PROLACERTA AND THE PROTOROSAURIAN REPTILES.

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PART II.

COMPARISONS.

Prolacerta differs from modern lizards and agrees with the Upper Permian eosuchians *Youngina*, *Youngopsis* and *Youngoides* in the following characters:

1. Quadratojugal present
2. Jugal with a long quadrate process
3. Dentition thecodont (pleuro-thecodont)
4. Pterygoids broadened and extending forward to the vomers
5. Postfrontal separate from postorbital and primitive in position and shape
6. Interparietal present (?)
7. Squamosal short and wide, postfrontosquamosal arch short and stout
8. Basioccipital short and narrow
9. Nasals extensive

Prolacerta also has the following presumably primitive characters not found in modern lizards and not yet recorded in eosuchians:

10. Exoccipitals and paroccipitals separate
11. Odontoid separate
12. All cervical vertebrae with ribs
13. Epipterygoid stout and with a quadrate process
14. Articular and prearticular separate (this point is doubtful)

Prolacerta shares with certain primitive geckonid lizards the following:

15. Vertebrae amphicoelous, notochordal
16. Cervical intercentra small and crescentic
17. All median elements of the skull roof paired
18. Stapes perforated at base (?)

Prolacerta agrees with most lizards and differs from *Youngoides* in having:

19. Streptostylic quadrate
20. Symphysis of lower jaws ligamentous (?)
21. Basipterygoid process fused with basisphenoid
22. Postorbital arch narrow

Prolacerta appears to differ from most lizards and *Youngoides* in:

23. Absence of a supratemporal bone (fused with squamosal ?)
24. Absence (or extreme reduction) of the pineal foramen
25. Presence of a reduced kinetic quadratojugal
26. Posterior process of jugal nearly reaching the quadrate

Prolacerta agrees with *Sphenodon* and *Youngoides* and differs from lizards in having:

1. A quadratojugal
4. Pterygoids which reach forward to articulate with the vomers
8. Basioccipital short and narrow

Prolacerta agrees with *Sphenodon* and differs from lizards in the following:

27. A longitudinal ridge of teeth on the palatine bones
28. Squamosal squarish with four subequal processes
29. Absence of a separate supratemporal bone (?)
30. Presence of a paired proatlas
31. Orbits large
32. Dorsal temporal fenestra nearly circular
33. Epipterygoid stout and expanded at base

Prolacerta agrees with the type specimen of *Protorosaurus speneri* in:

34. All characters of the vertebrae and cervical ribs so far as shown
35. The pleuro-thecodont insertion of the teeth (cf. Seeley 1888)
36. The general shape of the skull and the arrangement of the skull elements: elongate nasals, narrow maxillaries, shape of the frontals, and prefrontals, narrow elongate vomers with teeth, large orbit with bony sclera, slender lower jaws with splint like splenial reaching far forward, angular and surangular not extending to tip of retroarticular process

Prolacerta may differ from the type of *Protorosaurus speneri* in some of the following characters:

