THE COTYLOSAURIA

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The studies of Broili, and especially of Case, have furnished much welcome information concerning the Permian reptiles of America within recent years. But our knowledge of many of them is yet meager, and much obscurity yet prevails as to their rank and affinities, and especially as to their relationships with the known European and African types. The ordinal name Cotylosauria has, within the past few years, come into rather general use for many of the early stegocrotaphous reptiles to the exclusion of other terms which had previously been applied to them. A brief historical review of the origin and use of the term will be of interest.

Cope early introduced and made use of the term Theromorpha, afterward changed to Theromera, to include many of the older reptiles now recognized as quite diverse, and which he later so recognized, abandoning it. In 1880[1] he proposed the subordinal term Cotylosauria for a division of this group, founded exclusively on the Diadectidae of Texas, and based upon a real or apparent dicondylar structure of the skull. Later,[2] he expressed doubt of its validity as follows:

> I am still inclined to question whether the extraordinary characters of the cranio-vertebral articulation I have described justify the separation of the Diadectidae as a third suborder of the Theromorpha, which I have called the Cotylosauria, or whether they are not due to the loss of a loosely articulated basioccipital bone.

The two other suborders of his Theromorpha to which he refers were the Pelycosauria and Anomodontia—this latter of course in its wide sense. In 1889[3] he included in his order Theromera the following six suborders: Placodontia, Proganosauria, Parasuchia, Anomodontia, Pelycosauria and Cotylosauria. His Pelycosauria included

[1] *American Naturalist*, p. 334.

[2] *Proceedings of the American Philosophical Society*, 1882, p. 448.

[3] *American Naturalist*, p. 886.

the families Clepsydropidae, Pariotichidae and Bolosauridae; his Cotylosauria, the Diadectidae and Pareiasauridae; the Proganosauria, the Mesosauridae, Procolophonidae, Paleohateriidae, Proterosauridae, and Rhynchosauridae (equivalent, it is seen, plus the Rhynchocephalia and Choristodera, to Osborn's Diaptosauria). In 1891,[1] Cope defined the Cotylosauria, now for the first time considered an order, as including four families, the Diadectidae, Pareiasauridae, Pariotichidae, and Elginiidae. In the later publication he erected the order Chelydosauria for the Otocoelidae proposed a few years before for certain new reptiles from Texas, defining it as having the scapular arch internal to the ribs, a dermal carapace, and the temporal roof excavated posteriorly for the auricular meatus. Until this time *Pariotichus* had been included among the Pelycosauria. In 1896,[2] however, he referred one species described as *Pariotichus*, *P. hamatus*, to a distinct genus, *Labidosaurus*, which he provisionally placed among the Pareiasauridae.

In a few words, it is seen that Cope based the suborder Cotylosauria upon the Diadectidae, and not until his later papers did he unite any other American forms with it in the same group. In 1905,[3] Case brought evidence to show that the essential characters assigned to the Chelydosauria were also common to *Diadectes* and its allies, and he has withdrawn the family from the Cotylosauria to include it, with the Otocoelidae, in the Chelydosauria, leaving *Pariotichus* and certain other less well-known forms as the sole American representatives of the Cotylosauria. But this contravenes the basal rules of nomenclature. The group originally was based exclusively upon the Diadectidae, and, while we may add as many other families as we choose, we may not substract the one upon which it was alone based. The name Cotylosauria, of which Chelydosauria is purely a synonym, must accompany the Diadectidae wherever the family is placed.

With the elimination of Chelydosauria we have three ordinal terms which have been proposed for the primitive stegocrotaphous reptiles: Cotylosauria Cope (suborder, 1880, order 1891); Pareia-

[1] *Amer. Naturalist*, p. 644; *Syllabus of Lectures on the Vertebrates*, p. 68.

[2] *Proceedings of the American Philosophical Society*, p. 136.

