II. ZOÖLOGY.

1. On the Homologies of some of the Cranial Bones of the Reptilia, and on the Systematic Arrangement of the Class. By Edward D. Cope, of Philadelphia, Penn.

The great group of Reptilia may be considered as well circumscribed by the characters presented by their skeletal strutcure. They may be defined as vertebrates, with mandibular arch suspended from the cranium by the intervention of an os quadratum, or extra-auricular malleus; with the basis of the cranium formed of the cartilage bones, basisphenoid, sphenoid, and usually presphenoid; with a coracoid bone; and with metatarsals, metacarpals, second row (and usually first row) of tarsal and carpal bones distinct, and not coösified.

Within these limits there exists perhaps a greater variety of structure, in other respects, than in any other vertebrate class. The homologizing of the elements which present this variety is therefore a point not attainable without much study, while the homologizing of the same with their representatives in other classes is still more difficult. In the present essay a few points of this nature are, it is hoped, elucidated, especially with reference to the structures of the crania in the orders Ichthyopterygia and Anomodontia. Finally, the bearing of these and other points on the systematic arrangement of the class are alluded to.

1. *Homologies and Composition of the Cranial Arches.*

The bony arches which connect the facial part of the cranium with the posterior part of the brain-case, in nearly all Vertebrates, are primarily only two in number; viz., the zygomatic and the quadratojugal. They, however, form connections with each other and adjoining portions of the cranium, so as to complicate their determination, which is increased when one or other of their usual connections is, under these circumstances, atrophied or omitted.

The zygomatic arch takes its name from the only one which is present in the Mammalia; and that arch which is homologous with it throughout lower vertebrata must retain the name. It is then the arch connecting the maxillary with the squamosal (or squamosal part of the temporal) bone, and is therefore composed in large part of the malar.

The quadratojugal arch, as its name implies, is that which connects the maxillary with the quadrate bone. As the quadrate bone only exists as the malleus within the ear-chamber in the Mammalia, it is obvious that it cannot exist in that class. It can only be found in the vertebrata, from and including the birds, downwards. As the quadratum is projected below the squamosal, the position of this arch is always inferior to that of the zygomatic. It is composed normally of the malar (or jugal) and quadratojugal.

A third arch, which is especially characteristic of the Reptilia, connects the parietal bone with the superior extremity of the quadrate. The connection is accomplished by the intervention of the opisthotic or squamosal, or both.

The character of the arches existing in the different types of the vertebrata, above the Dipnoi, may be expressed schematically by the following table: —

I. Neither zygomatic nor quadratojugal arches.
  α. Without parieto-quadrate arch.
 Batrachia Urodela except Pleurodelidæ; Ophidia.
 Lacertilia Ophiosauri and Typhlophthalmi.
 Testudinata Chelydidæ.
 Mammalia Edentata (part).
  αα. With parieto-quadrate arch.
 Lacertilia Nyctisaura.
 Testudinata (Hydromedusa Platemys Rhinemys).
II. Quadratojugal only.
  α. Without parieto-quadrate arch.
  β. With quadratojugal bone.
 Aves.
  ββ. Without quadratojugal bone.
 Batrachia Anura in general.
III. Quadratojugal and zygomatic arches present.
  1. No postorbital arch.
 Batrachia Anura (Discoglossus).
  2. A postorbital arch.
  α. Without postorbital bone.
 Crocodilia.
  αα. With postorbital bone.
 Batrachia Stegocephali (Apateon).
 Ichthyopterygia.
 Rhynchocephalia (Sphenodon).
 ? Sauropterygia.
 Ornithosauria.
IV. Zygomatic arch only.
  1. With postorbital arch.
  α. With postorbital bone.

* Malar portion of zygomatic arch absent.
Lacertilia Varanidæ.
** Malar portion present.
Lacertilia in general.
Anomodontia.
Sauropterygia (? all).
Testudinata in general.*
a a. Without postorbital bone.
* Malar portion wanting.
Batrachia Urodela Pleurodelidæ.
Pythonomorpha.
** Malar portion present.
Batrachia Gymnophiona.
Mammalia Quadrumana, Artiodactyla, Perissodactyla (part).
2. Without postorbital arch.
Mammalia Carnivora Proboscidia Perissodactyla (part), Cetacea, Rodentia, Edentata (part), Monotremata.

From the above table, it will be observed that each class, and sometimes single orders, present many or several of the various types of structure of the arches. These arches are more or less protective or fixative in their use; that is, they protect the orbit, the temporal muscle, or the oral cavity, or fix the quadrate and prevent its motion. As adaptive characters, they are thus those which define very subordinate representatives of all the orders.

From want of analysis, the proper determination of the arches has not always been made, and the identification of the component and adjacent bones vitiated. This is no doubt owing to the fact, that in many Reptilia, where the orbits are large, and the temporal fossa small, — *e. g.*, Ichthyopterygia, Crocodilia, etc., — the zygomatic arch makes a strong sigmoid flexure, leaving the quadratojugal to take the more direct course to its terminus. Thus Owen (Palæontology) homologizes the quadratojugal arch of Ichthyosaurus with the zygomatic of Mammals, and the true zygomatic with the temporal fascia of the same. In the same way (*l. c.*, p. 210), he homologizes the quadratojugal arch of Nothosaurus with the zygomatic, thus: "The lower one (*i. e.*, arch) is formed by the malar (27) and squamosal (28), the latter answering to the true zygomatic arch in Mammals." The figures obviously refer, in the cut, to the malar and quadratojugal bones; while the "mastoid"

* The postorbital is prolonged so far downwards in Chelone and Chelydra, as to look like a quadratojugal.

in this, as in other determinations of the same author, is the squamosal.*

In the same way Günther, in describing Sphenodon (Philos. Trans., 1867), calls the quadratojugal arch the zygomatic, and the zygomatic the "temporal arch," employing a new name to designate it. Stannius (Zootomie der Amphibien) appears to have correctly identified the zygomatic arch in Lacertilia, but erroneously in the Crocodilia.

Before proceeding to determine more exactly the homologies of the posterior cranial bones, I will describe the cranial structures of Ichthyosaurus and Lystrosaurus, as our literature appears as yet to be deficient in these points.

2. *On the Cranium of the Ichthyopterygia.*

Commencing with the foramen magnum and occipital condyle, as fixed points, the connections of the bones, as they succeed each other forwards, may be safely considered.

All four of the occipital elements contribute to the margin of the foramen magnum, the supraoccipital not being excluded as in Crocodilia, Anomodontia, etc. The external or lateral margin of both exoccipitals and basioccipital are excavated by a large foramen. The continuous margin of both between these points is united to a bone which extends outwards and upwards, and which contributes by its superior and inferior margins to the outlines of the foramina just mentioned. Exterior to these, from the basioccipital to near the apex of the supraoccipital, there are no bones suturally united, and there is a vacuity in this position not seen in any other Reptilian cranium.

From the exterior margin of the inferior foramen, a subcylindric bone extends outwards. It is contracted medially, and is not in sutural connection with any other. Immediately exterior to it is a flat subvertical bone, which, as it bears the articular condyle for the mandible on its lower extremity, is no doubt the quadrate. That it is such is also proven by the fact that it is anteriorly connected to the malar bone by a quadratojugal.

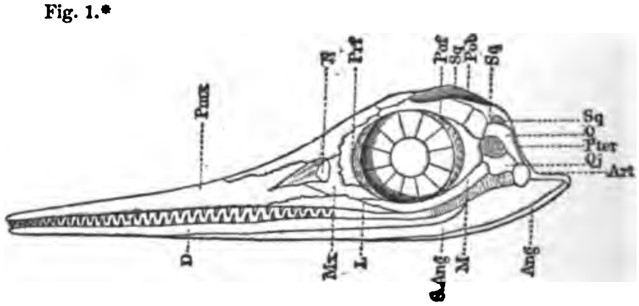
If we now turn to the lateral view of the skull, we observe the zygomatic arch, as determined above; *i. e.*, the superior of the two extending from the malar, and that which supports the postorbital arch. The bone which forms its posterior half must be the squa-

* This description, by the way, differs from Von Meyer's figures of Nothosaurus, where but one arch is represented.

mosal, not only on this account, but because, as in other Reptilia, it is articulated with the summit of the quadrate.

Turning again to the posterior face of the cranium, we may be in a position to determine the two bones described above as lying outside of the occipitals, and between them and the quadrate and the squamosals. The superior (Op. O, fig. 2) occupies the position of the "external occipital" of Cuvier, in the tortoise, both by its articulation with the exoccipital (Ex. O) and its direction towards the squamosal (Sq). Its separation from the supraoccipital, and contact with the basioccipital, are against this determination, yet

Fig. 1.*



the weight of these arguments is much less than that of those for it; and therefore I suppose it to represent that bone, which is the opisthotic of modern nomenclature.

The large foramen below the last, and exterior to the basioccipital, is in the position of the opening of the internal ear in the Lacertilia, as regards its relation to the latter bone, the opisthotic being separated from it by the extension outwards of the exoccipital. Its relation to the opisthotic is the same as that in the Cheloniidæ, where it is separated from the basioccipital by an inferior process of the exoccipital. It is probably the fenestra ovale; and, if so, the second bone in question (stap) becomes the *stapes*.

It is a question, however, to what extent this element is really

* Fig. 1.—Ichthyosaurus; lateral view (from specimen from Barrow, Leicestershire).

Pmx. . Premaxillary bone.	Qj. . . . Quadratojugal.
Mx. . . Maxillary.	Q. . . . . Quadrate.
N. . . . Nasal.	Pob. . . Postorbital.
Fr. . . . Frontal.	Sq. . . . Squamosal.
Prf. . . Prefrontal.	D. . . . . Dentary.
Pof. . . Postfrontal.	An. . . . Angular.
Pa. . . Parietal.	Ar. . . . Articular.
L. . . . Lachrymal.	S. Ar. . Subarticular.
M. . . . Malar.	Pter. . . Pterygoid.

stapes. In existing reptiles, it is only proximally expanded, and distally a slender rod terminating in the cartilaginous expansions called by Huxley* suprastapedial and extrastapedial; the latter being, as the same author shows, the support of the stylohyoid and other elements of the hyoidean arch, and with the suprastapedial the homologue of the incus. The expanded distal end of the bone marked *stap*, in Ichthyosaurus, looks as though it were the homologue of the cartilaginous expansions mentioned, in which case that bone becomes stapes and incus combined. This seems to us very probable.†

As a whole, this bone is in that case homologous with the hyomandibular of the Sharks and Teleostei. This has been pointed out by Huxley on embryological grounds to be the case with the incus. If the element (stap) in Ichthyosaurus represent both stapes and incus, the same is probably true of the hyomandibular.

Turning again to the squamosal, we find it appears to possess an extraordinary development. Besides forming the posterior portion of the zygomatic arch, as in other vertebrata, and forming part of the combination which supports the quadrate, as in Reptiles and Batrachia generally, it sends down behind the quadrate a plate for more than one-third the length of the latter to the superior margin of the stapes. Instead of joining the parietal or opisthotic at its posterior margin, it is continued inwards to near the apex of the supraoccipital, and bending forwards continues, in company with its fellow of the opposite side on the inner face of the temporal fossa, to a point above the middle of the orbit, where it unites suturally with what may be called the pari-

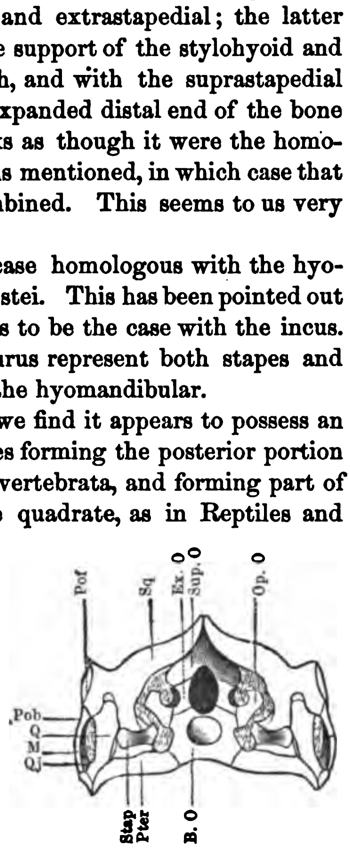


Fig. 2. ‡

* In a most valuable essay on "The Representatives of the Malleus and the Incus of the Mammalia" (Proceed. Zoöl. Soc., 1869, p. 891).

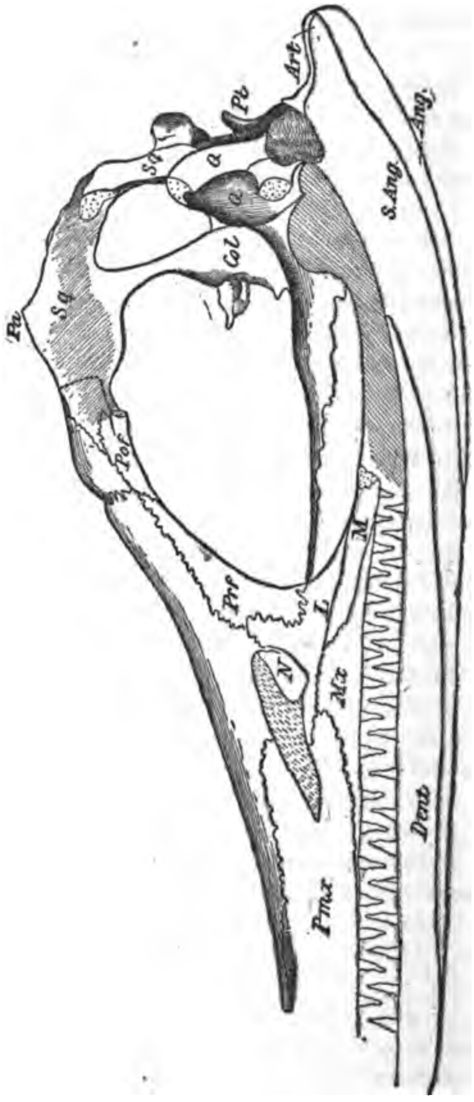
† In the serpent *Xenopeltis unicolor*, a superior process of the stapes (suprastapedial) is ossified, and a separate element at the end of the bone (extrastapedial v. stylohyal?) is also ossified. (See fig. 2.)

