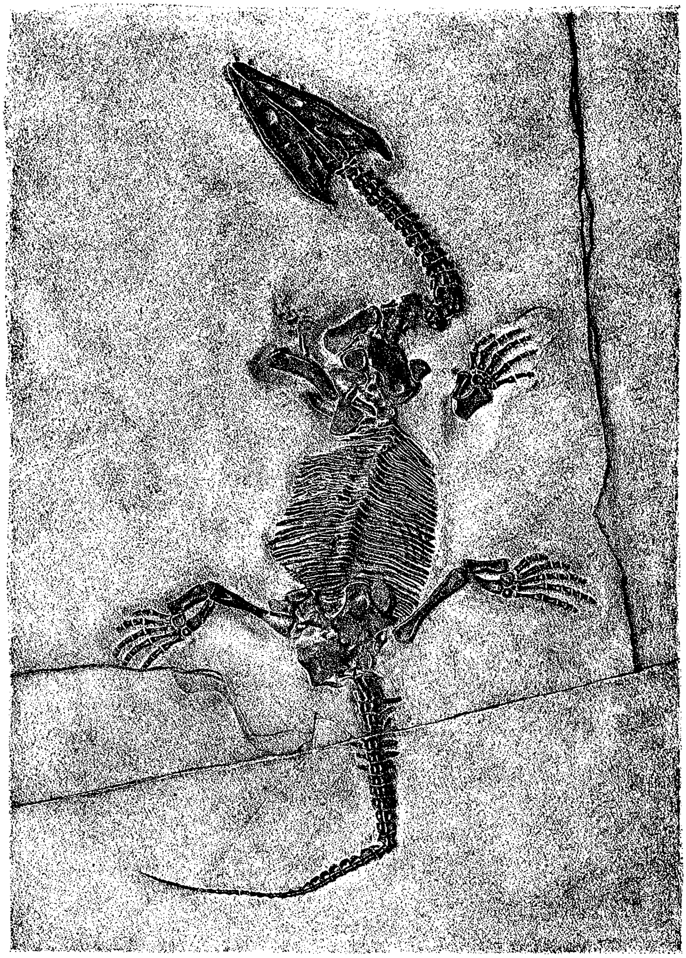

FIG 1.— A primitive Plesiosauroid Synapsidan, *Lariosaurus balsami.* After Boulenger. × ½.

The student will perhaps gain as valuable a lesson by considering the anatomical philosophy, true or false, which has prompted different systems of classification.

False Principles of Classification.

Superficial Resemblances.— In Brogniart's system of 1799 the Lacertilia and Crocodilia are wrongly united on limb structure as (II) Saurii, as distinguished from (III) Ophidii, and (I) Chelonii.

The similar scaly covering led Latreille (1820) to rightly unite the Ophidia and Lacertilia as Squamosa ; previously Oppel (1811) grouped the Lacertilia and Ophidia as Squamata ; this, however, is the single instance in which epidermal resemblance happens to coincide with underlying fundamental characters.

As instances of errors based upon epidermal characters, we may cite the union of the Testudinata and Crocodilia by Klein as Cataphracta ; or the union of the same animals by Merrem as Loricata.

Resemblances in Single External Organs.— So able a palæontologist as von Meyer (1830) attempted to classify the reptiles by resemblances in foot structure. He thus divided the Saurii, or limbed reptiles into (1) Dactylepodes, including Lacertilia and Crocodilia ; (2) Nexipodes, including the Ichthyosauria and Sauropterygia (*Plesiosaurus, Nothosaurus*) ; (3) Pachypodes, including the Iguanodontia and Megalosauria ; (4) Pterodactylii, including the Pterosaurs — a false system.

Classification of Analogous Adaptations.— De Blainville (1835) united the Ichthyosauria and Sauropterygia as Enaliosaurii, or sea lizards. Owen (1839) adopted the order Enaliosauria as embracing the Ichthyopterygia (1859) and Sauropterygia (1859), but remarked that these animals "do not form a strictly natural group."

Classification by single Internal Characters.—This method was especially characteristic of Cope. In 1869 he defined the Archosauria as differing from the Monimostylica of Müller only by the exclusion of the order Testudinata ; he observed that close sutural attachment of the quadrate bone "was the important feature which characterizes the order" ; by this feature he united the Sauropterygia (Nothosaurus, which was selected as a type) the Crocodilia, the Thecodontia (suborder of Dinosauria), the Dinosauria, the Anomodontia, and the Rhynchocephalia ; a totally unnatural and transitory grouping, because based upon the possession of a single primitive character, namely, the *fixed quadrate*.

We find that almost every attempt to classify the reptiles by superficial characters, by external organs, by general external adaptations, by single internal organs, has proved unnatural.

True Principles of Classification.

The conclusion is that there are three ruling principles in classification.

First, as to *priority*, we owe it to our palæontological forebears not to abandon the lower or higher groups they have proposed except in cases of absolute necessity. In some instances we must give a group a higher or lower rank than the author originally assigned to it, or a different position in the system. Priority has no force where a group is based on a false conception or on a false grouping of types, as in the definitions of Theromorpha and Archosauria by Cope.

Second, as to *phylogeny*, classification is a formal expression of our knowledge of phylogenetic relationships; it must, therefore, constantly shift and change as new relationships are discovered. The final classification will be the phylogenetic tree. This being the case, it is desired to include within a group its ancestral forms as soon as they have definitely branched off toward it. For example, Hyracotherium should not be placed in the Lophiodontidæ, as was done by Cope, but in the Equidæ. Again, if it should be demonstrated that the Protorosauria are ancestral to the dinosaurs and to no other reptiles, they should be placed in the superorder Dinosauria.