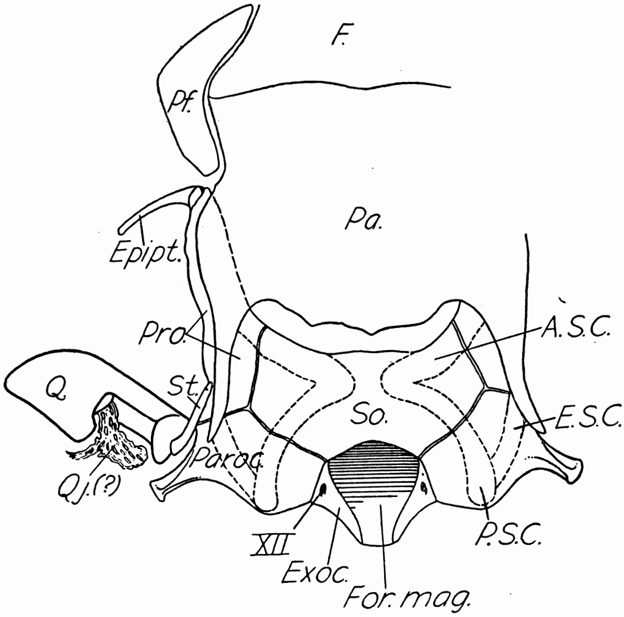

Fig. 7. Dorsal view of part of skull of *Coleonyx variegatus*, U. C. Mus. Vert. Zool. no. 26980, cleared specimen, adult, x 10. The "quadratojugal" (Qj?) occupies a recess in the quadrate similar to that of *Prolacerta.* A.S.C. = Anterior semicircular canal, E.S.C. = External semicircular canal, P.S.C. = Posterior semicircular canal; St. = Supratemporal ("Tabulare" of lizards). Nerve XII has a single internal opening and two external foramina.

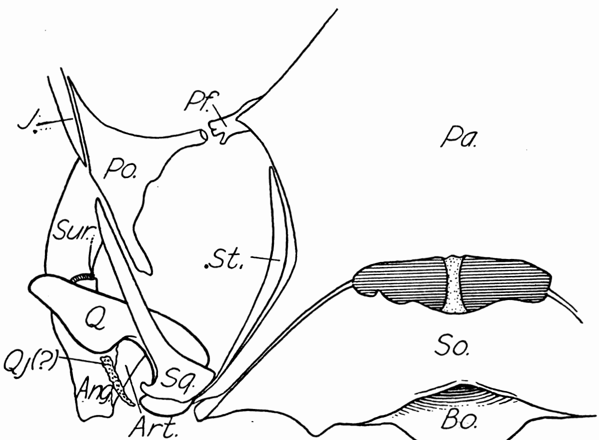

Fig. 8. Dorsal view of part of skull of *Sceloporus occidentalis*, U.C. Mus. Vert. Zool. no. 33865, cleared specimen, juvenile, x 10. The calcified tissue representing the "quadratojugal" (Qj?) occupies a position in the digastric fascia similar to the position in *Coleonyx* and other lizards.

37. Lack of a pineal foramen (?); small or absent (?) in *Protorosaurus*
38. Lack of a crest on the mid-parietal line; broken away in *Protorosaurus* (?)
39. Lack of a fenestra in front of the lacrimal; doubtfully present in *Protorosaurus*
40. Skull slightly smaller in *Prolacerta*
41. Cervical vertebrae about half the length of those in most of the known specimens of "*Protorosaurus*"

Some of these characters may now be discussed:

1. A quadratojugal has been questionably noted in skinks by Kingman (1932). Cleared specimens at hand of *Coleonyx*, *Sceloporus* and *Phrynosoma* show a small calcified "element" resting upon a mid-lateral facet of the quadrate (Text Figs. 7, 8) in about the same position as the quadratojugal of *Prolacerta*. In the more advanced lizards, *Gerrhonotus* and *Cnemidophorus* this element joins the upper head of the quadrate and lies at the origin of the quadrate slip of the digastric muscle. In all these lizards the element in question is a thin, calcified mass of somewhat indefinite form and boundaries, lying in the digastric fascia. It may well be a vestigial quadratojugal, for the similarity of its relation to the quadrate in ascalabotid lizards appears to be more than a coincidence.

2. The jugal has a short posterior process in the Cretaceous lizards *Polyglyphanodon* (Gilmore 1942) and *Macrocephalosaurus* (Gilmore 1943). The only recent lizard in which I have seen such a process is the xantusiid *Lepidophyma*, where the process is also short.

3. Thecodont or pleuro-thecodont teeth are present only in the embryos of modern lizards. The Cretaceous *Chamops* and the mosasaurs retain them. The alveoli in *Prolacerta* are deeper on the buccal than on the lingual side of the jaws and the old teeth are fused to the margins of the alveoli.