‡ Fig. 2.—Ichthyosaurus; cranium; posterior view. Lettering the same as in fig. 1, with the following additions: —

B. O. . . Basioccipital.
Ex. O. . Exoccipital.
Sup. O. Supraoccipital.
Op. O. . Opisthotic.
Stap. . . Suprastapedial, or hyomandibular.

etal. (See figs. 2, 3, Sq.) Though it cannot yet be asserted that this is one primary element, yet in the adult Ichthyosaurus there is

Fig. 8.



Cranium of Ichthyosaurus without arches.
Col, Columella. Pt, Pterygoid.
(The anterior extremity of the sphenoid is imperfect.)

no line of division to be discovered.* It will be seen later that the same structure exists in the Anomodontia and Sphenodon. It is not impossible that its anterior portion will be found to represent the element in Teleostei, called by Huxley, perhaps by error, Squamosal.

Returning to the external arches, we find the zygomatic is partially vertical, owing to the large size of the orbit and the shortness of the posterior region of the cranium, and that it is extended by a supernumerary bone not found in the Mammalia, for which I adopt the name given by Owen in this genus, of postorbital. (Figs. 2, 4, 13, Pob.) It is the temporal of the Testudinata of Cuvier, and one of the postfrontals of the Lacertilia of the same author. It is most erroneously called quadratojugal by Stannius, and by Günther, who follows him, in Sphenodon.

Anteriorly it articulates with the malar, here a long slender bone on account of the size of the orbit, and which, as usual, articulates anteriorly with the maxillary. Posteriorly the extent of the postorbital separates it from the squamosal, as is the case with some Lacertilia; while a short quadratojugal connects it with the quadratum, precisely as in the Crocodilia. This latter bone is the squamosal of Owen, who, on account of this erroneous determination, was compelled to apply a new name to the true squamosal, calling it "supratemporal." (See Palæontology, p. 198.)

Posterior to the postfrontal and postorbital, is an ovate bone connecting them with the squamosal. This is also peculiar to this order, and is the supersquamosal of Owen.

The postorbital arch is quite horizontal, and is composed of the postfrontal exclusively.

Turning to the superior aspect of the cranium, if we assume that the two posterior elements bounding the temporal fossæ are continuous with the squamosal, as has been above shown, there is no difficulty in determining the elements in front of them. Thus the undivided bone with large fontanelle near the posterior margin, bounding the squamosals anteriorly, would be the parietal. The posterior half of each of these bones is concealed by the anterior portion of the laminar squamosal as in Sphenodon: they descend beneath the latter to a point a little before the line of the middle of the temporal fossa. It scarcely touches its fellow on the median line behind the fontanelle. The general shape of the bone is

* I have since found a suture in two of our Ichthyosaurus crania, and Dr. Seeley states that that is the normal structure.

square. Each half is united to the bone behind it, except at the median suture, by a double squamosal suture, the squamosal bone sending a plate below as well as above it. Medially the suture is single and serrate. Suspecting that the bone here determined to be parietal might possibly be frontal, I searched for a bone posterior to it, beneath the prolongation of the squamosal, but without success. That the squamosal should contribute to the brain-case is apparently anomalous among Reptiles, though not among warm-blooded Vertebrates; but if we suppose the anterior plate to be the epiotic the difficulty is much lessened.

It might be objected that the position of the fontanelle was rather in favor of the determination of this bone as frontal, since it is, as in the Lacertilia, pierced in its posterior margin, and therefore probably, as in that order, included between the frontal and parietal. But in reply it may be asserted that the position of the fontanelle in the two orders most nearly allied to the Ichthyopterygia — *i. e.*, the Anomodontia and Rhynchocephalia — justifies the interpretation I have placed on this bone. Thus, in the former, it is pierced in the middle of the parietal with a suture extending from it to the occipital suture. In the latter it lies near the posterior margin of the parietal, so far as visible; for the latter bone is doubtless overlaid by the squamosals, as in Ichthyosaurus. Günther is probably correct in describing this median bone as parietal in Sphenodon.

The long paired bones, immediately anterior, which extend to near the middle of the muzzle, are the frontals. They extend to the premaxillaries, a junction only found in Reptiles with posterior nostrils, as Pythonomorpha, Varanidæ, etc., but common among Fishes. In Sphenodon the frontals are unusually produced in front.

Articulating with them on each side, and bounding the anterior and post and superior margins of the orbit, are the pre and postfrontals in their usual positions. The former almost excludes the latter from contact with the frontals, and leaves its connection with the parietal more extensive. Anterior to the frontals comes the elongate premaxillary. This of course bounds the nares in front; and as the latter are far removed posteriorly, in this order of Reptiles, the nasal bones have a posterior position also. The latter are much reduced in size, and have a very short suture with the frontals, being more extensively united with the lachrymal. They are entirely separated from each other by the anterior prolongation of the frontal, and are chiefly to be recognized by their position as roofing the nares posteriorly, and their connection with the frontal. In one of our crania I observe that they are absent.

The maxillary is much reduced, in connection with this position of the nares. It is separated from union with the prefrontal by the large lachrymal, which extends to both the frontal and the premaxillary.

Such a determination of the bones of the roof of the cranium differs materially from that of Cuvier and Owen. The former (Ossemens Fossiles, Tab. 257, figs. 1–5, and p. 103, V, 2 plates) laid a wrong basis by assuming the bones (figs. 2, 3, Sq) to be the parietals: the parietals become then frontals, and the frontals are called nasals, the true nasals being entirely overlooked. Owen (Palæontology and Comp. Anat. Vertebrates) follows Cuvier in these points. Günther falls into error as regards the squamosal branches in Sphenodon, uniting them with the true parietal as parietals. The frontals he names correctly. The parietal in Sphenodon is shown by Günther's figure to be a simple medial element, as in Ichthyosaurus.

Having, however, observed a suture separating the squamosal from its supposed anterior plate in one young and one adult Ichthyosaurus cranium, it has occurred to me that possibly the specimen here described may have a coalescence of two elements really distinct. In that case the anterior bone will not be homologous with that in same position in Lystrosaurus, but may be, as usually stated, the parietal. The other bones in front of them would then retain their usual names, the supposed nasals (*n*) remaining without determination.

Turning to the base of the cranium of Ichthyosaurus, we observe that the palatines and ectopterygoids are broad, flat bones, whose exterior margin is in contact with the maxillary and malar to opposite the posterior margin of the orbit, flooring the latter (fig. 3, Ectp). The pterygoids, on the other hand, contract abruptly behind this point, and support the columella. They then expand to a degree unusual in the Reptilia, and extend over the whole space between the basioccipital and the quadrate, joining both closely, and projecting behind their posterior plane. Its margin is recurved as far as the stapes (Pt, figs. 1, 2, 3).

The columella is very stout at its point of contact with the pterygoid, and above it; but higher it contracts much, and then expands anteriorly into the parietal branch of the ? squamosal with which it seems to be continuous, as I cannot see any suture separating them.

The basis cranii is incomplete, and is formed of basioccipital and basisphenoid. The latter (Cuvier, Oss. Foss., Tab. 257, figs. 12, 13) supports an alisphenoid on each side.

In considering the affinities of Ichthyosaurus as exhibited by the cranium, it may be premised that the structure of the limbs separates it as a very distinct order among Reptilia. The peculiar disposition of the squamosal is only paralleled among Anomodontia and Rhynchocephalia, and the character of the columella resembles only that of the former in its connections. The occipital elements have more the disposition of those of Sphenodon than of any other type, but there is a great difference in the position of the opisthotic. The arches are also those of the same genus, except that in the latter the quadratojugal is obsolete, or coössified with the malar. The structure of the front and base of the skull, and of the mandible, in Sphenodon, have no resemblance to those of Ichthyosaurus. The anteriorly unossified brain-case is that of several other Reptilian groups, while the presence of the alisphenoid furnishes a point of resemblance to the Crocodilia.

In general there are few points of affinity to the Crocodilia. The characters of the parietal bone are those of Sphenodon. The vertebræ are intermediate between those of that genus and the Lacertilia, and those of the Anomodontia; for the capitular and tubercular processes are confluent on the former, and widely separated in the latter, the tubercular being elevated to the neural arch. In the Ichthyopterygia they are separated, but both are on the centrum.

Thus the Reptilian affinities are divided between the Anomodontia and Rhynchocephalia, and are not very close to either. They are much less with the Lacertilia, and still less with the Testudinata and Crocodilia.

There are some extra-reptilian indications worth observing. The most important of these is the great extent of the pterygoids backwards and inwards, paralleling only in this some Batrachia, *e.g.*, Rana (fig. 21, Pt). The large size and form of the stapes are similar to that seen in Cœcilia. The posterior development of the squamosal is alluded to later, in the discussion of the homologies of that bone.

3. *On the Cranium of the Anomodontia.*

The bones of the superior and palatal surfaces of the cranium of the genus Dicynodon have been described by Owen; and the structure of the internal walls of the palatal and nasal cavities, with the occipital and mandibular bones, have been described by Huxley, from the Ptychognathus murrayi. The relations of the elements of the lateral walls of the brain-case, and the attachment of the os quadratum, have, so far as I am aware, never been made out. As these points are of the first importance in determining the affinities of the Anomodontia, I take the favorable opportunity for elucidating them, furnished by the very complete cranium of the Lystrosaurus frontosus, Cope, kindly placed at my disposal by Dr. E. R. Beadle.*

The maxillaries articulate posteriorly and externally with the ectopterygoid bone. This is vertico-oblique in position, its depth twice as great as its length. The pterygoid, which articulates with it posteriorly, is seen laterally, a flat hour-glass shaped bone, the anterior extremity embracing the ectopterygoid by a superior and an inferior process, whose articular faces are at right angles with each other. The contracted portion presents a longitudinal external angle, which disappears on the posterior part of the maxillary. At this point the pterygoid is arched upwards and inwards: it is then deflected outwardly and downwards to the extremity of the quadratum.

The relations of the pterygoid to the bones forming the anterior walls of the brain-case are of much interest, and throw great light on the vexed question of the homologies of the columella of the Lacertilian and Rhynchocephalian Reptiles. The adjacent bones may be first described.

The presphenoid is a flat lamina with arched superior margin, resembling that of the Crocodilia. It extends forwards in this species to the line of the frontal tuberosity. The inward and upward expansion of the pterygoid behind its median contraction, already described, appears to be in contact with the inferior margin of the presphenoid. It is not likely that this expansion belongs to the presphenoid, though it is difficult to perceive the suture. The expansion is subvertical. Posteriorly it expands backwards and outwards, forming the fundus of a deep subvertical groove, and unites suturally with the antero-interior margin of a bone,

* For description of this species, see Proceed. Am. Philos. Soc., 1870, p. 419.

Fig. 4.

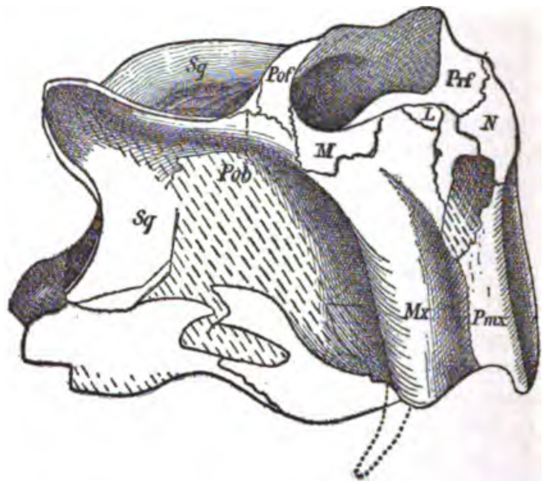
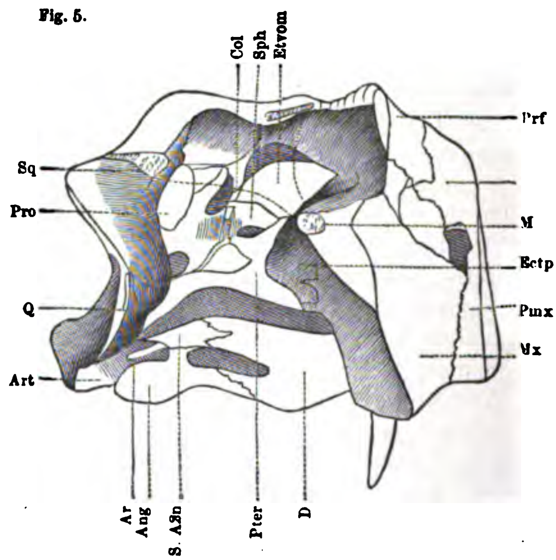


Fig. 5.