Third, as to *definition*, classification, like phylogeny, should be based on a number of characters of different parts of the body having different functions, in order to diminish the danger of being misled by analogous evolution, otherwise known as parallelism, convergence and homoplasy.

The neglect of one or other, and in some cases of all these three principles and the loss of the clarifying mind of George Baur have led to great and rapidly increasing confusion in the arrangement of the Reptilia in recent years. Smith Woodward, Broom and von Nopsca, have been working in the right direction.

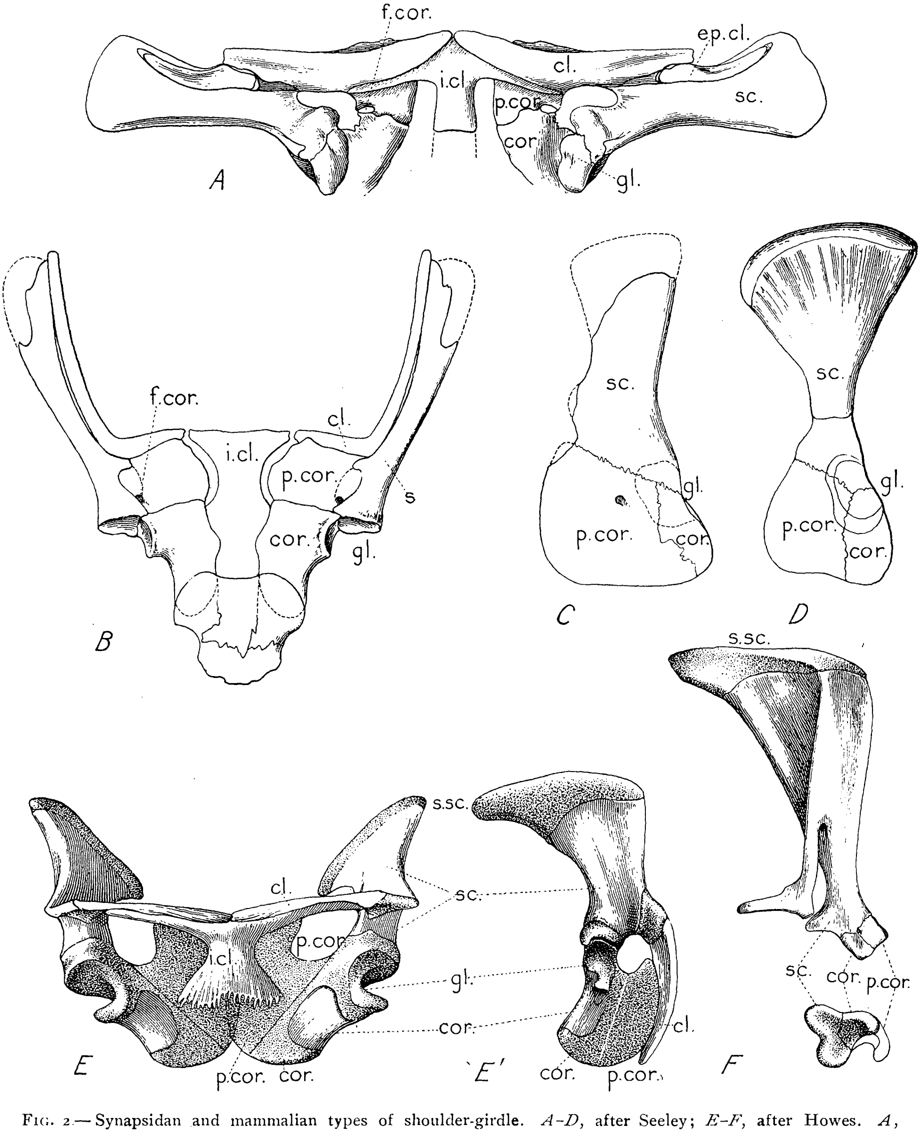

Fig. 2 — Synapsidan and mammalian types of shoulder-girdle. *A–D*, after Seeley; *E–F*, after Howes. *A*, *Pareiasaurus bainii*; *B*, *Keirognathus cordylus*; *C*, Deuterosaurus; *D*, Rhopalodon; E, ventral, *E'*, lateral views of Ornithorhynchus; F, Lepus.

PROPOSED RECLASSIFICATION.

At the Washington meeting, 1902, of the American Association, I presented a joint paper with Dr. J. H. McGregor on the diphyletic arrangement of the reptiles, based on comparison of a large number of characters. I have since made a more searching study of the same problem, designating these two groups as the subclasses SYNAPSIDA, or primitively single-arched reptiles, and DIAPSIDA, or primitively two-arched reptiles, and have grouped all the most primitive forms of Diapsida in the superorder DIAPTOSAURIA, a group equivalent in taxonomic rank to the Squamata or the Dinosauria. I now propose to briefly describe the reptiles which fall within these two groups.

SUBCLASS SYNAPSIDA Osborn.

The chief distinction of the single arched reptiles is that there is either no opening at all in the temporal region (Cotylosauria), or a single large supratemporal opening (Anomodontia, Plesiosauria, Testudinata) as in the upper view of the skull of a plesiosaur, a turtle, or a mammal. This supratemporal fossa is large, because the cranium or brain case is long while the facial portion of the skull is relatively short, these proportions being directly reversed in the Diapsida. The temporal arch consists primitively of two arches combined. The squamosal is always a large element. The quadrate is correspondingly more or less reduced; it is never movable, and is functionally supported by the squamosal. In the shoulder girdle the coracoid and procoracoid are separate, or united by suture. The phalangeal formula is primitively 2. 3. 3. 3. 3, like that of mammals.

I. *Order* COTYLOSAURIA Cope

Pareiasauria Seeley.

These are the most primitive of reptiles, retaining many Stegocephalian (amphibian) characters, and a solid cranial roof with temporal openings rudimentary or not developed at all.