4. The extent and shape of the pterygoids in *Prolacerta* resemble *Youngoides* and *Sphenodon* more closely than the lizards. In most reptiles, including *Sphenodon* and the lizards, a flange is developed along the juncture of the pterygoids and ectopterygoids, to guide the lower jaws into exact occlusion. This flange seems to be very weakly developed in *Prolacerta* as well as in *Youngoides*.

The pterygoids of *Iguana*, according to Lakjer (1927) and Olson (1936), meet the vomers. Olson says this union is concealed in the adult by ventral overgrowths of the median wings of the palatines. The only *Iguana* skull immediately available to me shows a dorsal overlap of the palatines upon the pterygoids and the pterygoids are widely separated from the vomers.

Lakjer (1927) announces a "separate" element which he has named "hemipterygoid." This is described and figured as extending from the tip of the true pterygoid to the vomer along the inner margin of the palatine, in an embryo of *Iguana tuberculatus*. Lakjer also finds a so-called hemipterygoid in a young *Anolis cristatellus* and other forms. I have at hand cleared specimens of embryo *Phrynosoma* and young *Sceloporus*. Here the pterygoids are widely separated from the vomers and the median parts of the palatines are not separate from the outer. The only evidence of an "hemipterygoid" is a slight longitudinal slit extending a short distance into the palatines.

Olson's figure of *Youngoides* shows no teeth on the vomers, but there is an extensive anterior tooth bearing process of the palatine. These teeth correspond in position to the teeth on the ridges of the vomers in *Prolacerta* so it may be that Dr. Olson has not correctly placed the sutures between the palatines and the vomers. With this exception the palatal resemblances bring *Prolacerta* closer to *Youngoides* than to any other reptile in which the palate is well known.

The palate of *Prolacerta* will also bear close comparison with *Sphenodon*. The elongate, laterally placed internal nares, the meeting of the wide vomers along the midline, the anterior extension of pterygoids, the peculiar shape of the palatine, the course of the sutural contact of the palatine and vomer, and the presence of longitudinal, tooth bearing ridges on the palatines and vomers, are similar in *Sphenodon* and *Prolacerta*. In fact, the resemblances in the palate alone would indicate closer relationship to *Stenaulorhynchus* and *Sphenodon* than to the lizards. The nature of the union of pterygoid and quadrate, the presence of a small pterygo-palatine fenestra (not found elsewhere among reptiles), the shape of the ectopterygoids, the narrow interpterygoid space, the small basioccipital, the shape of the squamosal, the large orbit and the circular shape of the supratemporal fenestra are further resemblances to *Sphenodon*.

Lakjer's (1927) studies on the shape and structure of the internal choanae of lizards are of interest. From comparison of palatal structures of various reptiles he would derive the lizards from the rhynchocephalians and these in turn from cotylosaurs. He divides the lizards into: I *Palaeochoanatae* (Agamidae, Iguanidae, Helodermatidae, Anguidae, Geckonidae, Pygopodidae and Chamaeleontidae) in which the choanae and palatal bones are of a simpler "more primitive" type, more similar to *Sphenodon*, than are the: II *Neochoanatae* comprising the skinks, teiids, zonurids, lacertids, gerrhosaurids, varanids and amphisbaenids. By these criteria the palate and choanae of *Prolacerta* appear to be similar to *Sphenodon*; and more similar to agamids and iguanids than to other lizards.

5. Postfrontals in lizards are often larger than in *Prolacerta*, and this occurs secondarily among the Scincidae. The primitive diapsid position, shown in *Prolacerta*, is modified in recent lizards. Primitive relations are most nearly preserved in *Polyglyphanodon* and *Lepidophyma* where the parietals are narrow anteriorly as in *Prolacerta*. Owing to the anterior expansion of the parietals in modern lizards, the postfrontal acquires a concavity along its inner margin. This is foreshadowed in the Upper Jurassic *Ardeosaurus* which Broili (1938) believes to be related to the Xantusiidae.