Figs. 4 and 5. — Lystrosaurus frontosus (from Cape Colony); profiles. (Fig. 5, diagram with arches removed.) Lettering as in figs. 1 and 2, with the following additions: —

Etvom. . Ethmovomerine.
Sph. . . . Sphenoid.
Pro. . . . Proötic.
Pter. . . . Pterygoid.
Col. . . . . Columella.
Ectp. . . . Ectopterygoid.
Subart. . Subarticular.

which I suppose to be the proötic. From the anterior and more horizontal portion of the pterygoid expansion, a thin laminar bone rises, which presents an angle outwardly. Superiorly and inwardly it appears to be continuous with a slender prolongation of the anterior angle of the parietal plate already mentioned. Not suspecting its existence, I destroyed a portion of this rod, in removing the matrix; but a piece from a point intermediate between the parietal and pterygoid extremities remains attached to the specimen in place. This element is, no doubt, the columella, whose existence in this group of Reptilia has not heretofore been suspected. It encloses a narrow vertical antero-posterior foramen with the presphenoid.

Two openings into the brain-case are visible: that between the parietal plates, common to most Reptilia, and the foramen, transmitting the fifth cranial nerve, the combined foramina ovale and rotundum. Another foramen is enclosed between the pterygoid and the element which bounds the proötic in front and below. A narrow bone with rounded edge extends from the superior origin of the columella, downwards and outwards to the proötic, bounding the foramen ovale above. It resembles the rod-like projection of the columella of Testudinata (see fig. 5), but that is below, not above, the foramen.

The exact composition of the suspensoria of the os quadratum is a little difficult to determine, owing to the obscurity of the sutures. The posterior parietal arches (fig. 7, Pa) are narrow and short, the posterior boundaries of the temporal fossa being chiefly formed by the squamosals. The latter commence on each side of the parietals, a little behind the anterior extremity, and form the overhanging margin of the temporal fossa, inwardly as well as posteriorly. The posterior plate of the parietal on each side is proximally enclosed between the squamosal and supraoccipital, then between the former and a thin laminiform bone, which extends laterally from the supraoccipital, and above the exoccipital. It is in contact with the squamosal for most of its length, but does not extend to opposite the zygomatic arch, and of course not to the os quadratum. This element, in spite of its exclusion from articulation with the quadratum, appears to be homologous with that which in Iguana extends from the same position to that articulation, and which is evidently homologous with the opisthotic of the Testudinata.

The squamosal is very largely developed in Lystrosaurus. Continuing round the temporal fossa, it sends forwards the usual zygomatic arch, and — what is noteworthy — unites with both postfrontal and malar, leaving the usual tripodal supplementary postorbital as a wedge-shaped plate, bounding the antero-inferior angle of the temporal fossa. The squamosal continues without interruption to the inferior extremity of the quadratum, concealing the latter entirely on a posterior view. I find no suture separating it from the superior portion already described, on either side of the cranium; and on reference to Owen's figure of Ptychognathus declivis,* I find that he found them continuous in that species. He calls this element the "masto-tympanic," which would be the Cuvierian nomenclature for opisthotic-quadrate of modern anatomists. I find, however, that it does not include the quadrate which is situated immediately anterior to it, and does not appear to contain the opisthotic, which, as already described, is distinct. It is in fact figured by Owen in Pt. declivis, and named parietal, the close squamosal suture separating it from the posterior arches of the latter bone not having been detected.

When the supposed quadrate bone is fractured, it is found to consist of two vertical plates, of which the anterior bears the narrow transverse articular face for the mandible, excluding the posterior one. This I take to be the os quadratum. Its width is not so great as that of the posterior plate or squamosal, and it does not ascend much more than half way to the zygomatic arch. Its superior margin appears to be received by the margin of the thicker superior portion of the squamosal, which somewhat overhangs it. I cannot trace its inner margin. A descending portion of the inner face of the squamosal approaches very near the posterior part of the pterygoid, and it is doubtful whether the quadratum extends interior to this point. The bony wall which appears below the proötic has been already alluded to as continuous with the pterygoid expansion, but it may represent the lateral processes of the sphenoid, or even part of the alisphenoid.

The squamosal or parietal sends down on each side a vertical plate, which terminates in a slender bony prolongation from its anterior margin. The plate is subquadrate, and twice as deep as wide antero-posteriorly. The osseous ethmovomerine septum extends posteriorly to between the anterior margins of these laminæ, and is prolonged inferiorly to the presphenoid, the suture with the latter extending beyond the anterior line of the above-mentioned

* In Proceed. Geol. Soc., Lond., xiv., Tab. 1.

laminæ. I can find no suture separating these plates from the squamosal above, and am therefore disposed to doubt whether they do not belong to these rather than to the parietals.

The ? epiotic is a subovate bone with truncate extremities, which has its long axis directed upwards and inwards. It is in contact with the parietal and the descending anterior plate of the squamosal, and inferiorly with the bone described in the next paragraph as proötic. It occupies a position similar to that seen in Sphenodon, excepting that it does not appear to extend to the quadratum. It might be questioned whether this bone is not really the proötic. The element below and anterior to it (fig. 5, Pro) is emarginated for the exit of the fifth nerve (V); and though I cannot find its inferior borders, and the portion behind the above foramen is narrow, it appears to me to answer more nearly to the proötic of

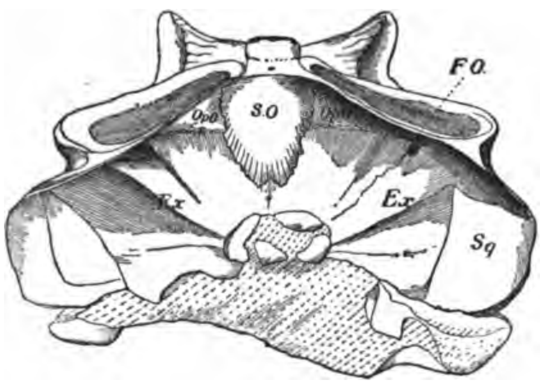


Fig. 6.— (Cranium from behind.)

Lacertilia than to an alisphenoid, which it would otherwise be. This is the more probable, in view of the fact that the supposed epiotic has its counterpart in Sphenodon, in which case this must be proötic.

The fenestra ovale (fig. 6, FO) is not readily discovered, but appears to be represented by a rather small oval foramen-like emargination of the exoccipital. It is situated just within the quadrate plate of the squamosal, and beneath the zygomatic process. I find no stapes. If it existed, it extended outwards beneath the overhanging margin of the squamosal, on the plane of the superior margin of the os quadratum.

Turning now to those portions of the cranium which are better known in allied species, I find the exoccipitals undivided, as did Owen in Pt. declivis, and Huxley in Pt. murrayi. I do not even find a median suture separating that of the right side from the left. Each presents a strong rib extending to opposite the zygomatic arch. The inferior portion is a subtriangular plate, continuous superiorly with the rib just mentioned. It is also raised

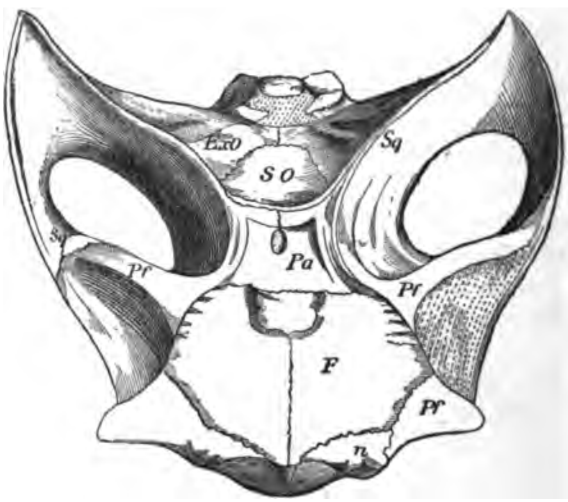


Fig. 7.—(Cranium from above.)
Lystrosaurus frontosus. (Lettering as in figs. 1 and 2.)

on the median line, and the inferior outline is concave and directed downwards. The supraoccipital is vertically ovate, and separated from the parietals by squamosal sutures. It does not reach inferiorly to the occipital foramen.

The parietals viewed from above form together a subquadrate plate, with the angles much prolonged; the anterior broadly to the postfrontals; the posterior as laminæ between the squamosals and opisthotics forming the parieto-squamosal arch. They embrace a rather large fontanelle, from which the median suture is distinct posteriorly, but invisible anteriorly.

The frontals are marked posteriorly by a large tuberosity, which bounds inwardly a concave surface on each side between it and the raised margins of the orbits. These margins are continued posteriorly. This raised margin is turned inwards above the postfrontals, giving the orbits a slight postero-superior notch, which is much less developed than in Pt. declivis, according to Owen's description. It is slightly rugose in consequence of transverse grooves. They are prolonged into the prefrontal tuberosities, which are very large, more developed than in any other species, resembling rudimental horns. They present a sharp edge outwardly, as the front margin of the orbits and the superior and anterior planes are at right angles to each other. The middle line of the front, descending more gradually, causes the angle between it and the premaxillary to be rather more open.

The premaxillary region is remarkably contracted; and its length from the front is about equal to the distance between the prefrontal horns, producing a T-shaped outline. On the middle line it presents a high laminar keel, which separates two parallel sulci. These extend to the end of the muzzle, and are bounded externally by a strong longitudinal angle. The external face of the maxillary is occupied by a wider longitudinal concavity parallel to the last. The posterior angle of the bone flares out behind it. The posterior (superior) "spine" of the premaxillary extends far between the nasals, and nearly to the anterior prolongation of the frontal.

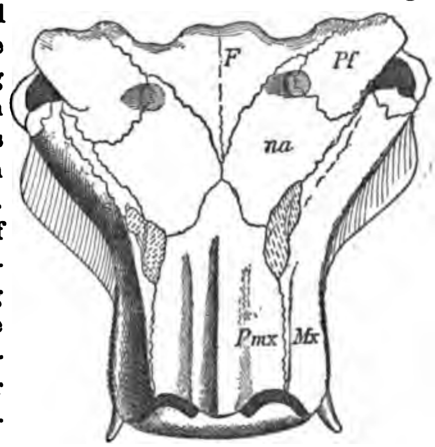


Fig. 8. — Lystrosaurus frontosus. (Lettering as in fig. 1.)

The nasals are prominent, each presenting a low boss forwards, which enclose a concavity on each side with the tuberosity of the premaxillary spine. They overhang the nares superiorly.

The lachrymal is a small bone intercalated between the prefrontal and the maxillary. In front of and below it, a larger bone extends to the nostril, constituting the principal part of its posterior boundary. This bone is described by Owen in the Pt. latifrons. Its homologies are not determined.

The alveolar margin of the upper jaw is undulating, presenting a short median beak-like prominence, then a concavity, and posteriorly a convexity to the tusk. The edge of the mandibular arch is correlated between these cutting edges, but its extremity is three-lobed. These lobes correspond to three grooves within the premaxillary portion of the edge of the jaw, which are separated by two ridges. The section of the tusks is cylindric, and where broken, at the alveolar margin, the pulp cavity is minute.

The malar bone is small, and of a subtriangular form, one apex being posterior. The antero-superior angle extends to the lachrymal, thus excluding the maxillary from the circumference of the orbit.

The dentary bone extends far posteriorly, and forms the greater part of the circumference of a longitudinal foramen, which pierces the middle of the ramus. The angular is prolonged into a keel-like plate below, which is truncate behind, and rises gradually anteriorly. Its margin, which articulates with the articular, is cut out by a deep foramen.

The angular and articular bones are both horizontal. The coronoid appears to be broken off, interior, or wanting. The angular extends to the symphysis.*

The palatal surface is not exposed.

Affinities of the Anomodontia.

The attachment of the os quadratum, with the Mammalian type of rib articulation, and the elongate sacrum, induced me to regard the Anomodontia as a subgroup of the Archosauria. The absence of the quadratojugal arch, usual in the latter order, and the lack of information respecting the mode of attachment of the os quadratum, rendered it probable that the group was aberrant, or even not properly referable to it. The extension of the exoccipital bones, so as to close the parieto-squamosal arch, is found among Lacertilia in the Stenodactylus guttatus, and a very few other species; but its extension to the quadratum below the proximal articulation does not occur.

The immovable articulation of the quadratum throughout its length to the squamosal, and by its whole inner margin (as I suspect, but cannot see without too much injury to the specimen) to the exoccipital, removes the Anomodontia from the Lacertilia, and associates them with the Archosauria, in accordance with the indications furnished by the ribs, sacrum, etc. The withdrawal of

* See Trans. Amer. Philos. Soc., 1869, pp. 27, 33,

the proötics and opisthotics from its support constitutes a step towards the liberation of the quadratum, and places it nearest the Lacertilia, in the order. This indication is confirmed by the simple premaxillary bone, and the lack of quadratojugal arch.

Among Lacertilia, the Chamæleontidæ make the nearest approach, though a remote one. This is seen in the posterior prolongation of the dentary bone, and the often rudimental dentition.

The nearest approach outside the Archosauria is to the Rhynchocephalia, as represented by the existing genus, Sphenodon.* Here the canine teeth begin to show an increased development, and the other teeth to become obsolete or confluent. The nearest approach to the great development of the squamosal in Anomodontia is seen in this genus, and they both possess an ossified septum orbitorum. In both, the posterior extremity of the pterygoid is much expanded, and supports a columella.

In summing up, the following significance may be attached to the above characters. From this it will be seen that the Anomodontia present a remarkable combination, and well deserve the appellation of a "generalized type." Characters of Crocodilia are: 1. Presphenoid keel; 2. Expanse of pterygoid to unite with it; 3. Foramen of the mandible; 4. Reduction of zygomatic bone. Testudinata: 1. Edentulous jaws; 2. Coössified mandibular rami, with foramen. Rhynchocephalia: 1. Largely developed squamosal; 2. Osseous interorbital septum; 3. Distinct ? epiotic; 4. Biconcave vertebræ; 5. Columella; 6. Foramen parietale;— the last two belonging also to the Lacertilia, which have further in common with Lystrosaurus: 1. Absence of quadratojugal arch; 2. Simple premaxillary bone (mostly).