[3] *Journal of Geology*, No. 2, 1905, p. 126.

sauria Seeley (1892);[1] and Procolophonia Seeley (1889).[2] The question of immediate interest is, in which of these two latter groups, if either, can *Pariotichus* and the other forms eliminated by Case from the Cotylosauria be placed. Its interest has led me to re-examine in the light of the recently accumulated facts concerning the older reptiles, the excellent specimen in the Chicago University collections described by Case some years ago[3] as *Pariotichus incisivus* Cope. For the general description of the specimen the reader is referred to the cited paper. By further preparation of the specimen I am able to make some additions of interest.

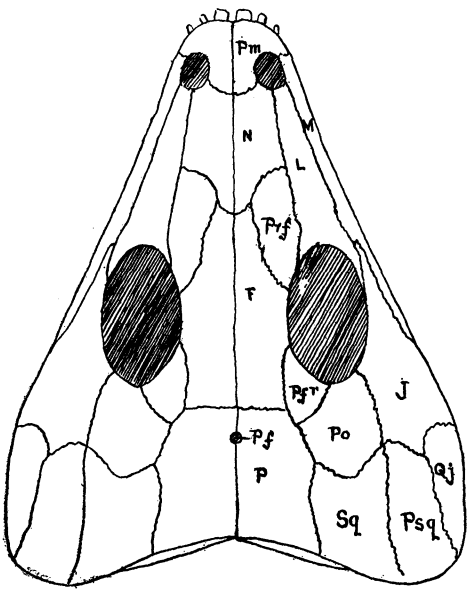

FIG. 1.—Skull of *Labidosaurus incisivus*, upper surface; one-half natural size. *Pm*, premaxilla; *N*, nasal; *M*, maxilla; *L*, lachrymal; *F*, frontal; *Prf*, prefrontal; *Pof*, postfrontal; *Po*, postorbital; *J*, jugal; *Pf*, parietal foramen; *P*, parietal; *Sq*, squamosal; *Psq*, prosquamosal; *Qj*, quadratojugal.

My determination of the upper elements of the skull (Fig. 1) made independently, agrees well with Case's. On the under surface, however (Fig. 2), I am quite unable to differentiate the pterygoids, palatines, and vomers anteriorly, they are so closely fused together. I do not feel at all sure about the distinction of the paroccipital as a separate element. The epiotics may be present, but I am not sure.

Eighteen presacral vertebrae were collected by Professor Case with the specimen, and he was inclined to the belief that this was the full number. Four of these, without rib attachments, are connected

[1] *Philosophical Transactions*, 1892, p. 106.

[2] *Ibid.*, 1889, p. 270.

[3] *Zoölogical Bulletin*, Vol. II, 1899, p. 231

yet with the sacrum and pelvis. Six are united in a series lying over the pectoral girdle, with ribs or portions of ribs attached. In addition, there are two united pairs, and two single vertebrae. Between the two series there are quite evidently several missing, since the diapophyses end abruptly with the pectoral series. From the size and shape it seems apparent that the two pairs belong here, making at least fourteen dorsals. Both of the single vertebrae have small rib diapophyses; they are also smaller in size. I have placed them in the neck in the restoration (Fig. 6). However, *Labidosaurus hamatus* has, according to Broili,[1] at least twenty-two presacral vertebrae; and *Telerpeton*, according to Boulenger,[2] twenty. It is probable, hence, that two or more vertebrae have been lost in the present specimen from in front of the sacrum. The neck could not have been longer than is represented in the restoration, perhaps not so long, since so broad and ungainly a head would have been sadly unmanageable on a slender neck. At least four presacral vertebrae bore no ribs, but I believe