- Subclass **SYNAPSIDA** Osborn 1903.
  - Order COTYLOSAURIA Cope 1880 (Pareiasauria Seeley 1889)
- Superorder ANOMODONTIA Owen 1860. (Theromorpha Cope 1878, in part.)
  - Order THERIODONTIA Owen 1876.
    - Suborder Therocephalia Broom 1903.
    - Suborder Cynodontia Owen 1861.
  - Order DICYNODONTIA Owen 1860.
  - Order PLACODONTIA *auct. ex* H. von Meyer[3] 1863 Incertæ Sedis.
  - Order SAUROPTERYGIA Owen 1860.
    - Suborder Simosauria *auct. ex* Gervais[1] 1845. (Nothosauria Seeley 1882.)
    - Suborder Plesiosauria *auct. ex* Quenstedt[2] 1852.
  - Order TESTUDINATA *auct. ex* Shaw[4] 1802.
    - Suborder Pleurodira *auct. ex* Duméril and Bibron[5] 1835.
    - Suborder Cryptodira *auct. ex* Duméril and Bibron[6] 1835.
    - Suborder Trionychia[7] *auct. ex* Pictet 1853.

- Subclass **DIAPSIDA** Osborn 1903.
- Superorder DIAPTOSAURIA Osborn 1903.
  - Order PROCOLOPHONIA Seeley 1867.
  - Order PROTOROSAURIA Seeley 1887.
  - Order PROGANOSAURIA Baur 1887.
  - Order GNATHODONTIA Owen 1680. (Rhynchosauria Osborn 1903).
  - Order PELYCOSAURIA Cope 1878.
  - " CHORISTODERA Cope 1877.
  - " RHYNCHOCEPHALIA Günther 1868.
  - Order PARASUCHIA Huxley 1875.
    - Suborder Aëtosauria Nicholson and Lydekker 1889.
    - Suborder Phytosauria Baur 1894 *ex* Jaeger 1828.
  - Order ICHTHYOSAURIA Blainville 1835 *ex* Jaeger 1824. (Ichthyopterygia Owen 1860.)
  - Order CROCODILIA[9] Wagler (?) 1830.
    - Suborder Mesosuchia Huxley 1875.
    - Suborder Eusuchia Huxley 1875.
    - " Thalattosuchia Fraas 1901.
- Superorder DINOSAURIA Owen 1840.
  - Order THEROPODA Marsh 1881.
    - Suborder Megalosauria *ex* Fitzinger 1843. (Thecodontia Owen 1860.)
    - Suborder Symphypoda Cope 1867. (Compsognatha Huxley 1870.)
  - Order OPISTHOCŒLIA Owen 1860. (Sauropoda Marsh 1881.)
  - Order ORTHOPODA Cope 1866. (Predentata Marsh 1894.)
- Superorder SQUAMATA Oppel 1811.
  - Order LACERTILIA[9] Owen 1839.
  - Order MOSASAURIA *auct. ex* Gervais[8] 1845.
  - Order OPHIDIA[9] Brogniart 1802.
  - Order PTEROSAURIA *auct. ex* Kaup 1834.

[1] "Simosauriens."

[2] "Plesiosauri."

[3] "Placodonten."

[4] "Testudines."

[5] "Pleurodères."

[6] "Cryptodères."

[7] "Trionychides."

[8] "Mosasauridés."

[9] The dates and authors assigned for the earliest recognition of the supergeneric rank of several of these groups may be altered by future investigations.

The large South African Pareiasauridæ are more specialized than the Texan Pariotichidæ and Diadectidæ, the latter being the type of the order.

Theoretically some unspecialized members of this order gave rise to all other reptiles including both Synapsida and Diapsida.

II. *Superorder* ANOMODONTIA Owen.

This was originally defined by Owen (1860) as an 'order' embracing the "families" Dicynodontia, Cryptodontia and Gnathodontia (Rhynchosaurus). The reference of the latter 'family' proves to have been an error. In 1861, in the second edition of his *Palæontology*, Owen included in the Anomodontia the 'family' Cynodontia, based on the types Galesaurus and Cynochampsa; thus raising the Anomodontia to the rank of a superorder which is equivalent in part to the superorder Theromorpha Cope.

This 'superorder' includes two orders, which represent an adaptive radiation from more primitive truly reptilian types (Therocephalia Broom) into the more mammal-like Cynodontia, both with full sets of teeth, and finally into the highly specialized Dicynodontia, in which the teeth are greatly reduced. All these animals retain, however, some primitive or cotylosaurian and stegocephalian characters.

I. *Order* THERIODONTIA Owen.

1. *Suborder* Therocephalia Broom.

Broom has recently published an admirable paper on the "Classification of the Theriodonts and their Allies,"[1] in which the Therocephalia[2] are defined from the types Scylacosaurus, Ælurosaurus, Ictidosuchus, Deuterosaurus, Titanosuchus, Gorgonops, as representatives of six families. These are medium sized reptiles, and apparently the most primitive of the Anomo-

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[1] *Rep. So. Afr. Assoc. Adv. Sci.* 1903, pp. 362–369.

[2] This is defined as an order by Broom and may prove to be of full ordinal rank; it is here provisionally grouped with the Anomodontia as a suborder of Theriodontia.

dontia. The teeth are differentiated as in mammals into incisors, canines (sometimes double), and molars; the molars, however, are simple, and the palate is simple, like that of the Cotylosauria, that is, there is no secondary palate.

2. *Suborder* Cynodontia Owen.

This was originally defined as the "family" Cynodontia by Owen in 1861, and may be embraced within the order "Theriodontia" Owen of 1876, which was based on the same types, viz.: Galesaurus and Cynochampsa.