Ichthyopterygia: 1. Parietal and quadrate branches of squamosal; 2. Sessile suspensorium of quadrate; 3. Posterior flat opisthotic.

Dinosauria: 1. Elongate sacrum; 2. Ribs continued to sacrum; 3. Capitular and tubercular attachment for ribs on neural arch and centrum, respectively.

From the preceding evidence, it is clear that the Anomodontia constitute the most generalized order of Reptilia of which we have any knowledge; and occupying, as it does, almost the first or oldest place in geologic time among the Reptilia,— *i. e.*, in the Triassic period,— it justifies the statement that the peculiarly older

* See Günther, Trans. Royal Society, 1867, Pt. II., p. 1.

forms of life are the more generalized in structure than the later, and that this generalization is increasingly evident the further back we carry our inquiries.

4. *On the Homologies of the Opisthotic Bone.*

This element, distinguished by Huxley from those which compose with it the "temporal bone" of anthropotomists, has been called "mastoid" by Owen, and "external occipital" and "mastoid" by Cuvier.

Its position is exterior to the exoccipital, posterior to the proötic, and beneath and behind the squamosal.

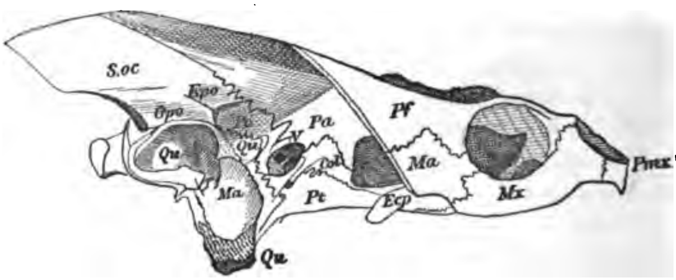


Fig. 9. — Chelydra serpentina; cranium, with squamosal and postorbital bones removed. Epo, Epiotic; Pro, or Po, Proötic. Ma, Meatus Auditorius. Ecp, Ectopterygoid. V, Foramen ovale.

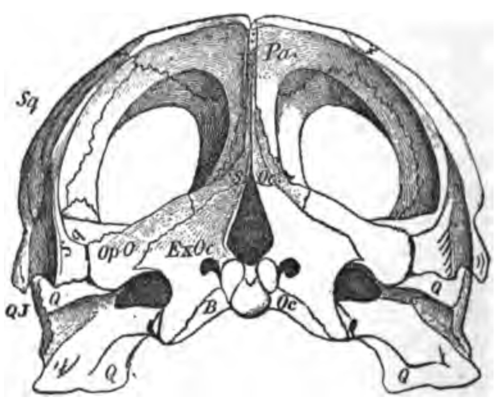


Fig. 10. — Chelone midas; cranium from behind. (Lettering as in fig. 2.)

In Mammalia it is confluent with the elements mentioned, remaining distinct from the exoccipital, and forming part of the "mastoid and petrous portions of the temporal." (Huxley.)

In Aves it is early confluent with the exoccipital. (Parker.)

In Reptilia it is distinct in all the orders except the Crocodilia, where it is confluent with the exoccipital. (Fig. 11, Exo.)

This group resembles the higher vertebrates in the close union of the quadratum with the proötic and other cranial bones; and we pursue the line of extreme Reptilian divergence in following the gradual removal of the quadrate from the cranial walls, on the

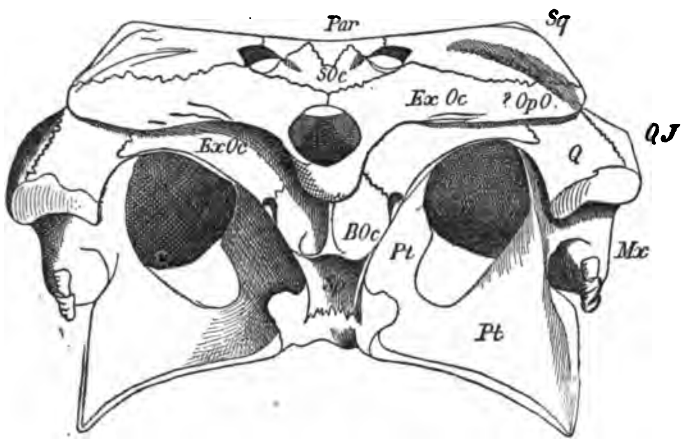


Fig 11. — Alligator mississippiensis; cranium from behind.

extremity of a suspending cylinder, which reaches its highest expression in the Ophidia. First in this succession comes the separation of the opisthotic.

We have already seen its position in Ichthyopterygia (fig. 1, Opo) where it is peculiar in separation from the supraoccipital and connection with the basioccipital. We have also seen an element in the Anomodontia identified with it (fig. 6, Opo) which differs in its connections, by being attached to the supraoccipital and exoccipital only.

Passing to the Testudinata, the element maintains the same connections, with the addition of that with (fig. 10, Opo) the proötic anteriorly, and is extended externally over the proximal extremity of the quadratum, a connection not observed in the types just described.

If we now turn to the Rhynchocephalia, as represented by Sphenodon,* we find the exoccipital greatly prolonged laterally, and carrying with it the opisthotic. It is carried apparently beyond any connection with the proötic (alisphenoid of Günther), but is less distant from the supraoccipital, or rather the epiotic (paroccipital, Günther), which is here, according to Günther, not entirely separated from the supraoccipital, as in the Testudinata, though more so than in the latter. Its superior and anterior extent is remarkable in this genus, forming a connection with the postorbital above and the malar below, peculiarities not noticed in any other reptile. Superiorly it rises into the parieto-quadrate arch, which it forms with the squamosal, the parietal not entering it; another peculiarity, the only parallel to which is to be found in the Anomodontia, where this arch is however depressed into close contact with the occipital segment of the skull.

The type exhibited by the Lacertilia is intermediate between that of the last and that of the Tortoises, and serves to reconcile them. Here, also, the opisthotic is carried beyond connection with the other otic elements. In Iguana it contributes largely to the formation of the parieto-quadrate arch, but with the parietal instead of the squamosal, and on the under instead of the upper side, as in the genus Sphenodon. (See figs. 13, 14, OpO.) In Chamæleo it is a mere wedge articulating with the proximal end of the quadratum, and not entering into the parieto-quadrate arch.

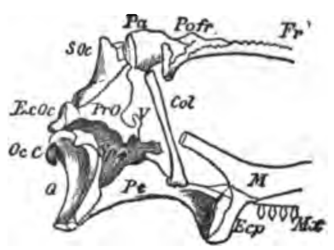


Fig. 12.—Iguana tuberculata; posterior arches removed.

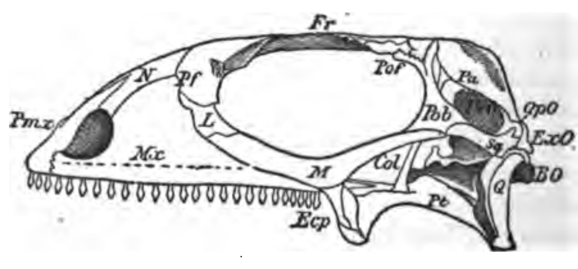


Fig. 13.—Iguana tuberculata; lateral view, with arches.

* I rely on the figures and descriptions of Günther, in his paper on the Anatomy of Hatteria (Philos. Trans., London, 1867).

In the Pythonomorpha its character as "suspensorium" of the quadrate is still more pronounced; yet, though it forms part of a cylindric bar extended transversely from the brain-case, it maintains a sutural union with the proötic (see fig. 15, OpO), and to a slight degree in Clidastes, with the supraoccipital, or ? epiotic portion of it. If there be any parieto-quadrate arch (a doubtful point), it probably enters into it posteriorly.

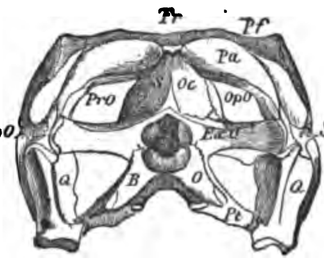


Fig. 14. — Iguana, from behind.

In the Ophidia it exhibits an important range of variation. I have not been able to find it in Typhlops.* In Cylindrophis it is

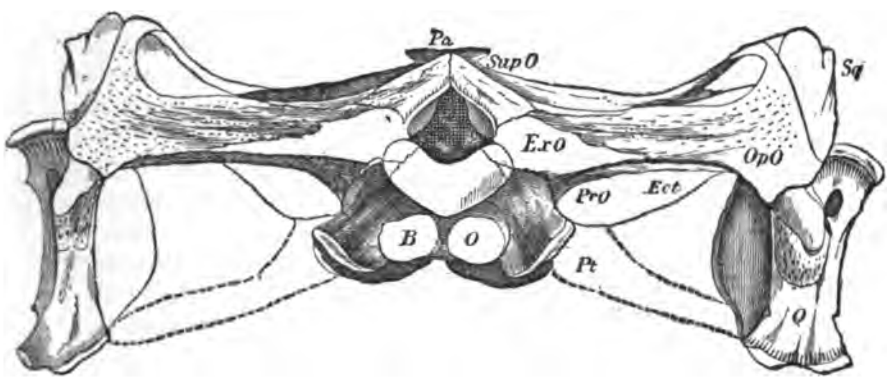


Fig. 15. — Clidastes propython, Cope; cranium from behind.

enclosed as usual between the exoccipital behind, the proötic anteriorly and inferiorly, the parietal above, and a small area enclosed between the latter and the exoccipital, which is either the extremity of the supraoccipital or a distinct element, perhaps epiotic. (See fig. 16: BO, Basioccipi-

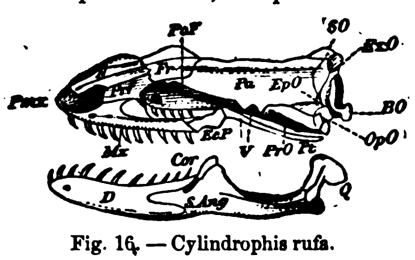


Fig. 16. — Cylindrophis rufa.

* In an osteological system of the scaled Reptilia, published in "Proceedings of the Academy of Natural Science," Phila., 1864, p. 224, an error occurs, in

tal; ExO, Exoccipital; SO, Supraoccipital; OpO, Opisthotic; PrO, Proötic; EpO, Epiotic; Fr, Frontal; PoF, Postfrontal; Prf, Prefron-frontal; N, Nasal; Pmx, Premaxillary; Mx, Maxillary; Ecp, Ectopterygoid; Q, Quadrate; Art, Articular; Cor, Coronoid; D, Dentary; V, Foramen ovale.) The obtuse extremities of the opisthotic and exoccipital support together the os quadratum.

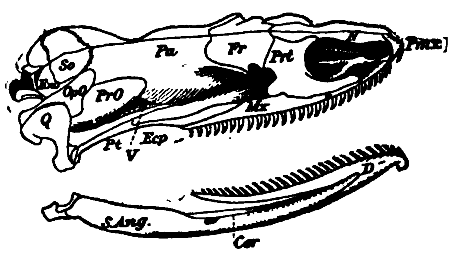


Fig. 17. — Xenopeltis unicolor (Siam).

In the rather more specialized Xenopeltis, the opisthotic is no longer intercalated between the proötic and exoccipital, but lies over the common suture of the two, united by a squamosal suture. This important change transfers us from the Tortricina to the Asinea, as defined by Müller. (See fig. 17, OpO.) Throughout the latter suborder it only increases in length, which prolongation reaches its highest expression in the venomous serpents of the suborder Solenoglypha. It has been homologized with the squamosal in these groups by Huxley (Elements of Comparative Anatomy), but incorrectly, as I believe, and attempt to show in considering that bone.

Among the Batrachia this element is not distinct, except in Necturus. (See fig. 22, posterior view of cranium of Rana mugiens.) I have failed to find it entirely distinct in larvæ of various ages of Amblystoma, Spelerpes, and Gyrinophilus; for though a suture from the fenestra ovale to the foramen condyloideum sepa-

which I say in the definition of the Scolecophidia, p. 230, "no prefrontal." This should have read "no opisthotic." The prefrontal is largely developed in Typhlops, while the maxillary is much reduced, and concealed on the inferior face of the cranium alongside the vomers. In the portion devoted to the Lacertilia, p. 225, several expressions occur which need explanation, owing to the fact that the homologies of some of the elements were not at that time worked out. Thus the "temporal bone" is the proötic, and the "mastoid" is the opisthotic. I must also correct the nomenclature of the elements of the mandible here, and in Clidastes, as published in Trans. Amer. Philos. Soc., 1870, pp. 214–16. Angular should read *articular*, articular should read *surangular*, and subarticular should read *angular*. In cut 51, figs. 3 and 5 belong to one bone, which is the *angular*.

rates it inferiorly from the exoccipital in several species, the superior suture is wanting or invisible.

The opisthotic is known to be distinct in osseous Ganoids and Teleostei.

5. *On the Homologies of the Squamosal Bone.*

As this bone derives its name from its Mammalian representative, it will be well to trace it from that class. It may be defined as the bone which occupies the space between the proötic in front, the opisthotic behind, and the parietal above, which subtends the auricular bones or meatus superiorly, and forms the posterior extremity of the zygomatic arch.

In the Birds the zygomatic arch does not exist, and the malleus is produced from beneath it, as the os quadratum, for the support of the mandible (Parker).* Here then it first assumes the position of the external shield of the quadrate, which it continues to hold throughout the series of Vertebrata below this point.