6. An "interparietal" is described by Kingman (1932) in recent skinks. He figures this element as a nodule lying in or above the tissue connecting the mid-dorsal border of the supraoccipital with the parietals.

7. If previous observations on eosuchians are correct, the squamosal of *Prolacerta* may represent the fused supratemporal (=tabulare of Broom) and the squamosal of *Youngina*, *Youngoides* and *Youngopsis*. This fusion may indicate that *Prolacerta* is not directly in the line of ancestry of the lizards. But such fusions may not be significant.

8. A short, narrow basioccipital occurs in *Youngoides* and *Sphenodon* as well as in *Prolacerta*. The condition in *Prolacerta* strongly suggests that of *Youngoides* and the tubera are weak in both.

9. The great extent of the nasals is another important point of resemblance between the Permian eosuchians and *Prolacerta*. These bones are never so well developed in lizards, even in *Ameiva*, mosasaurs, and others with an elongate antorbital region.

Characters 15-18 are found in the geckos, among modern lizards. All the skull elements are paired in *Youngina*, *Youngopsis* and *Youngoides*, and in some modern geckos. The stapes is perforate in the geckos *Pachydactylus*, *Hemidactylus* and *Terentola; Coleonyx* (Fig. 9) has a large fenestra. These are the only lizards in which this primitive character is known to occur.

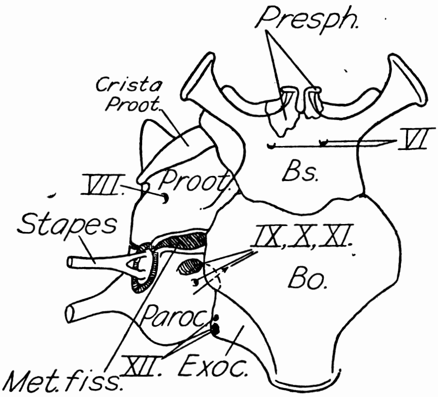

Fig. 9. Ventral view of part of skull of *Coleonyx variegatus*, Mus. Vert. Zool. no. 26980, cleared specimen, adult, x 10. The stapes has a larger fenestra than in other known geckos. The metotic fissure (Met. fiss.) remains open. Nerves IX, X and XI have three foramina, the anterior also contains the perilymphatic sac. There is no parasphenoid. The paired presphenoid (Presph.) is separated by suture from the basisphenoid.

19 and 20. The lack of a direct articulation between the jugal and the quadrate, and the loose articulation of the quadrate with the squamal and quadrotojugal in *Prolacerta* makes it apparent that the skull was streptostylic, but not exactly as in lizards. The ligamentary symphysis of the lower jaws and the long digastric process of the angular is further evidence of streptostyly. In the face of so many obvious resemblances to *Youngina* and *Youngopsis* one might well hesitate to apply the criterion of streptostyly so strictly as to exclude *Prolacerta* from the eosuchians. *Prolacerta* is the earliest known streptostylic reptile and illustrates the way in which complete streptostyly probably arose, with the quadratojugal itself involved in the kinetism.

24. The pineal foramen is so variable in lizards (cf. Camp 1923, p. 394) that its apparent absence in *Prolacerta* may not be significant.

25. The quadratojugal was apparently movable along with the quadrate but in a slightly different direction. With a fore and aft movement of the foot of the quadrate, the quadratojugal would have moved dorsally and ventrally; at the same time its lower end would swing fore and aft in a short arc where it is loosely attached to the lateral margin of the quadrate.

Prolacerta seems to illustrate an early stage of streptostyly in which the initiation of movement in the quadrate has accompanied an equivalent movement in the reduced quadratojugal.

26. The slender posterior process of the jugal, which approaches but does not join the quadrate and quadratojugal seems to be another character intermediate between eosuchians and lizards. A similar posterior process of the jugal is also found in *Thalattosaurus* and the general similarity of the temporal region in *Thalattosaurus* and the eosuchians seems to indicate relationship between these groups.