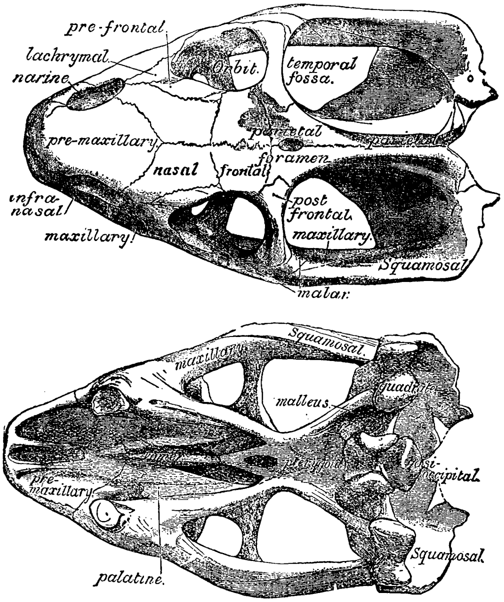


FIG. 3.— Synapsid Type. Palatal and superior views of the skull of Dicynodon, showing the elements as interpreted by Seeley. Note especially the exposure of the prevomer, the large extension of the squamosal, the pre- and postfrontals, the single squamoso-maxillary bar. After Seeley.

These are intermediate anomodonts of medium size. In contrast with the Therocephalia the squamosal is more expanded and the quadrate is greatly reduced. Approaching the mammals also, there is the secondary palate, formed of the maxillaries and palatines, also the double condition of the occipital condyles which are single in Therocephalia. These cynodonts have lost several of the other more primitive characters of the therocephalians, such as teeth in the palate; and their specialization is in the direction of the mammalia. The phalangeal formula is 2. 3. 3. 3. 3. They include three families, typified respectively by the genera Lycosaurus, Cynognathus, and Gomphognathus.

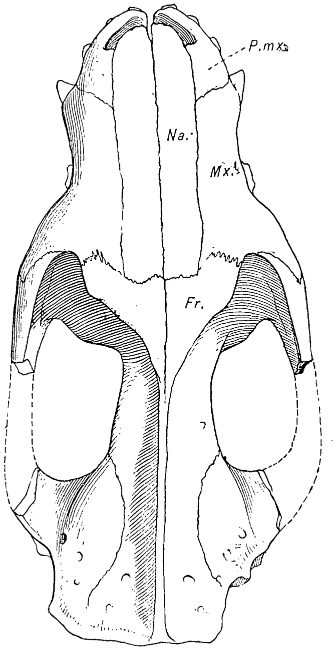


FIG. 4.— Synapsid Type Top view of the skull of a primitive amblypod ungulate, Pantolambda. × ½.

2. *Order* DICYNODONTIA Owen.

This term was originally used as a "family" term, under Anomodontia, by Owen in 1859; Huxley raised it to the rank of an order from the types Dicynodon, Oudenodon. The latter, Owen (1859) had placed in the "family" Cryptodontia, in reference to the absence of teeth. Despite the high specialization of the dentition, these animals retain the more primitive features of the single condyle, of the cleithrum or epiclavicle, of the large quadrates. On the other hand, like the cynodonts, they show a rudimentary secondary palate. They approach the mammals also in the loss of the prevomers and development of the vomer (parasphenoid).

In the most primitive family of Endothiodontidæ one or more series of molar teeth are present on the maxillaries and dentaries; the interclavicle is a rounded plate as in the Stegocephalia. In the more specialized Dicynodontidæ, maxillary teeth are absent, or present as a pair of tusks, and there are no teeth in the lower jaw; the interclavicle is elongated, and a cleithrum is present. The third family, Lystrosauridæ, exhibits a small interclavicle, and no cleithrum. A fourth family, Cistecephalidæ is doubtfully ranked here by Broom.

Broom has contributed a large number of papers on the structure and arrangement of the South African reptiles, which for the first time throw a perfectly clear light on their relationships to each other.

3. *Order* PLACODONTIA.

(*Incertæ sedis.*)

The position of this order as typified by the genus Placodus, is still very doubtful. It is characterized by very large teeth in the palate, and by the absence of teeth on the maxillaries and premaxillaries. It includes littoral, shell-eating forms, which may be an independent offshoot of the Anomodontia, or may be more nearly related to the Sauropterygia.

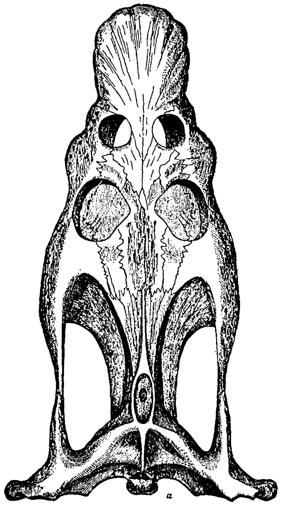


Fig. 5.— Synapsid Type. Dorsal aspect of skull of *Nothosaurus andriani?* A primitive plesiosauroid reptile. After Cope.

III. *Order* SAUROPTERYGIA Owen.

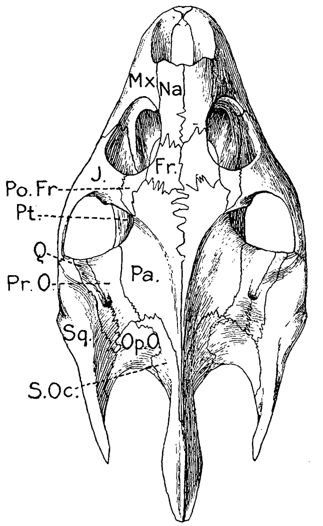


Fig. 6.— Synapsid Type. Dorsal view of skull of Trionyx.