In tracing its homologies in the Reptilia, we commence with those in which the quadrate is most nearly sessile on the cranium, as in the Birds, and proceed towards those in which the latter is supported at the extremity of a prolongation of the posterior elements of the cranium, or a "suspensorium."

I may add here that the former relation of the quadrate, being most similar to that found in both the Birds and the Stegocephalous, and other tailed Batrachia, is the most generalized;

Fig. 18. — Alligator mississippiensis; cranium, with arches removed, and a pointer passed behind the columella.

* On the Development of the Skull in the Ostrich Tribe (Philos. Trans., London, 1865, p. 118).

while the suspensorial type is the most divergent from other Vertebrata, and most specialized. Hence the successional relation of the orders of Reptilia is to be estimated by reference to their degree of approximation to either of these extremes, as will be considered further on.

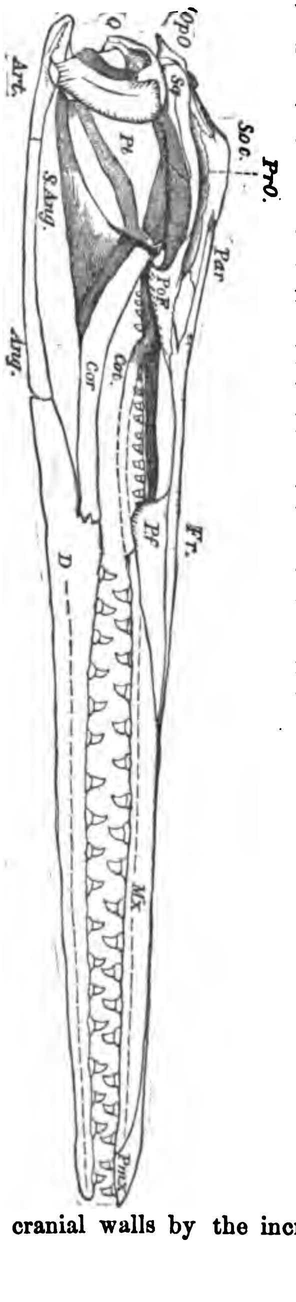


Fig. 19. — Clidastes propython; profile of cranium, with arches.

If we seek for that element, in the Crocodilia, which fulfils the requisites of the squamosal as above defined, we find it on the posterior superior lateral angle of the cranium. (See fig. 18, Sq.) It sends forwards an anterior process, which completes the zygomatic arch posteriorly, and with the postfrontal (Pf) bone encloses the temporal fossa. As its union with the quadratum is on the under side of the latter, it is concealed from view in fig. 18, chiefly by the superior prolongation of the quadratojugal (QJ).

In the Testudinata, the quadrate being removed from the cranial walls, the position of the squamosal is more exterior. (Fig. 10, Sq.) In Chelone, it sends an extension upwards to the parietal, forming the parieto-quadrate arch, which is not observed in most other Testudinata. The enclosed space is much more expanded than in Crocodilia (fig. 11), where it is in fact reduced to a foramen above each supraoccipital.

The position of the squamosal in the Pythonomorpha is very similar to that seen in the last order, but it is further removed from the cranial walls (fig. 19, Sq), in consequence of the greater length of the suspensorium.

In the Lacertilia it is carried far from the cranial walls by the increased length of the exoccipital, from

which, as in the Testudinata, the opisthotic separates it. (See figs. 13, 14, Sq.) In most of the order it has no contact with the parietal, the parieto-quadrate arch being supported below by the opisthotic, as above pointed out. But in the Rhiptoglossa (Chamæleo) the squamosal sends a long process upwards, which meets a prolongation of the parietal, which is however single and median, and not bifurcate as is usual. The opisthotic does not rise with it. In the Ophiosauri (Amphisbænia), it appears to be wanting, as Müller has already indicated; and there are various stages of reduction to be observed among the Typhlophthalm lizards which approach them.* In the Aniellidæ it is wanting, while it exists in a rudimental state in the Acontiadidæ. (Fig. 20, Ramus mandibuli, quadrate, and suspensorium of Acontias meleagris, Sq.)

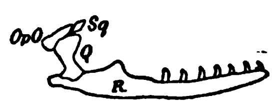


Fig. 20.—Acontias meleagris, S. Africa; mandible and suspensorium.

In the Ophidia the squamosal is obviously wanting. This is proven in two ways: first, by the serial homology of the opisthotic, from Lacertilia through Pythonomorpha (fig. 15), or Tortricina (fig. 16), with the single suspensorium of the quadrate in typical snakes; and, second, by the successive diminution of the squamosal in the Lacertilia from the Leptoglossa through the Typhlophthalmi, where it is rudimental in Acontias (fig. 19), and wanting in Aniella, and in the succeeding group of Amphisbænia. Therefore its identification with the suspensorium in Ophidia, proposed by Huxley, must be abandoned.†

Returning to the earlier types of Reptilia, we may recall the features of the squamosal already ascribed to the Ichthyopterygia and Anomodontia. The first peculiar feature, the anterior prolongation on each side of the cranium, on the inside of the temporal fossa, separating widely the supraoccipital and parietal, was shown to exist also in the Rhynchocephalia. The question of the real pertinence of this prolongation to the squamosal may be raised, as it is remote from the position of that bone in most of the Lacertilia, and in some specimens of Ichthyosaurus is separated by suture from it. Its relations in Chamæleo throw much light on the point, and render it highly probable that the cranial prolongation in the three groups just mentioned is really continuous with it. As pointed out above, the squamosal in Chamæleo extends inwards to the parietal, forming the greater part of the parieto-quadrate

* See Essay on Primary Groups of Reptilia Squamata (Proceedings Academy of Natr[illegible] Phila., 1864, p. 230).

† [illegible]rpha, Trans. Am. Philos. Soc., 1869, p. 178.

while the suspensorial type is the most divergent from other Vertebrata, and most specialized. Hence the successional relation of the orders of Reptilia is to be estimated by reference to their degree of approximation to either of these extremes, as will be considered further on.

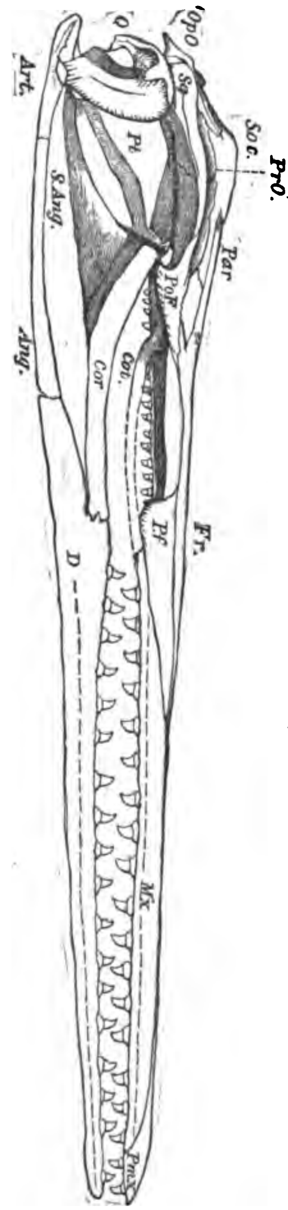


Fig. 19.—Clidastes propython; profile of cranium, with arches.

If we seek for that element, in the Crocodilia, which fulfils the requisites of the squamosal as above defined, we find it on the posterior superior lateral angle of the cranium. (See fig. 18, Sq.) It sends forwards an anterior process, which completes the zygomatic arch posteriorly, and with the postfrontal (Pf) bone encloses the temporal fossa. As its union with the quadratum is on the under side of the latter, it is concealed from view in fig. 18, chiefly by the superior prolongation of the quadratojugal (QJ).

In the Testudinata, the quadrate being removed from the cranial walls, the position of the squamosal is more exterior. (Fig. 10, Sq.) In Chelone, it sends an extension upwards to the parietal, forming the parieto-quadrate arch, which is not observed in most other Testudinata. The enclosed space is much more expanded than in Crocodilia (fig. 11), where it is in fact reduced to a foramen above each supraoccipital.

The position of the squamosal in the Pythonomorpha is very similar to that seen in the last order, but it is further removed from the cranial walls (fig. 19, Sq), in consequence of the greater length of the suspensorium.

In the Lacertilia it is carried far from the cranial walls by the increased length of the exoccipital, from

which, as in the Testudinata, the opisthotic separates it. (See figs. 13, 14, Sq.) In most of the order it has no contact with the parietal, the parieto-quadrate arch being supported below by the opisthotic, as above pointed out. But in the Rhiptoglossa (Chamæleo) the squamosal sends a long process upwards, which meets a prolongation of the parietal, which is however single and median, and not bifurcate as is usual. The opisthotic does not rise with it. In the Ophiosauri (Amphisbænia), it appears to be wanting, as Müller has already indicated; and there are various stages of reduction to be observed among the Typhlophthalm lizards which approach them.* In the Aniellidæ it is wanting, while it exists in a rudimental state in the Acontiadidæ. (Fig. 20, Ramus mandibuli, quadrate, and suspensorium of Acontias meleagris, Sq.)

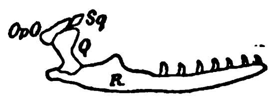


Fig. 20.—Acontias meleagris, S. Africa; mandible and suspensorium.

In the Ophidia the squamosal is obviously wanting. This is proven in two ways: first, by the serial homology of the opisthotic, from Lacertilia through Pythonomorpha (fig. 15), or Tortricina (fig. 16), with the single suspensorium of the quadrate in typical snakes; and, second, by the successive diminution of the squamosal in the Lacertilia from the Leptoglossa through the Typhlophthalmi, where it is rudimental in Acontias (fig. 19), and wanting in Aniella, and in the succeeding group of Amphisbænia. Therefore its identification with the suspensorium in Ophidia, proposed by Huxley, must be abandoned.†

Returning to the earlier types of Reptilia, we may recall the features of the squamosal already ascribed to the Ichthyopterygia and Anomodontia. The first peculiar feature, the anterior prolongation on each side of the cranium, on the inside of the temporal fossa, separating widely the supraoccipital and parietal, was shown to exist also in the Rhynchocephalia. The question of the real pertinence of this prolongation to the squamosal may be raised, as it is remote from the position of that bone in most of the Lacertilia, and in some specimens of Ichthyosaurus is separated by suture from it. Its relations in Chamæleo throw much light on the point, and render it highly probable that the cranial prolongation in the three groups just mentioned is really continuous with it. As pointed out above, the squamosal in Chamæleo extends inwards to the parietal, forming the greater part of the parieto-quadrate

* See Essay on Primary Groups of Reptilia Squamata (Proceedings Academy of Natural Science, Phila., 1864, p. 230).

† See, on Pythonomorpha, Trans. Am. Philos. Soc., 1869, p. 178.

while the suspensorial type is the most divergent from other Vertebrata, and most specialized. Hence the successional relation of the orders of Reptilia is to be estimated by reference to their degree of approximation to either of these extremes, as will be considered further on.

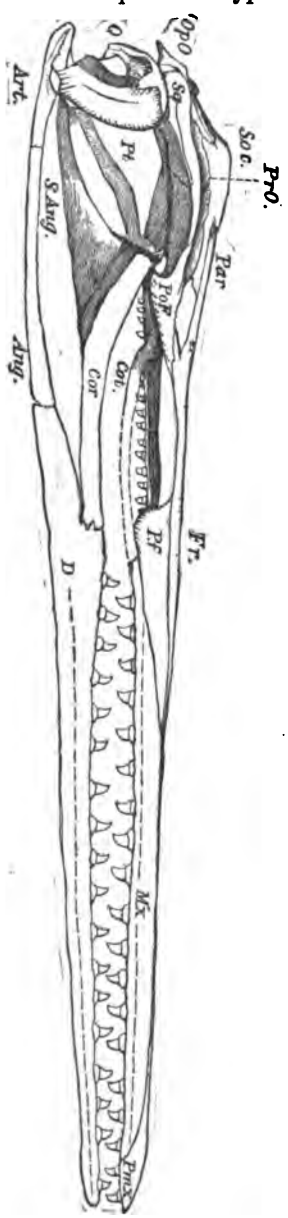


Fig. 19. — Clidastes propython; profile of cranium, with arches.

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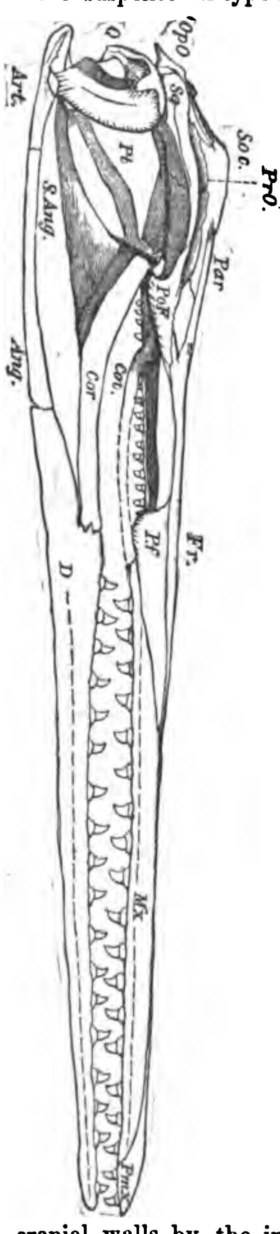

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system at present includes, the definitions of our groups will rest upon single characters only, and the history of the origin of those characters will be the history of the origin of the groups.