27-33. The similarities between *Prolacerta* and the rhynchocephalians serve to emphasize their relationships and support the view (Broom 1922; and Huene 1938b) that the rhynchocephalians as well as the lizards are derived from Permian eosuchians, (see also points 1, 4, 8, 15-18, and 23).

Comparison with Tangasaurus.—*Prolacerta* seems to resemble *Tangasaurus* (Haughton 1924, 1929; Huene 1926b) in its amphicoelous, notochordal vertebrae, presence of cervical intercentra, unkeeled atlantal intercentrum, small basioccipital with tubera, basisphenoid with divergent posterior crests and prominent basipterygoid process, slender, elongate parasphenoidal rostrum, interpterygoid vacuity, at least one long row of large teeth on pterygoid, slender lower jaws with elongate retroarticular process, and stout curved first ceratobranchials.

The vertebrae in *Tangasaurus* are smaller and shorter, the neck is much shorter, the basioccipital tubera are more prominent, and the ceratobranchials are larger.

What remains of the dorsal skull roof in *Tangasaurus* is sufficiently like *Prolacerta* to be interesting. The frontals are narrow, the parietals are broader and form a squarish plate bounding a circular, closed temporal fenestra. The specimens preserved in the Paris Museum are figured by Piveteau (1926, Pl. IX, Figs. 1 and 2).

My own sketches of these specimens are shown in Text Figs. 10 and 11. The impression in Text Fig. 10 is probably the ventral surface of the skull roof. The skull of *Tangasaurus* is, of course, imperfectly known.

Fig. 10. Ventral view (?) of skull roof of *Tangasaurus menelli,* from a plaster impression in the Museum d'Histoire Naturelle, Paris, x 1, (cf. Piveteau 1926, pl. IX, fig. 2).

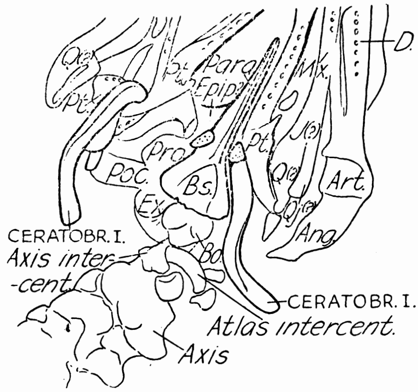

Fig. 11. Palatal view of part of skull of *Tangasaurus menelli,* from plaster impression, x1, (cf. Piveteau 1926, pl. IX, fig. 1).

34-41. *Comparison with Protorosaurus.*—The cervical regions of *Protorosaurus speneri* (Meyer 1856, Pl. 1, Fig. 1: Seeley 1888; and Huene 1926a) and *Prolacerta* will bear scrutiny. The cervical vertebrae are nearly identical and the cervical ribs as well, except that von Meyer has described the ribs of *Protorosaurus* as single headed. The division between the cervical rib heads in *Prolacerta* is weak and such a division may have been undetected in *Protorosaurus*. *Gracilisaurus* (Weigelt 1930), an apparently related genus, has bicipital ribs.

The centra are biconcave, elongate, and compressed below in *Protorosaurus* and *Prolacerta* and they both show ventral, arched muscle scars. The axis is shorter than the next three centra, and the fourth and fifth centra are the largest in each genus. The neural arches are nearly as long as the centra, especially on the axis, and their heights are less than the diameters of their centra. The neural arches decrease in length toward the rear. The zygapophyses are large, elongate, and those on the fifth vertebra are the longest. The diapophyses are small and occur at the extreme anterior margin of each centrum.

The post-axis intercentra are very small. Ribs occur on all the cervicals. The anterior ribs are extremely long and needle-like, and those behind become slightly expanded below the tuberculum.