The theory of the relationship of the plesiosaurs to the Synapsida and especially to the Anomodontia and Testudinata still requires confirmation. The skull structure is typically synapsidan. The shoulder girdle structure, so far as known, in the Triassic plesiosaurs is certainly more synapsidan than diapsidan. Numerous resemblances to the Testudinata have been pointed out. On the other hand, certain of the oldest Triassic plesiosaurs, such as Lariosaurus, (Fig. 1) closely approach the Diapsida in the phalangeal formula.

IV. *Order* TESTUDINATA (*ex* Shaw.)

The kinship of the Testudinata to the Synapsida is indicated both by the skull structure and by the phalangeal formula. The shoulder girdle structure, like that of the plesiosaurs, is still in dispute; the main question being as to the homologies of the anterior ventral processes variously known as the "procoracoid" or "proscapula."

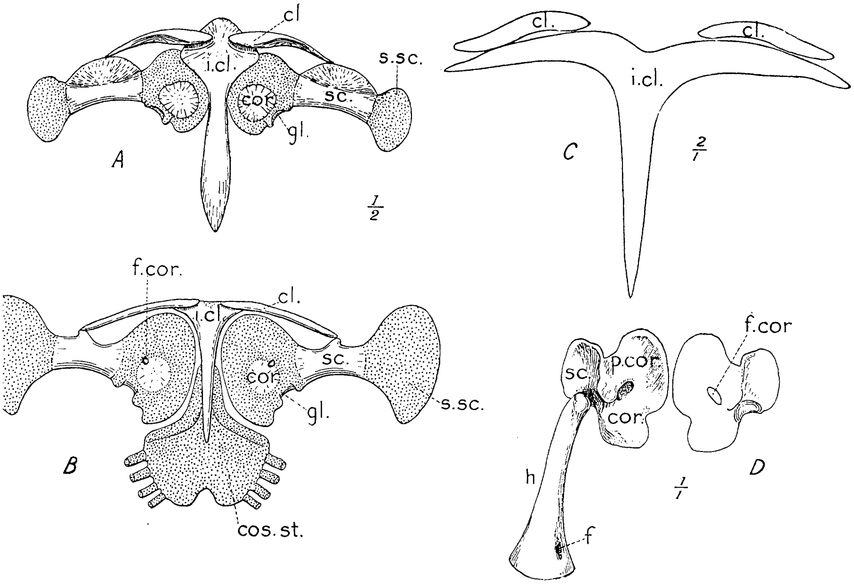


FIG. 7.—Diapsidan types of shoulder-girdle. *A*, Palæohatteria. After Credner. The cartilaginous areas are entirely restored. Restoration by J. H. McGregor. × ½. *B*, Sphenodon juv. (15 cm.); modified from Howes. By J. H. McGregor. × $\frac{8}{1}$. *C*, Pleurosaurus. Cartilaginous elements omitted. After Dames. × $\frac{2}{1}$. *D*, *Mesosaurus tenuidens*. Modified from Gervais. × $\frac{1}{1}$.

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

SUBCLASS DIAPSIDA Osborn.

All these animals are readily distinguished by their general likeness to the existing Hatteria. In contrast to the Synapsida the cranium is short; the temporal region is primitively fenestrated by two distinct openings, the supra- and latero-temporal fenestræ, bounded by the supra and latero-temporal arches, one or both of which may secondarily disappear. In further contrast with the Synapsida, the squamosal is a relatively small element, frequently separate from the prosquamosal, and never entering into articulation with the lower jaw; the quadrate, on the other hand, is a relatively large element, uncovered, and sometimes secondarily movable. In the shoulder girdle we find a most distinctive character in the early coalescence of the coracoid and procoracoid into a single bone, or in the degeneration of the procoracoid. Another highly distinctive character is the phalangeal formula, 2. 3. 4. 5. 3–4, which is secondarily modified in the aquatic forms.

There appear to have been two great adaptive radiations among the Diapsida. The *first* is that which occurred during the upper Carboniferous and Permian, branches of which are already well separated in the Permian and have been collectively grouped in the superorder Diaptosauria by Osborn. The *second*, or later radiation of the Diapsida, partly sprung from terminal branches of the first, is known in the Triassic, and includes the great orders Parasuchia, Ichthyopterygia, Crocodilia, the superorder Dinosauria, the superorder Squamata, and finally the Pterosauria.

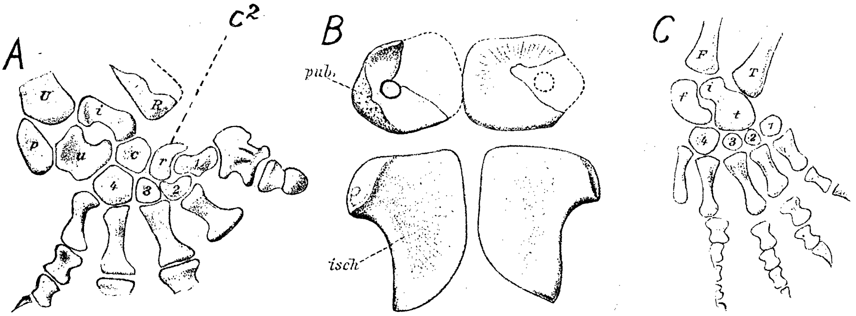
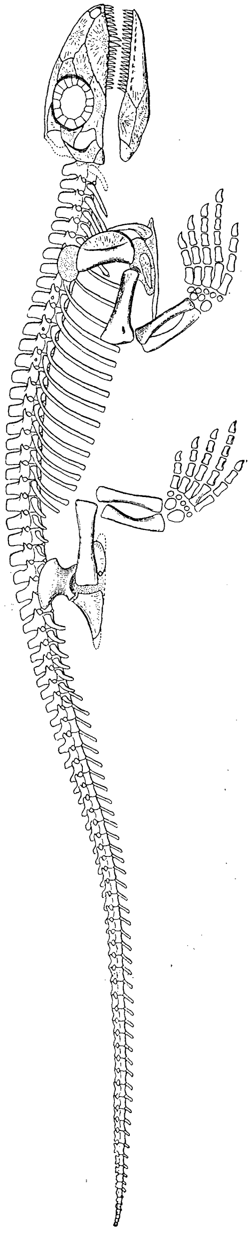


FIG. 8.—The most primitive known Diapsidan. *A*, manus, *B*, pubis and ischium, and *C*, pes, of *Procolophon trigoniceps* Owen (Order PROCOLOPHONIA). After Broom. $\times \frac{1}{1}$.