It is the proper discrimination of the relative values of these single characters which in our estimation determines the "naturalness" of a system; and the principle on which such discrimination reposes is the key to that perplexing question which often renders the conclusions of naturalists so different in appearance, while the objects of their investigations are the same. But by misusing "technical" or single characters — that is, by misinterpreting their values — the most erroneous approximations may be made, and systems constructed which well deserve the term "artificial" applied to them by those who, in their search for the "natural" system, are opposed to the use of "technical" characters. Perhaps the best known example of this misuse is to be found in the Linnæan system of botany, where the value of the numbers of stamens and pistils in determining affinity was placed much too high. Though this system has been utterly abandoned, yet Linnæus's characters are still of great importance in a lower grade of relations.

As the number of primary groups of the animal kingdom is but small, I will commence with the principle on which all subordinate divisions may be distinguished, and their value ascertained.

I. Given primary divisions, and given that such divisions present in some members greater resemblance (or unity of minor characters) to members of other primary divisions, and in other members especial diversity from the same, — the primary subdivisions of said first divisions are those which express the successional degrees of resemblance to or difference from the other divisions of first rank.

II. Given primary subdivisions, their subdivisions of first rank are estimated, as in Prop. I., by reference to the characters presented by their extremes of likeness to or diversity from the members of the other primary subdivisions. The value of characters of the groups contained in each of last grades mentioned to be determined by the same test.

For primary divisions, in Prop. I., might be read *class;* for primary subdivision, *order;* and for subgroup of the latter, *family.* The same principle applies to genera, which is expressed in Prop. VI. of a series designed to render clear the basis of the theory of evolution, published in a "Monograph of the Cyprinidæ of Pennsylvania." * The I., II., and III. propositions are prefixed as preliminary: —

I. That genera form series indicated by successional differences of structural character, so that one extreme of such series is very different from the other, by the regular addition or subtraction of characters, step by step.

II. That one extreme of such series is a more generalized type, nearly approaching in characters the corresponding extreme of other series.

III. That the other extreme of such series is excessively modified and specialized, and so diverging from all other forms as to admit of no type of form beyond it.

VI. That therefore the differences between genera of the same natural series are only in those characters which characterize the extreme of that series.

For the highest groups in the animal kingdom we must accept the definition of Cuvier, Von Baer, and Agassiz, for the present, that they are primary, because they represent different primary plans of structure. For the lowest grade of groups (genera) the definition above given (Prop. VI.) will be found to represent groups to which the definition given by Agassiz † will also apply; viz., that "their special distinction (*i. e.*, of genera) rests upon the ultimate details of their structure." I believe that the definitions given by Agassiz to the three intervening grades of divisions — viz., of families, orders, and classes — are far nearer a representation of nature than any other ever given. They are as follows: —

Classes are defined "by the manner in which the plan of the branch is executed; *Orders*, by the degrees of complication of that class-structure; *Families*, by their form as determined by structure." Natural science is under great obligations to Professor Agassiz in this, as in other points.

These definitions are, however, better perceived after the groups are constituted, but in practice are not sufficiently exact to serve as the crucial test in the cases which may arise. The simple method indicated in our propositions above will, it appears to us, serve to solve many of the more difficult questions which arise during the attempt to state the true relations of organic beings.

We may now apply these principles to the groups of the class

* Trans. Am. Philos. Soc., 1866, p. 397.
† Contrib. Nat. Hist. U. S., i. pp. 163, 170.

Reptilia, not only as an illustration of their meaning, but of their use.

β. On the System of Reptilia.

The points of resemblance to the other classes of Vertebrata presented by the Reptilia are, of course, to those below them and those above them. Relationships to the class Batrachia are as yet doubtful, unless indeed the remarkable relations of the squamosal and quadrate in Anomodontia have such a significance. The extremities of the genus Ichthyosaurus present a remarkable structure not seen elsewhere in the class, nor in the classes above it; viz., in lacking all differentiation between the elements external to the proximal element, — the humerus and femur. So far as form is concerned, the ulna and radius, tibia and fibula, tarsus carpus, metacarpus, metatarsus, and phalanges, are identical. This type is only found below the Reptilia, approximately among Crossopterygian fishes and Elasmobranchi; and it is to the latter class that we must appeal, says Gegenbaur, for an explanation of their structure. No other resemblance of real importance has been observed to exist between the two groups.

The extension downwards of the squamosal over the quadrate region constitutes a point of remote resemblance to the Fishes. The ? continuation of the ? frontals to the premaxillaries in Ichthyosaurus is seen in the lower tailed Batrachia.

Resemblances to the classes above the Reptilia are seen in the groups Crocodilia, Dicynodontia, Ornithosauria, and Dinosauria. In the first, the presence of a vermis in the cerebellum, and quadripartite heart are points of equal affinity to the Mammalia and Aves. In the three others, the double-headed ribs, with capitular articulation on the centra of the vertebræ, and generally elongate or complex sacrum, are points of resemblance both to Mammalia and Birds. In the Dicynodontia, other resemblances to either class are wanting, but the case is different in the other orders. The pelvis and hind limbs of the Dinosauria are especially bird-like; while, according to Seeley, the Ornithochiræ had epipubic or marsupial bones as in Mammalia, a brain with infero-lateral optic lobes as in Aves, and even confluent metatarsi as in the same class. In fact, it seems quite evident that Seeley is right in referring that group to the Birds; but this does not necessarily remove the true Pterodactyles from the Reptilia. These have distinct tarsals and metatarsals, though their epipubic (marsupial) bones and other characters ally them most closely to the Ornithochiræ.

Serial divergence from these lower and higher orders to an extreme of special peculiarity, such as is mentioned in Prop. III. above, has been alluded to in the discussion of the homologies of the opisthotic and squamosal bones. This is seen in the successive prolongation of the elements on the sides of the posterior region of the cranium into a "suspensorium," and the successive liberation of the quadrate bone from several sutural articulations, to a condition as a mobile fulcrum for the mandible. This succession is seen first in the Rhynchocephalia, where the suspensorium is produced, but the quadrate fixed; the Testudinata, where the quadrate is freed from a quadratojugal bone; in the Lacertilia, where the quadrate is movable, but the opisthotic not produced; in the Pythonomorpha, where the opisthotic is produced as suspensorium; the extreme being reached in the Ophidia, where the suspensorium itself becomes movable, and with it the elements which usually form the solid surface of the palate.

This series then, it is evident, is like that of the Teleostei, among the lower Vertebrata, a special divergence from the main line of succession to the higher classes. The reptiles which retain and increase the close contact of the quadrate bone with the periotic elements are evidently those which conduct us to the Mammalia. The highest group in this succession is the Crocodilia. Those which consolidate the periotic elements, but retain the partial freedom of the quadrate, on the other hand, lead to the Avine class. These are the Ornithosauria, and perhaps, when we come to know the cranium, the Dinosauria. At least this may be predicated, if the structure of the foot and ear bones are correlated in this group as they are elsewhere.

The primary importance of this series is confirmed by the correlation with it of the serial modification of the modes of attachment of the ribs. These differences were first used in systematic work by Owen,* and later more fully by Huxley.† The latter subdivides the Reptilia in accordance with it alone, and, while pointing out important affinities thereby, fails to recognize others from his neglect of the modifications of the quadrate and supporting bones.

In the most generalized form (represented by Ichthyosaurus), the capitular and tubercular articular surfaces are near together, but distinct, and situate on the sides of the vertebral centra.

* Palæontology. † Jour. Geol. Society, London, 1870.

From this point two lines of modification can be traced. The one, coinciding with that in which the quadrate and suspensorial bones are received into closer cranial articulation, is characterized by the wider separation of the two surfaces. The inferior becomes marginal and sessile, remaining on the centrum; the superior rises, and on the dorsal region is supported on an elongate basis from the sides of the neural arch. Thus, in this point also, this series tends towards the Aves and Mammalia. The second, or special series, in correspondence with the liberation of the quadrate, etc., sees a fusion of the two articular surfaces, and their usual retention on the centrum. In one group (Sauropterygia) this fused basis rises to the top of the neural arch in the dorsal region: on the cervical region they are distinct.

In the Crocodilia, the capitular articulation does not rise to meet the tubercular in front of the posterior dorsal region; and they are united and rise from the neural arch on the lumbar region. These two orders are otherwise allied, and form a point of connection between the groups defined by the characters of the rib articulations.

In the Testudinata, the ribs are single headed as in this series, but the convexity is sometimes in contact with the transverse expansion of the neural spine. There appears, however, to be no true articulation here, nor any diapophysis.* The space between the vertebral expansion and the tubercular region of the rib is filled by a later and distinct ossification. The capitular articular facets are sessile, and at the point of contact of two centra. The majority of this order present a special peculiarity in the expansion of the ribs into an osseous upper shield: a similar expansion of abdominal elements (perhaps abdominal ribs), with the clavicles† and mesosternum (interclavicle, Parker), forms an inferior shield. As these characters are not developed in Sphargididæ, they need not be necessarily regarded as ordinal.

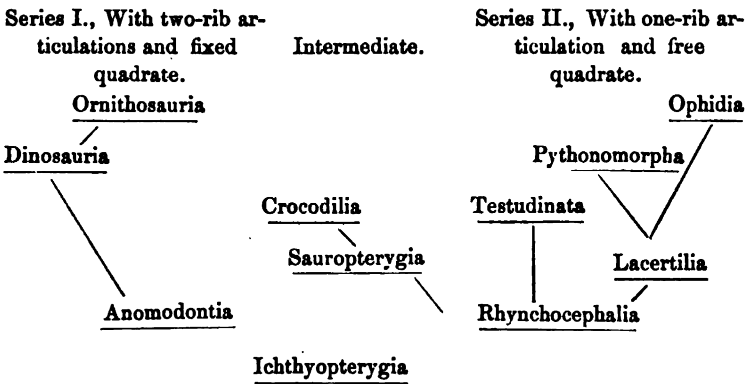
A similar character is to be found in the Pythonomorpha and Sauropterygia, whose fore limbs are specialized into swimming organs or paddles. Since we see this last modification of the truly differentiated limb to be subordinated to the characters of the order in the Testudinata (*e. g.*, in Cheloniidæ and Sphar-

* In a young *Testudo mauritanica* the proximal extremities of the ribs are decurved to their capitular articular facets, without touching the expansion of the neural spine (vertebral bones of carapace), and without sending tubercle or process to meet them.

† See Parker on the shoulder girdle.

gididæ), I do not regard it as necessarily of ordinal value, but subordinate to characters already mentioned, of the posterior regions of the cranium, the tarsus, pelvis, etc. The forms of the articular extremities of the vertebræ have also a subordinate value.

The affinities of the Orders are most easily expressed in the following outline scheme:—



A tabular arrangement destroys expression of more than one line of affinities, but is most convenient for presentation of diagnoses. The above-named groups possess different degrees of relationship to each other, and have been combined into groups by authors, which are supposed to represent natural divisions. This presents some difficulties as yet, on account of our ignorance of the structure in certain orders. They may, however, be provisionally placed as follows:—

A. Extremities beyond proximal segment not differentiated as to form.

I. Tubercular and capitular articulations for ribs distinct, on centra. Os quadratum immovably articulated to squamosal, etc. No sacrum. ICHTHYOPTERYGIA. Including one order, *Ichthyopterygia.*

B. Extremities differentiated.

II. Tubercular and capitular surfaces united. Os quadratum articulated with squamosal and opisthotic by ginglymus. Sacrum very small. STREPTOSTYLICA, with the orders *Lacertilia, Pythonomorpha,* and *Ophidia.*

III. Tubercular and capitular surfaces united. Os quadratum articulated with squamosal, opisthotic, etc., by suture. Sacrum small. SYNAPTOSAURIA, with the orders *Rhynchocephalia, Testudinata,* and *Sauropterygia.*

IV. Tubercular and capitular surfaces separated; former on diapophysis, latter on centrum. Os quadratum articulated by suture with its suspensorium. Sacrum generally of several vertebræ. ARCHOSAURIA; orders,—*Anomodontia, Dinosauria, Crocodilia,* and *Ornithosauria.*

CATALOGUE OF THE FAMILIES OF THE REPTILIA.*

I. ORNITHOSAURIA.

Bonaparte, Fitzinger, Seeley; *Pterosauria*, Owen.
Dimorphodontidæ; Dimorphodontæ, Seeley, l. c.
Pterodactylidæ; Rhamphorhynchæ et Pterodactylæ, Seeley, l. c.

II. DINOSAURIA.

Owen, Cope, Seeley; *Pachypodes*, Meyer. *Ornithoscelida;* Huxley.

1. Symphypoda.

Cope; *Compsognatha*, Huxley.
Compsognathidæ; Compsognathus, Wagner.
Ornithotarsidæ; Ornithotarsus, Cope.

2. Goniopoda.

Cope; *Harpagmosauria*, Haeckel.
Megalosauridæ; Huxley (part). Cope, Trans. Am. Philos. Soc., 1869, p. 99.
Teratosauridæ; Teratosaurus, Plateosaurus, Meyer, etc. Cope, Trans. Am. Philos. Soc., 1869, p. 90.

3. Orthopoda.

Cope; *Therosauria*, Haeckel.
Scelidosauridæ; Cope, Trans. Am. Philos. Soc., 1869, p. 91; Huxley, Jour. Geol. Soc., London, 1870, p.
Iguanodontidæ; Cope, l. c.; Do. (in part), Huxley, l. c.
Hadrosauridæ; Cope, l. c.; Iguanodontidæ, Huxley (part).

III. CROCODILIA.

Crocodilia et *Thecodontia* (part), Owen, 1841.

1. Amphicœlia.

Belodontidæ; Thecodontia, Owen (part). Cope, Trans. Am. Philos. Soc., 1869, p. 32.
Teleosauridæ.

* The extinct groups and synonymes are indicated by italics.