The skull of the type of *Protorosaurus speneri* is best described by Seeley (1888). Its outlines indicate a long, low muzzle, slender jaws, and posterior orbit—large in *Gracilisaurus* and provided with sclerotic plates in both genera. The general outlines and proportions are similar to *Prolacerta*. There are many points of striking similarity, so there can be little question as to the close relationship of *Protorosaurus* and *Prolacerta*.

The teeth are sharp, single pointed, and slightly recurved in both reptiles. The adult teeth are fused to the margins of their sockets with more of the tooth base exposed lingually than buccally. The vomers bear teeth in both forms. The shape of the visible skull elements is much the same, the lower jaws are similar.

There is a possibility of further comparison between *Protorosaurus* and the skeletal parts shown in eosuchians.

In *Youngina* Broom (1922, 1924) has found a slender tibia and a tarsus somewhat similar to *Protorosaurus* in the disposition of the elements. There is, however, a fifth tarsale in *Youngina*, not apparent in *Protorosaurus*. The humerus of *Youngina* is also similar in shape. But there was an entepicondylar foramen in *Youngina* and *Palaeagama* (Broom 1926) not shown in von Meyer's figures of *Protorosaurus*. According to Peyer (1937) there are no humeral foramina in *Macrocnemus* and *Tanystropheus* which Peyer regards as related to *Protorosaurus*.

Weigelt (1930) refers to the entepicondylar foramen found by Etzold in *Protorosaurus*. He also calls attention to the *Sphenodon*-like shoulder girdle of his *Gracilisaurus*. In *Gracilisaurus* the cervical vertebrae and ribs are like those of *Protorosaurus*. The frontal bones are deeply sculptured, and the coracoid is single.

Prolacerta then closely resembles *Protorosaurus* and *Gracilisaurus* in the characters available for comparison, and these genera should be placed in the same general group. This could be expressed by mergence of the Protorosauridae with the "Eosuchia." Peyer (1937) and Huene (1938a) have already noted resemblances between some of these forms and Welles (1943) indicates the rather wide separation between *Protorosaurus* and *Araeoscelis*. Welles also has suggested placing *Protorosaurus* in the Eosuchia.

It would seem preferable to substitute Huxley's name *Protorosauria* for Broom's Eosuchia. Eosuchia was proposed later; furthermore the original genus *Eosuchus* is a crocodilian. "Eosauria" might be suggested but *Eosaurus* has turned out to be an amphibian.

SYSTEMATIC POSITION.

A. *Prolacerta* retains the following primitive reptilian characters:

Median elements of skull roof all separated by suture, brain case largely membranous, external nares anterior and paired, epipterygoid with a quadrate process, quadratojugal present, vertebrae notochordal, intercentra present, ribs on all cervical vertebrae, ribs bicipital, no cranial osteoderms.

B. The upper and lower temporal fenestrae of *Prolacerta* place it in the subclass Diapsida, although the jugal-quadratojugal arch is incomplete.

C. The skull, dental and vertebral characters of *Prolacerta* relate it most closely to *Protorosaurus*.

D. *Prolacerta* agrees with *Youngina*, and *Youngopsis* (Broom 1936, 1937, Olson and Broom 1937) in the arrangement of the elements of the skull roof and jaws. The palate is similar to *Youngopsis* and the posterior palatal elements resemble those of *Tangasaurus*. These may now be placed in the superorder Protorosauria (=Eosuchia).

E. *Prolacerta* possesses a streptostylic quadrate and in this respect agrees with the Squamata, and is probably ancestral to the lizards, in a general way.

F. The Squamata must then be regarded as diapsids rather than parapsids, despite their lack of a lower temporal arch.

G. *Prolacerta* resembles *Sphenodon* and the rhynchosaurians in the shape of the squamosal, the fusion or loss of the supra-temporal, the forward extension of the pterygoids and in other features. This would justify derivation of the Rhynchocephalia as well as the Squamata from the Protorosauria.