I. *Superorder* DIAPTOSAURIA Osborn.



This superorder embraces the Rhynchocephalia of Günther, the Pelycosauria of Cope, which certainly represent distinct orders of reptiles, and the more or less distinct orders or suborders Protorosauria, Procolophonia, Proganosauria, Choristodera, Gnathodontia, Rhynchocephalia. They have appropriately been termed 'rhynchocephaloid' reptiles by Broom.

The common characters of these primitive or stem Diapsida, are as follows: cranium with two complete temporal arches; vertebræ typically amphicœlous and often perforated by a notochordal canal; hypocentra frequently present throughout vertebral column; ribs on all vertebræ from first cervical to eighth caudal inclusive, generally single-headed or incipiently two-headed; large abdominal ribs or plastron always present; coracoid and procoracoid early uniting into a single bone; pubis and ischium ventrally in continuous contact or secondarily fenestrated.

The adaptive radiation of these mostly small sized animals into ambulatory, littoral, amphibious, and fully aquatic types, together with specializations of the skull and dentition for a great variety of feeding habits has resulted in a divergence sufficiently profound and ancient to form seven groups which have been variously assigned the rank of orders or suborders as follows:

FIG 9.—A primitive diapsidan. *Palæohatteria longicaudata.* Restoration by J. H. McGregor. × ⅓. Order PROTOCOSAURIA.

1. *Order* PROCOLOPHONIA Seeley.

This includes the most primitive of the Diaptosauria; those closest to the Cotylosauria, and distinguished by the entire absence of lateroemporal fenestræ,[1] by the persistence of the epiotics and auditory notch of the cotylosaurs, and other very primitive characters. These animals are thus far recognized in the Permian of South Africa only.

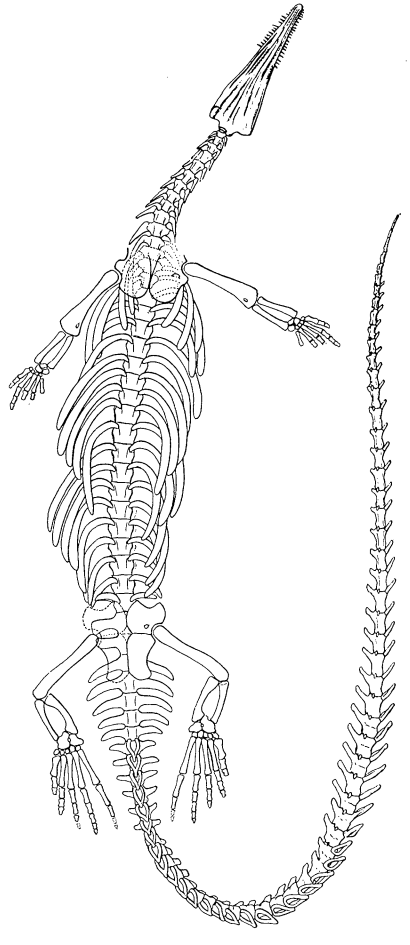


FIG. 10. *Stereosternum tumidum.* Restoration by J. H. McGregor. × 1/3. Order PROGANOSAURIA.

2. *Order* PROTOROSAURIA Seeley.

This land group includes Protorosaurus, Palæohatteria, Kadaliosaurus, distinctively ambulatory and in part leaping reptiles, certainly carnivorous; distinguished by the straight limbs, strong development of the hind limbs, correlated with a dorsally expanded ilium and from two to three sacral vertebræ.

These animals show all the characters which we should expect to find in the ancestors of carnivorous Dinosauria; the three genera known are too far specialized in the direction of ambulatory and predatory types to have given rise to any of the other known Diaptosauria.

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[1] Dr. R. Broom has just made this important observation.

3. *Order* PROGANOSAURIA Baur.

This aquatic or amphibious group, which has been confused with the Protorosauria, is at present represented only by the genera Mesosaurus Seeley and Stereosternum Cope, closely allied forms from the Permian of South Africa and South America. These are typical swimming or amphibious types, with greatly elongated rostrum, delicate, prehensile teeth, very heavy ribs with highly modified capitular attachments; the vertebræ are also highly distinctive and unique in structure.

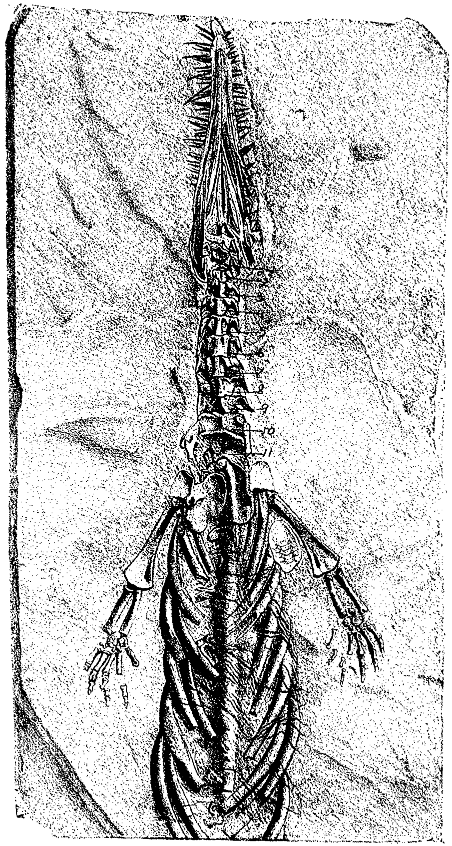

FIG. 10a.—*Mesosaurus tenuidens*. After Gervais. × ½. Order PROGANOSAURIA.