2. PROCŒLIA.

Thoracosauridæ; Thoracosaurus, Leidy, Cope.
Gavialidæ; Gavialidæ, Gray; + Holops Thecachampsa, Cope, etc.
Crocodilidæ; Crocodilidæ + Alligatoridæ, Gray.

IV. SAUROPTERYGIA.

Owen.
? *Placodontidæ;* Placodus, etc.
Plesiosauridæ; Nothosaurus, Pistosaurus, Plesiosaurus, Pliosaurus, etc.
Elasmosauridæ; Elasmosaurus, Cimoliasaurus, etc.

V. ANOMODONTIA.

Owen.
Dicynodontidæ; Owen, Palæontology.
Oudenodontidæ; *Cryptodontia*, Owen, Palæontology.

VI. ICHTHYOPTERYGIA.

Ichthyosauridæ.

VII. RHYNCHOCEPHALIA.

Protorosauridæ; Protorosaurus, Meyer (elongate sacrum).
Sphenodontidæ; Hatteriidæ, Cope (Proceed. Acad. of Nat. Sci., Phila., 1864).
Rhynchosauridæ; Rhynchosaurus, Owen.

VIII. TESTUDINATA.

1. ATHECÆ.

Sphargididæ; Gray, Annals of Philosophy, 1825; Bell, Fitzinger, Agassiz.

2. CRYPTODIRA.

Cheloniidæ; Gray, Annals of Philosophy, 1825; Agassiz.
Propleuridæ; Cope, Sillim. Am. Jour. Sci., 1870, p. 137.
Trionychidæ; Gray, Bell, Dum., Bibr., Agassiz.
Emydidæ; Emydidæ and Chelydridæ, Agassiz.
Adocidæ; Cope, Proceed. Am. Philos. Soc., 1870, November.
Cinosternidæ; Agassiz, Contrib. Nat. Hist. U. S.; Cope, Leconte (part).

Testudinidæ; Gray, Agassiz, Cope emend.
Pleurosternidæ; Cope, Proceed. Acad. Nat. Sci., Phila., 1868, October.

3. Pleurodira.

Duméril, Bibron; *Chelyoidæ*, Agassiz.
Podocnemididæ; Cope, Proceed. Acad. Nat. Sci., Phila., 1868, October; Peltocephalidæ, Gray.
Chelydidæ; Gray, Proceed. Zoöl. Soc., London, 1869; Cope, l. c., 1868.
Hydraspididæ; Cope, l. c.; Gray, l. c.
Pelomedusidæ; Cope, l. c., 1865, p. 185, 1868, p. 119.
Sternothæridæ; Cope, l. c., 1868, p. 119.

IX. LACERTILIA.

Owen, Cope.

1. Rhiptoglossa.

Acrodonta Rhiptoglossa; Wiegmann, Fitzinger, Cope. *Chamæleonida;* Müller.
Chamæleontidæ; Wiegmann, Gray, et auctorum.

2. Pachyglossa.

Cope; *Acrodonta Pachyglossa*, Wagler, Fitzinger. Cope, Proceed. Acad. Nat. Sci., Phila., 1864, p. 226.
Agamidæ.

3. Nyctisaura.

Gray; Catal. Sauria Brit. Mus.; Cope, l. c.
Gecconidæ; Gray, et auctorum.

4. Pleurodonta.

Cope, Proceed. Acad. Nat. Sci., Phila., 1864, p. 226.

a. Iguania.

Anolidæ; Cope, l. c., pp. 227, 228.
Iguanidæ; Cope, l. c., pp. 227, 228; Iguanidæ (pars), auctorum.

b. Diploglossa.

Anguidæ; Cope, l. c.
Gerrhonotidæ; Cope, l. c.; *Zonuridæ* (part), Gray.
Xenosauridæ; Cope, l. c., 1866, p. 322.
Helodermidæ, Gray; Catal. Sauria Brit. Mus.; Cope, l. c., 1864, p. 228, 1866, p. 322.

c. Thecaglossa.

Wagler, Fitzinger, Cope.
Varanidæ.

d. Leptoglossa.

Wiegmann, Fitzinger, Cope.

Teidæ; *Teidæ* and *Ecpleopodidæ*, Peters, Cope, Proceed. Acad. Nat. Sci., Phila., 1866, p. 228; *Teidæ Anadiidæ Cercosauridæ Riamidæ*, Gray.

Lacertidæ; Gray; Catal. Sauria; Cope, l. c.; Lacertidæ et *Cricosauridæ*, Peters; *Xantusiidæ*, Baird.

Zonuridæ; *Zonuridæ* (part), Gray; *Lacertidæ* (part), Cope.

Chalcididæ; Gray, l. c.; Cope, l. c.

Scincidæ; Gray, l. c.; Cope, l. c.

Sepsidæ; Gray, l. c.; Cope, l. c.

e. Typhlophthalmi.

Cope, Proceed. Acad. Nat. Sci., Phila., 1864, p. 228; Do. (pars), Duméril et Bibron. Erpet. Gen.

Anelytropidæ; Cope, l. c. name; *Typhlinidæ*, Gray.

Acontiidæ; Gray; Catal. Brit. Mus.; Cope, l. c., 1864, p. 230.

Aniellidæ; Cope, l. c., 230.

5. Ophiosauri.

Cope, l. c., Merrem; *Annulati*, Wiegmann; *Ptychopleures Glyptodermes*, Dum., Bibr.; *Amphisbænoidea*, Müller.

Amphisbænidæ; —æ, Wiegmann, Fitzinger.

Trogonophidæ; *Trogonophes*, Wiegmann, Fitzinger.

X. PYTHONOMORPHA.

Cope, Trans. Am. Philos. Soc., 1870, p. 175; Proceed. Boston Nat. Hist. Soc., 1869, p. 251; *Lacertilia Natantia*, Owen; Palæontograph. Society, Cretaceous Reptiles.

Clidastidæ; Cope, l. c., p. 258.

Mosasauridæ; Cope, l. c., p. 260.

XI. OPHIDIA.

1. Scolecophidia.

Duméril; *Scolecophidia* et *Catodonta*, Cope, Proceed. Acad. Nat. Sci., 1864, p. 230.

Typhlopidæ; *Epanodontiens*, Dum., Bibr.

Stenostomidæ; *Catodontiens*, Dum., Bibr.; *Catodonta*, Cope, l. c.

2. Tortricina.

Müller, Cope, l. c.
Tortricidæ.
Uropeltidæ; *Uropeltacea*, Peters; *Rhinophidæ*, Gray.

3. Asinea.

Müller, Cope.

a. Peropoda.

Müller.
Xenopeltidæ; Cope, l. c.; Günther, Reptiles British India.
Pythonidæ; Cope, l. c.; *Holodontiens*, Dum., Bibr.
Boidæ; Cope, l. c.; *Aproterodontiens*, Dum., Bibr.
Lichanuridæ; Cope, Proceed. Acad. Nat. Sci., Phila., 1868, p. 2.

b. Colubroidea.

Achrochordidæ; Cope, l. c., p. 231; *Achrochordiens*, Dum., Bibr.
Homalopsidæ; Cope, Proceed. Acad. Nat. Sci., Phila., 1864, p. 167; *Natricidæ* (pars), Günther; *Potamophilidæ*, Jan.
Colubridæ; *Asinea* Group *β–bb*, Cope, Proceed. Acad. Nat. Sci., Phila., 1864, p. 231; *Calamaridæ*, *Oligodontidæ*, *Coronellidæ*, *Colubridæ*, *Dryadidæ*, *Dendrophidæ*, *Dryiophidæ*, *Psammophidæ*, *Lycodontidæ*, *Scytalidæ*, *Dipsadidæ*, etc., Günther, Catal. Brit. Mus., et op. alt.
Rhabdosomidæ; *Calamaridæ* (part), Günther.

4. Proteroglypha.

a. Conocerca.

Elapidæ; Cope, l. c., p. 231; *Elapidæ* (pars), Günther, l. c.
Najidæ; Cope, l. c.; *Elapidæ* (pars altera), Günther, l. c.

b. Platycerca.

Hydrophidæ; *Hydridæ*, Gray; *Hydrophidæ*, Schmidt, Fischer, Günther. Cope, Proceed. Acad. Nat. Sci., Phila., 1869, p. 75, 1864, p. 231.

5. Solenoglypha.

Duméril, Bibron; *Viperidæ*, Cope, Proceed. Acad. Nat. Sci., 1859, p. 333.
Atractaspididæ; Günther; Catal. Brit. Mus.; Cope, l. c., 1859, p. 334.
Causidæ; Cope, l. c., 1859, p. 334.
Viperidæ; Gray; Catal. Brit. Mus., p. 18; Cope, l. c.; Günther, Reptiles British India.
Crotalidæ; Gray, l. c., Cope, l. c., Günther, l. c., et auctorum.

8. *Critical Remarks on the System.*

1. In the "Transactions of the American Philosophical Society," 1869, part I. (August), I proposed a system in which the primary groups of the Reptilia were defined anew, and understood in some measure differently from those proposed by Owen. The system of the latter author, and that of Von Meyer, were the only ones extant previously; and additional discovery necessitated some modifications, while the meritorious portions of both it was intended to preserve. The groups, perhaps equivalent to "orders," retained, were the Ichthyopterygia, Archosauria, Testudinata, Pterosauria, Lacertilia, Pythonomorpha, and Ophidia. The form of attachment of the quadrate bone was regarded, after Johannes Müller, as an element of prime importance in the estimate of affinities, and of nearly equal value, the differentiation of distal elements of limbs, the opisthotic bone, the mode of attachment of ribs, etc.

Another systematic grouping of the orders was proposed by Professor Huxley in the "Journal of the Geological Society," London, 1869 (November), in which the position and character of the rib articulations to the vertebral centra were used exclusively in discrimination of the groups. The subclasses proposed were the Suchospondylia, which is our Archosauria; the Perospondylia, our Ichthyopterygia;* the Herpetospondylia, corresponding to our orders Ophidia, Pythonomorpha, Lacertilia, with the addition of the Sauropterygia. The last group is rendered unnatural by the presence of the latter order, which possesses the closely articulated quadrate bone of the Archosauria. I therefore omit it, and retain the three orders remaining, in one division, which has already been named by Müller the Streptostylica. Huxley's fourth subclass, the Pleurospondylia, includes the Testudinata only. This group I also recognized in the original memoir quoted, and I accept it with

* Some criticisms of Professor Huxley's in this essay, on my determination of the structures and relations of the Dinosauria, are so inapposite as to require notice. He quotes me as saying of the astragalus of Lælaps, that "one other example of this structure is known in the Vertebrata;" and adds, "but I shall show immediately that the astragalus is altogether similar in the commonest birds, and probably in the whole class Aves." This statement is so precisely the reverse of the fact, that I can only suppose it to be an inadvertence, or a *double entendre*, the latter being an impossibility in so fair a man as Professor Huxley. On page 85 he says: "Professor Cope has distinguished Compsognathus as the type of a division Ornithopoda, from the rest of the Dinosauria, which he terms Goniopoda (on the structure of the foot, etc.)... It seems to me precisely by the structure of the foot that Compsognathus is united with, instead of being separated from,

new definition, so much so indeed as to constitute a substitution. The Rhynchocephalia (an order which Huxley has not recognized), Testudinata, and Sauropterygia agree in the essential structures of the quadrate element, and the simplicity of the rib attachment; they also agree in the abdominal ribs and plane vertebral centra. The capitular rib articulations are on processes in the last, in the Testudinata in pits, but in Sphenodon almost sessile on the centra. If Rhynchosaurus be a Rhynchocephalian, it has tortoise-like jaws; so has the Sauropterygian Placodus in some respects. Natatory fins of Plesiosaurus, etc., are repeated in the turtle Sphargis. So, though this association into the subclass which I have called Synaptosauria appears at first sight unnatural, it probably has a basis in nature.

2. The Ornithochiræ of Seeley do not appear to belong to the Ornithosauria, but to the Birds, where they would enter the subclass Saururæ with the Archæopteryx. This depends on the accuracy of Seeley's statement that the metatarsi are united, and there seems to be no reason to doubt it. This learned author does not state whether the tarsal bones are distinct or not; though confluent metatarsi suggest union of these also, since the Dinosauria lose the distinctness of the tarsals, and preserve separate metatarsals. This group will be annectant to the Reptilia by their near allies the Ornithosaurian group of Dimorphodontæ of Seeley.

3. The arrangement of the Lacertilia is the same as that proposed by the author in 1864, with three exceptions. The Rhiptoglossa are separated from the Pachyglossa by a wider interval, and the two groups are regarded as of primary value. In the system quoted they are united into one primary group, — the Acrodonta. Secondly, the Sphenodontidæ (Hatteriidæ) are removed from the

the Ornithoscelida." I united Compsognathus with the Dinosauria in 1867, on account of the foot structure (as quoted by Professor Huxley, p. 24), but regarded its subordinate modification of arrangement as indicative of a subordinate division, Symphypoda. This is exactly the course adopted by Professor Huxley in 1869, only he changes the name of Symphypoda to Compsognatha, and gives different characters to it. As to the groups Ornithopoda and Goniopoda, as ascribed to me, they cannot be found in my papers. On page 24 Professor Huxley supports Cuvier's determination of the position of the tibia in Dinosauria, as different from mine, observing that "Cuvier was right from a morphological point of view, when he declared the tibia to be laterally compressed," etc. This point I never contested; but that Cuvier was wrong so far as actual position is concerned, as I have proposed, is evidently Professor Huxley's opinion, since he arranges the tibia in his descriptions and plates precisely as I did in 1867.