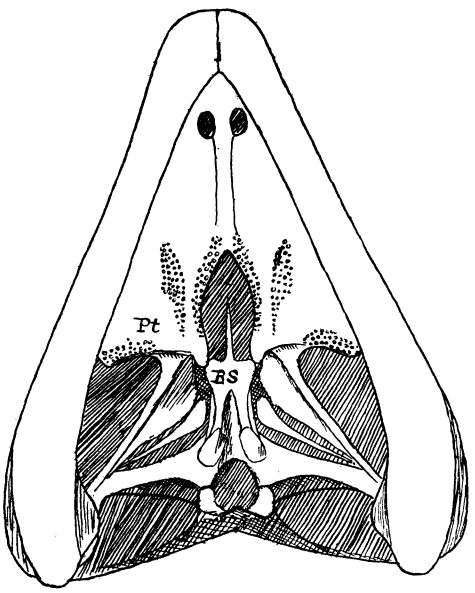

FIG. 2.—*Labidosaurus incisivus*, under surface of skull; one-half natural size. *Pt*, pterygoid; *Bs*, basisphenoid.

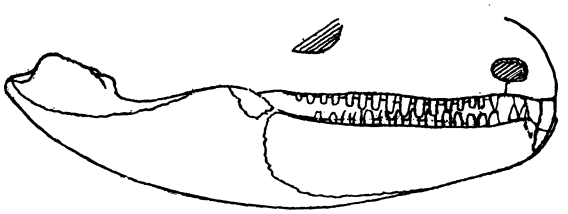

FIG. 3.—Mandible and maxillary teeth of *Labidosaurus incisivus*, one-half natural size.

[1] *Paleontographica*, 1904.

[2] *Proceedings of the Zoölogical Society*, London, 1904, p. 474.

that all the others, save perhaps the atlas, had such bones. Three caudal vertebrae are preserved together, in addition to two connected with the sacrum. They evidently bore ribs and indicate a short tail.

The pectoral girdle I am able to restore completely with assurance. The sutures between the scapula and the coracoid elements I find to be as represented in the drawing, with the exception of that between the scapula and the procoracoid anteriorly, of which I am in doubt, because of the absence of that part of the arch on the left side with

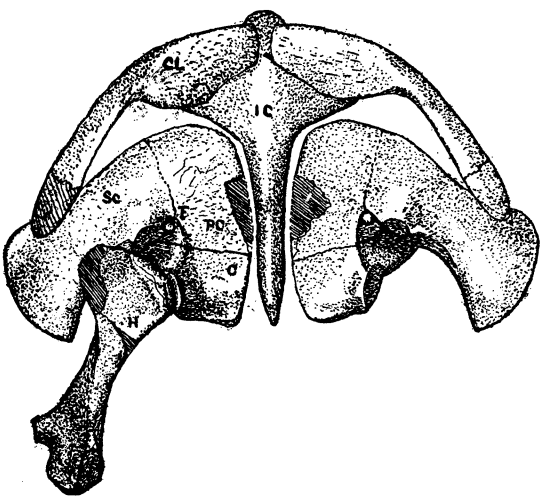

FIG. 4.—Pectoral girdle of *Labidosaurus incisivus;* one-half natural size. *I*, interclavicle; *Cl*, clavicle; *Sc*, scapula; *C*, coracoid; *Pc*, procoracoid; *F*, coracoid foramen.

its corroboratory evidence. There is a small but distinct, coracoid foramen between the procoracoid and the scapula. There is, as Case has said, no evidence of a cleithrum, nor is there any place where one could have been attached. The scapular surface of the distal extremity of the clavicle, of which the tip only is wanting, is striated, and the scapula presents a similar surface for its attachment in the position shown in the drawing. The diagrammatic position in which it is necessary to figure the arch distorts somewhat the relations of scapulae and clavicles. The distal extremity of the scapula was evidently turned dorsad at nearly a right angle with the plane of the

coracoid surface. The proximal end of the right humerus lies perfectly in position in the glenoid fossa. The distal extremity of the bone, twisted in a plane nearly at right angles with that of the proximal, presents not the slightest indication of an entepicondylar foramen, and the bone is not at all mutilated. The absence of this foramen is, however, extraordinary, since very nearly all the known reptilian vertebrates of the Permian have it, though not all, according to Cope. The thinned margin of the proximal expansion has been lost in the specimen. There is the possibility, a remote one I believe in view of the fact that the relations of the various bones of the skeleton had suffered little disturbance, that the humerus had been completely and perfectly reversed in the glenoid socket, and some indication of this reversion is furnished in that the so-called distal end agrees fairly well with the proximal end of some forms.