These forms also are too specialized to give rise to any of the higher Diapsida; they represent an isolated and dying out group.

4. *Order* GNATHODONTIA Owen.

Rhynchosauria Osborn.

Owen first proposed the "family" Gnathodontia in 1859, typified by Rhynchosaurus, at the same time that he proposed the "family" Dicynodontia. It seems proper that this term should be given priority over the order Rhynchosauria proposed by Osborn in 1903.

Here again we have a highly specialized division resembling the Procolophonia in general body and cranial form, but differing from these animals widely in the concentration of pavement-like teeth on the pterygopalatines and the development of a large edentulous bony beak. They were probably littoral, shell-eating animals far removed from the true Rhynchocephalia.

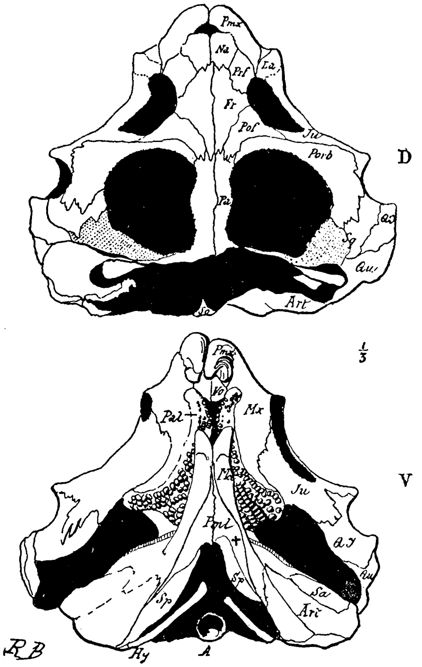

Fig. 11.—Skull of *Hyperodapedon gordoni*. *D*, dorsal, *V*, ventral aspect, × $\frac{1}{3}$. After Burckhardt. The black areas represent parts still covered by matrix. Order GNATHODONTIA.

5. *Order* PELYCOSAURIA Cope.

This land group, developed in the Permian of Texas and Bohemia, is distinctively ambulatory and carnivorous. It is characterized by the abbreviation of the tail, the enormous development of the spines of the dorsal vertebræ, also by the

the persistence in certain forms of a suture between the coracoid and procoracoid.

This line also became very highly specialized, and died out in the Trias.

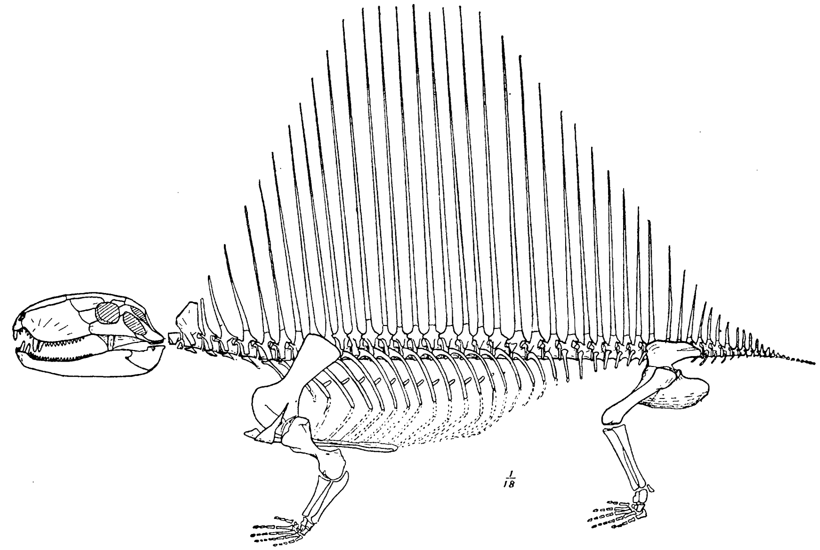

FIG. 12.—Restoration of Embolophorus (Order PELYCOSAURIA). About $\frac{1}{18}$ nat. size. After Case.

6. *Order* CHORISTODERA Cope.

These amphibious animals, found thus far only in the Cretaceous and in the Lower Eocene, represent a sharply defined division with a greatly elongated gavialoid rostrum, teeth acrodont and internally folded, dorsal ribs two-headed. They include the American Champsosaurus and the European Simœdosaurus; the latter being distinguished by more distinct adaptation to aquatic life were made the type of the order Simœdosauria by Dollo. The analogies are with the Proganosauria and the aquatic true Rhynchocephalia, but there are no phylogenetic relationships with these forms.

7. *Order* RHYNCHOCEPHALIA Günther.

These are the "Rhynchocephalia Vera" of Boulenger. They represent by far the most conservative of all the Diaptosauria because even the recent Sphenodon is in certain respects more primitive than most of its Permian relatives.

The order includes the Jurassic radiation of terrestrial, semi-aquatic, and fully aquatic types, with modifications paralleling those in the Choristodera and Proganosauria, also the existing terrestrial genus Sphenodon. The Jurassic forms are in many respects less primitive than the existing genus.