Pachyglossa, and associated with certain extinct forms into the order Rhynchocephalia. This is in consequence with the full statement of its structural characters by Günther, and I accept the new order proposed for it by this author, with some change of diagnosis. Third, the Zonuridæ are regarded as distinct from the Lacertidæ on account of their papillose tongue.

4. In the Ophidia, the Typhlopidæ and Stenostomidæ are united into one order, the Scolecophidia, as already done by Duméril and Bibron. I separated them in the system proposed in connection with that of the Lacertilia in 1864, on account of the supposed absence of the prefrontal bone in Typhlops while it is present in Stenostoma. I find, however, that the large bone I supposed to be maxillary in Typhlops, is really the prefrontal, and that the maxillary is concealed on the inferior face of the skull, being represented by a narrow strip alongside of the vomer.

9. *On the Rhynchocephalia and supposed Lacertilia of the Trias and Permian.*

The existence of Lacertilia in the Trias has been asserted by Professor Huxley, as indicated by the genera Hyperodapedon, Telerpeton, Rhynchosaurus, and Saurosternum.* For us the evidence furnished by these and other genera is conclusive only as to the presence of the Rhynchocephalia in beds of that age, while the existence of the Lacertilia remains undecided. The other genera are from Germany; viz., Proterosaurus, Sphenosaurus, and Phanerosaurus, of Meyer. Of these the first two are believed by Huxley to be Lacertilia.†

The characters of the Rhynchocephalia have been in part pointed out in the preceding pages. Other features, especially of the soft parts, can be learned by reference to Günther's Monograph of Sphenodon, already quoted.

Of the above genera, Hyperodapedon has the remarkable palatal structure characteristic of Sphenodon, and entirely unknown among the Lacertilia, and I have little doubt that the genus belongs to the same order; viz., the Rhynchocephalia. In all of the remaining genera, the vertebræ are flat or sub-biconcave as in Rhynchocephalia, and not procœlian as in Lacertilia. In defence of the position of Telerpeton as a Lacertilian, Professor Huxley cites the biconcave vertebræ of the Gecconidæ. These are, however, fish-like, and enclose within the adjacent conic cavities of

* Jour. Geol. Soc., Lond., 1869, p. 49. † Ibid., p. 87.

two centra a mass of cartilage. In the Batrachia, the ossification of this mass produces the ball which adheres to the centrum in front or behind, producing the procœlian or opisthocœlian vertebra. The vertebræ of Gecconidæ are therefore probably in the embryonic form of those of the other Lacertilia. Not so, however, with the Triassic genera in question. According to Meyer's figures, they are nearly plane, like those of Sphenodon and Dinosauria; and were probably developed round the chorda dorsalis, without retention of included-ball.

In Phanerosaurus, the neural arches are united to the body by suture, a character unknown in the Lacertilia. In general the vertebræ by which the genus is known might as well belong to a Sauropterygian. In Proterosaurus (See Von Meyer's "Saurier aus dem Kupferschiefer," Plates), the forms of the inferior pelvic bones and the presence of inferior abdominal ribs, are so entirely unlike any thing in the Lacertilia, and so much like the same parts in Sphenodon, that this genus also, I have no doubt, is a Rhynchocephalian. Every thing is in favor of the supposition that Rhynchosaurus and Sphenosaurus are Rhynchocephalians, since the parts preserved correspond with those of known types of that order, and none of the special peculiarities of Lacertilians, as distinguished from the former, have been discovered.

The only genera remaining are Saurosternum (Huxl.) and Telerpeton (Mant.). In the latter genus the palatine bones are said not to be separated by the pterygoids, and there is no quadratojugal represented by Huxley: if these characters exist, it suggests the Lacertilia rather than Rhynchocephalia. The latter is the more important point; but further examination is necessary to decide on it, as the postorbital arch is also omitted in the figure, which is possibly an inaccuracy, consequent on the state of the specimen. The form is in its dentition equally like the Lacertilian Uromastix and the Rhynchocephalian Sphenodon; but the transverse direction of the parieto-squamosal arch, and the plane or concave articulations of the vertebral centra, are those of the latter, not of the former.

As to Saurosternum, not enough is known of the only specimen to ascertain whether it belongs to the Lacertilia or Rhynchocephalia. There is no cranium, and the parts preserved or described are as characteristic of one order as the other.

10. *Stratigraphic Relation of the Orders of Reptilia.*

This is most readily shown in tabular form, as follows:—

Present				Rhynchocephalia		Crocodilia		Testudinata	Lacertilia		Ophidia
Pliocene						Crocodilia		Testudinata	Lacertilia		Ophidia
Miocene						Crocodilia		Testudinata	Lacertilia		Ophidia
Eocene						Crocodilia		Testudinata	Lacertilia		Ophidia
Cretaceous	Ornithosauria	Dinosauria				Crocodilia	Sauropterygia	Testudinata	Lacertilia	Pythonomorpha	
Jurassic	Ornithosauria	Dinosauria			Ichthyopterygia	Crocodilia	Sauropterygia	Testudinata	Lacertilia		
Triassic		Dinosauria	Anomodontia	Rhynchocephalia	Ichthyopterygia	Crocodilia	Sauropterygia	?	?		
Permian			?	Rhynchocephalia							

It will be observed, by this table, that the most specialized Reptilian order, the Ophidia, appeared last in time in the Eocene period; and that those which constitute the line of connection with the generalized reptiles appeared earlier as they approached the latter,—the Pythonomorpha in Cretaceous, and Lacertilia in Jurassic times. The Reptilian groups most specialized in bird characters (Ornithosauria and Dinosauria) appear on the other hand very early; the first and most Mammalian also,—the later of the two,—in Jurassic Beds. The Trias gives us in the Anomodontia and Ichthyopterygia, the two most generalized and lowest orders; while their contemporary, the Rhynchocephalia, almost as much generalized in Reptilian features proper, was already represented in the Trias. Strangely enough this order yet exists in the living Sphenodon of New Zealand. The Crocodilia, rather specialized in bird characters, accompanies the last in this wonderful persistency, beginning also in the Trias.

The inquiry as to the truth of the proposition that the more ancient types of animals are more generalized, and therefore more embryonic in the characters of a special nature* which characterized groups later introduced, is answered in a very imperfect way in the affirmative. It is like the shadow of a truth whose substance will shortly come before us. But when we come to compare the subdivisions of the orders themselves with each other, and with those of other orders, as we pass backwards in time, the weight of the affirmative answer to the above proposition is greatly increased. The oldest Ophidia are boæform, therefore approaching Lacertilia and Pythonomorpha. The oldest Tortoises have generally the most incomplete carapace and plastron; among them the Psephoderma allied to Sphargis, without carapace, and thus the most lizard-like of the order. The Lacertilia of European Jurassic strata are, some of them at least, acrodont, apparently Pachyglossa (*e. g.*, Acrosaurus), and, as such, nearer the Rhynchocephalia, which preceded them in time. The position of Homorosaurus and Piocormus is not determinable, as the dentition cannot be understood from the descriptions and figures of Wagner. The form of the mesosternum of the former refers it to either the Pachyglossa or Iguania, as I understand those groups. It may be assumed that since the order Lacertilia has diverged from the line of other Reptilia, while it took on in its special peculiarities it lost in the features characterizing the main

* The identity of these two propositions has not always been noticed by authors.

series with a higher tendency or terminus, thus *retrograding* in one sense. This is seen in the shortened sacrum, pleurodontu dentition, etc.

The Crocodilia of the Jurassic do not possess the ball and socket-jointed vertebræ of the recent genera, and exhibit the plane articular faces of all the Jurassic and Triassic Reptilia. Their basicranial region is also plane like that of other orders, instead of vertical as in the recent forms. The Triassic Crocodiles are still more generalized. Their ribs are extended to the pelvis, as in Dinosauria and Anomodontia: there are often three sacral vertebræ, an approach to the long sacrum of the same orders. The femur, with third trochanter, is an approach to that of the Dinosauria; and finally the position of the nostrils near the orbits (Belodon) is a Sauropterygian feature. In the Sauropterygia the shortened vertebral column, and long muzzle (Pistosaurus) in the oldest types (Triassic), are approximations to the Crocodilia. The Dinosauria display an increasingly Crocodilian character as we pass into the Triassic period. The femur (Palæosaurus, Megadactylus) loses the bird-like head, and assumes the ill-defined convexity of the Crocodiles; the tibia (Plateosaurus) loses the bird-like "spine," or crest. The ilium is shorter (Palæosaurus). Every student of the subject knows how much more difficult is the separation of the bones of Sauropterygia, Crocodilia, Anomodontia, and Dinosauria, of the Trias, than those of the Cretaceous. There are types allied to the Rhynchocephalia, whose systematic position is doubtful, owing to the generalized character of the parts we possess. Thus the Rhynchosaurus of the Trias of England is allied to that order, and to the Anomodontia. The Rhopalodon of the Permian has a large canine tooth, like the single one possessed by the Anomodontia; but with others associated, like those of the Rhynchocephalia. The Triassic Sauropterygia and Rhynchocephalia also agree in the anterior production of the pterygoid bones between the palatines to the vomer. Compare, for this point, Hyperodapedon and Nothosaurus.

We learn from such considerations as the above, and similar ones derived from the study of the Mammalia, that the successional relation of the faunæ of the periods in geologic time is more strikingly exhibited by the subordinate contents of the orders than by the orders themselves, in relation to each other. From this we decide that we must look for the origin of the orders in periods prior to those in which we now know them, if, as some suppose, they originated in still more generalized types. This accords with Huxley's view of the period of origin of the Mammalian orders.

It must also be remembered that the above deduction as to geological distribution is precisely that of geographical distribution; *i. e.*, that the homologous groups of different continents are not orders, but subordinate divisions of orders, the orders being universally distributed. This coincidence is remarkable, and justifies the view I have taken of the origin of higher types on the basis of retardation and acceleration, and of the nature of synchronism.*

Note in reply to Dr. Seeley's remarks on my interpretation of the structure of the cranium of Ichthyosaurus.

A brief abstract of the portions of the preceding paper, which relate to Ichthyosaurus and Lystrosaurus, having been published in the "American Naturalist," for 1870, Dr. Seeley publishes a criticism of the statements and conclusions therein contained, in the "Annals and Magazine of Natural History" for April, 1871. I will briefly reply to these remarks; and commence by saying that he discovers some errors in determinations of bones of the cranium of Ichthyosaurus, which are due to errors of the artist and proof reader; such are more likely to occur in an abstract issued early in a periodical, than in the essay itself. Thus he finds the lettering of the maxillary and lachrymal bones to be exchanged. This, as he supposes, is the artist's error, and one which was corrected on the proof which was not received in time. He also finds the nomenclature of the elements of the mandible to be erroneous. This resulted from a misconception by the artist of the lettering on my original drawing, which I find to be correct, and which in the present memoir is correctly copied. In the same way the small "supersquamosal" will be found described in the present paper.

The question as to the determination of the bones forming the roof of the cranium receives new light from Dr. Seeley's remarks. This has been much needed by American naturalists, for I have been unable to find in the whole range of the literature of the subject an English description of the osteology of the head of Ichthyosaurus, which is at all complete; and the figures are not more instructive. Dr. Seeley's statement, that the flat bone on the inner side of the temporal fossa, continuous in our specimen with the squamosal, is usually separated from the latter by suture, is valuable, and suggests that the element may be parietal and not homologous with the similar plate in Dicynodonts. This possibility has existed in my mind all along, but what are thus probably sutures in two of our specimens have looked as much like fractures. As to the bones suspected to be nasals, I find that of the left side present in a specimen of *I. intermedius*, besides that from Barrow, but wanting in one of *I. tenuirostris*. As observed by Seeley, the absence of a bone in a fossil has little weight in evidence of its

* Origin of Genera, 1868; Hypothesis of Evolution, 1870.

non-existence, as compared with its presence in evidence of its existence. Nevertheless, its absence in so many specimens as Dr. Seeley has had the opportunity of examining renders it necessary to ascertain whether the element in question is a dismemberment of some other bone or not. And this I must leave to those who have more extended material for examination. Dr. Seeley's objections to my determination of the frontals (? nasals) are not weighty, and are anticipated in the memoir itself.

On the whole, the probabilities of the Cuvierian nomenclature of the bones of the cranial roof being correct is rather increased by Dr. Seeley's remarks, but I have not been able to discover that any one has correctly determined the squamosal, quadratojugal, opisthotic, and stapedial bones before the reading of my paper.

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2. On the Embryology of Limulus Polyphemus. By A. S. Packard, Jr., of Salem, Mass.

(Abstract.)

The eggs on which the following observations were made were kindly sent me from New Jersey, by Rev. Samuel Lockwood, who has given an account of the mode of spawning, and other habits, in the "American Naturalist." They were laid on the 16th of May, but it was not until June 3d that I was able to study them. The eggs measure .07 of an inch in diameter, and are green. In the ovary they are of various hues of pink and green just previous to being laid, the smaller ones being, as usual, white. The eggs are simple, the ovarian eggs being formed of a single cell. The yolk is dense, homogeneous, and the yolk granules, or cells, are very small, and only in certain specimens, owing to the thickness and opacity of the egg-shell, could they be detected.

Not only in the eggs already laid, but in unfertilized ones taken from the ovary the yolk had shrunken slightly, leaving a clear space between it and the shell. Only one or two eggs were observed in process of segmentation. In one the yolk was subdivided into three masses of unequal size. In another the process of subdivision had become nearly completed.

In the next stage observed, the first indications of the embryo consisted of three minute, flattened, rounded tubercles, the two anterior placed side by side, with the third immediately behind them. The pair of tubercles probably represent the first pair of limbs, and the third, single tubercle the abdomen. Seen in out-