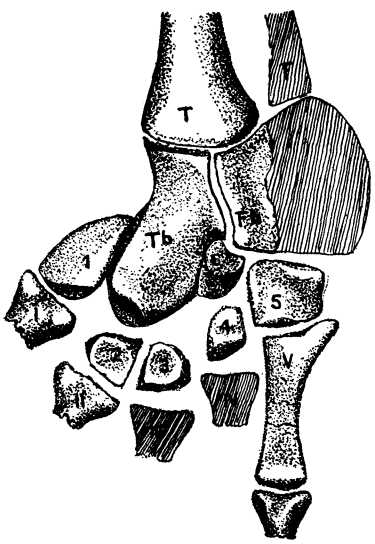

FIG. 5.—Hind foot of *Labidosaurus incisivus;* natural size. *T*, tibia; *F*, fibula; *Tb*, tibiale; *Fb*, fibulare; *C*, centrale; 1–5, distal tarsals; I–V, metatarsals.

In the structure of the feet I have no emendations to make of Professor Case's interpretations, save of the centrale of the pes. This bone I find, on removal of the bone lying over it, to be pretty well fused with the tibiale, the union shown, however, clearly in a sutural line. Broom has expressed a doubt of the structure of the feet in this specimen. There can be none. The number and arrangement of the bones of the carpus are assuredly as Case has figured them. As to the number of the phalanges in the digits I believe that they will be found to be as in *Procolophon* and *Telerpeton*, 2, 3, 4, 5, 3, or 4. The pelvic girdle in this specimen is typically that of the old reptiles, elongated, flat, plate-like pubes and ischia, closely united by suture and wholly without a thyroid foramen. It is the pelvis of *Procolophon*, *Telerpeton*, *Paleohatteria*, etc.

Briefly the important characters of this specimen may be summed up as follows:

Skull stegocrotaphous, with distinct elements; epiotic probably present; the lachrymal (postnasal of Jaekel) entering into the posterior border of the external nareal opening. Surface of skull sculptured; a pineal foramen between the parietals; orbital and nasal openings not large, the latter situated near extremity of face. Premaxillae with three teeth, the first one much elongated, the second less so. Maxillae with about sixteen teeth, inserted in a single row, with a pleurodont elevation internally, and not very different in size. Mandibular teeth in a single row, biting within the upper teeth, about seventeen in number, the front ones somewhat elongated; teeth thecodont, not transverse. Palate with small teeth in two or more rows each, inserted on pterygoids and probably palatines and vomers, dependent upon the location of the sutures. Internal nares small, situated far forward. A cordiform interpterygoidal space. Pterygoids articulating with basipterygoid processes, their dilated posterior processes united with quadrates.

Vertebrae deeply biconcave, with persistent intercentra. Coracoids and large procoracoids united by suture with scapula; a supracoracoid foramen between scapula and procoracoid. Interclavicle with an elongate posterior process and dilated anterior extremity; clavicles closely attached to interclavicle and scapula; no cleithra. Ribs functionally double-headed, attached to intercentra and diapophyses. Two sacral vertebrae. Pubes and ischia expanded, plate-like, without thyroid foramen. Caudal vertebrae with ribs. Carpus with three bones in the proximal row and four in the distal, and with two centrales; tarsus with two in proximal row, five in the distal and a partially fused centrale, possibly two. Phalangeal formula probably 2-3-4-5-3, 4.