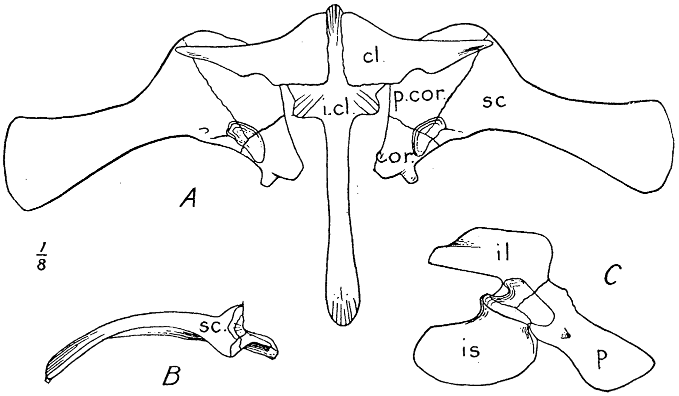

FIG. 13.—*A*. Shoulder-girdle of a Pelycosaurian (Embolophorus) *B*, Profile view of conjoined scapula and procoracoid of same. This is one of the few Diapsida in which the procoracoid is still separated by suture from the coracoid. *C*. Pelvis of same. After Case. × $\frac{1}{8}$.

11. *Order* PARASUCHIA Huxley.

This amphibious fresh water group, typified by Phytosaurus and Aëtosaurus, placed in the suborders Aëtosauria and Phytosauria respectively, has long been treated in connection with the Crocodilia, owing to Huxley's influence and authority; McGregor has shown that it has practically no affinity to the Crocodilia, its relationships being closer to the Ichthyosauria, although it constitutes an independent order, probably of freshwater, littoral, carnivorous, short snouted (Aëtosaurus) or long snouted (Phytosaurus, Mystriosuchus) forms, analogous in their habits to the modern Crocodilia.

The Parasuchia are found by McGregor to represent an undoubted modification of the rhynchocephaloid or diaptosaurian type.

III. *Order* ICHTHYOSAURIA Blainville.

The ichthyosaurs are also distinctively Diapsida, both in shoulder girdle and in basicranial structure. The latero-temporal fenestra, however, is closed, perhaps secondarily. The posterior position of the nares and the elongation of the snout in front, is analogous to that in the Parasuchia and may be indicative of divergence from a common stem.

The most primitive form, Mixosaurus affords a transition to the ambulatory limb type of the Diaptosauria. None of the known orders of Diaptosauria, however, can as yet be considered ancestral to the ichthyosaurs.

IV. *Order* CROCODILIA Wagler.

We must exclude from the Crocodilia the Parasuchia of Huxley and embrace only the Mesosuchia and Eusuchia of Huxley with the addition of the typical marine forms, the Thalattosuchia, recently monographed by Fraas.

V. *Superorder* DINOSAURIA Owen.

It is a mistake to raise this group to the rank of a subclass, as has been done by some authors, because its three great subdivisions certainly lead back to a common stem form in the Permian which was not dissimilar to the type represented by the Protorosauria.

The ordinal nomenclature still requires further study. At present I am disposed to place the carnivorous forms in the order Theropoda Marsh, including two suborders, (1) Megalosauria for the large types with solid, hour-glass shaped vertebræ, (2) Symphypoda Cope for the smaller types with hollow, cylindrical vertebræ.

The Opisthocœlia of Owen although proposed as a 'suborder' of Crocodilia appears to enjoy priority of definition over the Cetiosauria of Seeley or the Sauropoda of Marsh.[1]

Similarly the Orthopoda of Cope is distinctively prior to the admirable term Predentata of Marsh. In the selection of these terms we cannot be governed by our preferences; we are bound to stand by the law of priority.

VI. *Superorder* SQUAMATA Oppel.

This superorder ranks in value with the Diaptosauria and Dinosauria inasmuch as it includes the very wide adaptive radiation of three groups of animals which were undoubtedly closely related in origin, namely: (1) Lacertilia, (2) Mosasauria, (3) Ophidia.

The radiation of the Mosasauria from the Lacertilia is analogous to that which we have observed occurring independently in three orders of the Diaptosauria, namely, the Proganosauria, the Choristodera, and the aquatic Rhynchocephalia of the Jurassic.

VII. *Order* PTEROSAURIA Kaup.

There is no question as to the Diapsidan relationships of the Pterosauria and as to their original derivation from Rhynchocephaloid types, although their specialization has carried them to a very great extreme of separation from any known Diaptosauria.

CONCLUSIONS.

I trust that the reclassification of the Reptilia here outlined, and the order of arrangement here adopted will be found to simplify their study. Memoirs now in preparation by Broom on the Procolophonia, by Case on the Pelycosauria, by Brown on

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[1] Riggs, E. S. Structure and Relationships of Opisthocœlian Dinosaurs. Part I, Apatosaurus Marsh. *Field Columbian Museum Publ.* No. 82, Aug. 1, 1903.

the Choristodera, by McGregor on the Parasuchia, will further elucidate the still numerous and perplexing questions of phylogeny.

Origin of Aves.— The birds probably originated from a group of Diaptosauria identical with or closely related to that which gave rise to the Dinosauria. It is not true that birds have descended from dinosaurs, but there is very strong evidence that birds and dinosaurs are descended from a common stock.

Origin of Mammals.— There is no question that the mammals are affiliated with the subclass Synapsida rather than with the Diapsida; both in skull and shoulder girdle structure and in the phalangeal formula they are Synapsidan.

As to their nearer relationships they appear to be rather with the superorder Anomodontia and with the order Cynodontia or Theriodontia. The divergence of the mammal stem from these typical reptiles will probably be found to have occurred in the Permian or Lower Trias of South Africa. In fact Broom has recently described what he believes to be a mammal jaw, Karoomys, from the Karoo Beds of South Africa.

American Museum of Natural History,
December 28th, 1903.