As to the identity of our specimen I can be but a little more certain than was Case. That it does not belong in the genus *Pariotichus* is certain, since there is but a single row of teeth on maxillae and dentaries. That it is not specifically identical with *Labidosaurus hamatus* I believe is equally certain, that is if Broili has rightly identified that species, and I think that he has. It presents some differences from the species *incisivus*, as described by Cope, but it may provision-

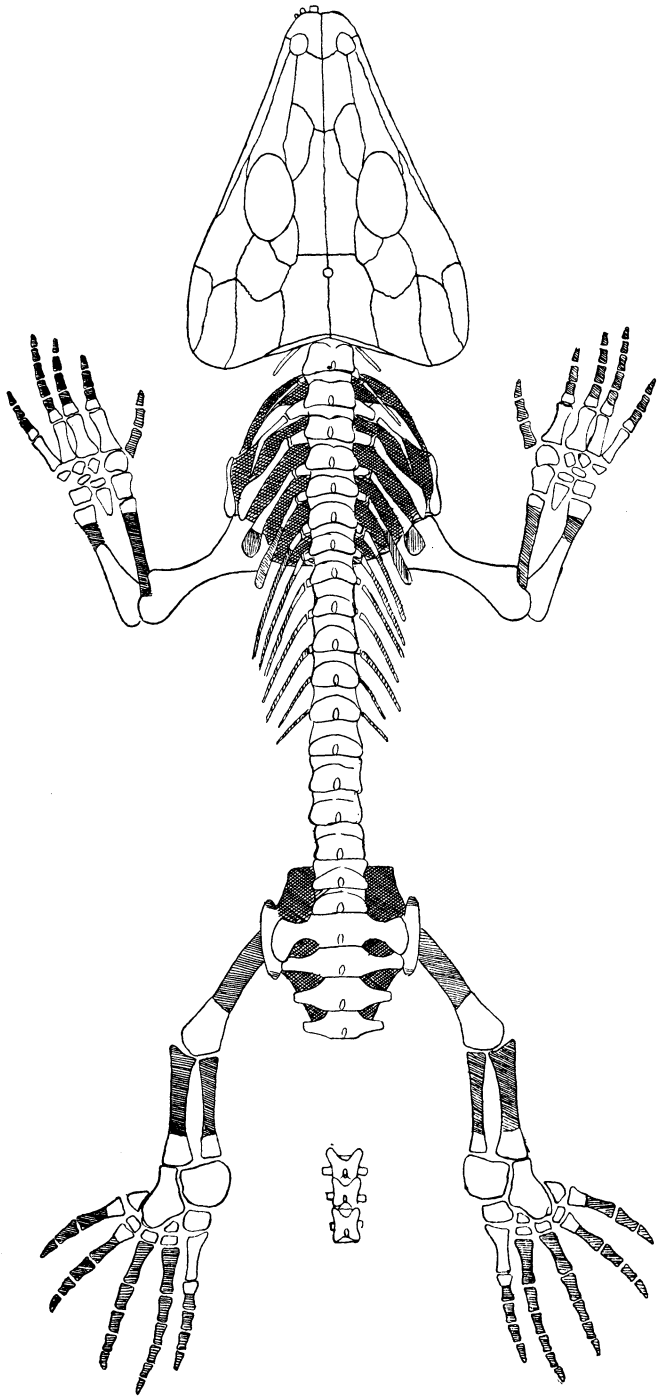

FIG. 6.—Restoration of *Labidosaurus incisivus;* a little less than one-third natural size.

ally be placed there, and in the genus *Labidosaurus* until such time as Cope's types have been examined and compared. The specific or even generic identity, however, matters little at present. The more important matter is, what relation does the form have to *Procolophon* and *Telerpeton* especially.

Boulenger has shown, forcefully I think, the relationship between *Procolophon* and *Telerpeton*,[1] about the only differences which he found being the absence of ventral ribs in *Telerpeton*. Seeley[2] and Broom[3] have, more recently, added to this the newly discovered characters of the acrodont and transverse teeth,[4] and it is on the strength of these differences, in face of the resemblances, that Broom would associate *Procolophon* with the Rhynchocephalia, *et al.*, in the superorder Diaptosauria and in the phylum Diapsida, arguing that, in any phylogenic classification the separation of the phyla should be carried back to the very beginning, even though the earliest forms may differ vastly more from the later ones than they do from those immediately preceding them. It is true that, so far, no reptile with a roofed over skull, save *Procolophon* (and of course the Chelonia) has been found to possess abdominal ribs, so commonly present among the saurocrotaphous reptiles. Indeed, of the single-arched reptiles only the Sauropterygia and Ichthyosauria have such ribs, and, carrying the argument to its extreme, Broom would unite both of these with the subclass Diapsida of Osborn, quite vitiating the original meaning of the term and requiring a new name for the modified phylum. But it is a more difficult thing to treat the Chelonia in the same way. No one has yet had the temerity to transfer the Chelonia to the Diapsida and we are forced to the inevitable conclusion that both of these reputed subclasses, the Diapsida and Synapsida, had abdominal ribs. And indeed such a conclusion is beyond dispute; certainly the oldest reptiles must have had ventral ribs and they must have been essentially Cotylosaurian in structure, for these reptiles, espe-

[1] *Proceedings of the Zoölogical Society*, London, 1904, p. 476.

[2] *Ibid.*, London, 1905.

[3] *Ibid.*, 1905.

[4] It is of interest to observe that the genera *Phanerosaurus* and *Stephanospondylus* according to Stappenbeck, have acrodont teeth placed transversely, and surely they are not also related to the Rhynchocephalia (*Zeitschrift d. deutsch. Geolog. Gesellschaft*, 1905, p. 379).

cially such forms as *Seymouria* Broili[1] are about as close to the temnospondylous amphibians, save in the palatal structure, as it would be possible to have them and still call them reptiles; unless, indeed, we accept Boulenger's rather improbable views and derive the double-arched forms from the Microsauria and the stegocrotaphous and single arched from the Temnospondyli. And here too, the Chelonia upset our best-laid schemes. Not all dinosaurs possess such ribs, and I do not think that their loss, without other important differences is of great moment. And by no means is it yet sure that the Cotylosauria, and the acleithral forms were without them. Indeed I believe that we shall find some of them with such ribs eventually.

Our "*Labidosaurus incisivus*" differs from *Telerpeton* chiefly in the sculptured skull, a character which that genus shares with *Procolophon* and *Sclerosaurus*,[2] and from *Procolophon* in that and the character of the teeth, and in practically nothing else. If *Procolophon* be admitted to a distinct order, superorder, and subclass from *Telerpeton*, what shall we do with *Telerpeton*, *Pariotichus*, *Labidosaurus*, *Elginia*, *Sclerosaurus*, etc.? They all lack the cleithrum; they are, for the most part at least, small, crawling reptiles and can hardly be united with *Pareiasaurus* nor with *Diadectes* and *Otocoelus*. Shall we erect a new order for them?

The resemblances between the pectoral and pelvic girdles of *Dimetrodon* and our present specimen are evident at a glance. But, the Pelycosauria, notwithstanding the two temporal vacuities of the skull, and its supposed membership in the Diaptosauria, have well developed cleithra, and that character must be added to the Diaptosauria as well as to the Cotylosauria and Pareiasauria!

I may add, by way of postscript, that, in a recent review of the literature of the reptilia, I find all of the older groups usually called orders have been raised in recent years by well-known writers to superordinal or subclass rank, save the Ichthyosauria and Chelonia, the two groups of all others most entitled to high rank! And most of the suborders have been elevated to orders—thirty or more. And what has been gained?

[1] *Paleontographica*, 1904.

[2] Von Huene, *Geologische pal. Abhandlungen*, X, 1902, p. 29.