H. *Prolacerta* seems possibly to lie near the point of divergence of the Rhynchocephalia from the Protorosauria. Its concert of characters seems to place it in the Protorosauria (=Eosuchia), and within the family Protorosauridae. It cannot be directly ancestral to the rhynchocephs because of the break in the lower temporal arch and the freeing of the quadrate.

I. The Thalattosauria have a slender posterior jugal process which probably did not reach the quadrate or quadratojugal. The structure of the two temporal arches and the position of the supratemporal bone may indicate derivation from the early Protorosauria.

J. *Araeoscelis* could be regarded as an example of an early Permian ancestor of the later "Parapsida" and the Diapsida. Resemblances to *Protorosaurus*, as well as to the Sauropterygia, appear to be present. The position of the ichthyosaurs is extremely doubtful.

K. Parrington (1935) has assigned *Prolacerta* to the "Theocodontia." This evidently follows Watson's and Smith-Woodward's use of that term in the last edition of Zittel, where the Eosuchia are placed in Theocodontia together with the Pelycosimia, Parasuchia, and Pseudosuchia. Owen (1860) includes the following "types" in his "Order VII, Thecodontia": *Thecodontosaurus* and *Palaeosaurus* from the Upper Triassic near

Bristol, *Cladyodon* of Warwickshire "with which, probably the Belodon of the Keuper Sandstone of Wirtemberg is generically synonymous," and *Bathygnathus* Leidy "which is probably a member of the present order which seems to be a forerunner of the next Order VIII Dinosauria."

So, Owen evidently intended his Thecodontia to include the archosaurian Pseudosuchia+Phytosauria (= Huxley's Parasuchia). If the term Theocodontia is to be retained it may be better not to include therein the Protorosauria (=Broom's "Eosuchia"). The Archosauria may then be conveniently retained as a group equivalent in rank to the Lepidosauria.

L. The earliest and most primitive known archosaurs appear to be the lower Triassic genera *Proterosuchus* and *Chasmatosaurus*. *Proterosuchus* is imperfectly known and it is possible that the two belong to the same genus. Both have a similar dentigerous pattern on the palate. The teeth are fused to the alveoli and have been described as "acrodont." It might be desirable to restrict the term acrodont to those types, such as rhynchocephalians and Agamidae, in which there is a higher state of fusion accompanied by a loss of tooth replacement in the adult. In Proterosuchidae the replacement teeth appear to be successional. All told, the insertion is of course not strictly thecodont and appears to be of the same type to be seen in *Prolacerta* and *Protorosaurus*.

The resemblances between the Proterosuchidae and *Prolacerta* and *Youngina* also include the presence of a short row of teeth on the transverse process of the pterygoid; similar relations between the vomers, the palatines and the pterygoids; similarly shaped pterygoids; narrow interpteryoid space; and elongate, rod-like parasphenoidal rostrum.

The skull of *Chasmatosaurus* differs from the lepidosaurs in having an antorbital fenestra as well as a phytosaur-like bony case around the forebrain. Laterosphenoids and orbitosphenoids are presumably present. There is a small interparietal bone in *Chasmatosaurus* but the tabular has not been recognized.

Huene originally regarded *Erythrosuchus* as the chief example of his new order Pelycosimia. Later this group was reduced to the rank of a superfamily, with the invalid name "Pelycosimioidea," to include all the known Pseudosuchia. For the present it might be preferable to separate the Pseudosuchia into at least two main groups: (1) the Aëtosauroidea to include *Euparkeria* and the armored stagonolepids, and (2) the

Proterosuchoidea (new name) to include the Erythrosuchidae. The Proterosuchidae appear to have been derived from the Protorosauria, theoretically from an early form such as *Youngina*, in which the lower temporal arch and quadrate are quite intact.

RELATIONSHIPS OF PROTOROSAURIA.

The phylogeny of the Protorosauria might be expressed as in the accompanying diagram (Text Fig. 12).

A suggested classification based on this phylogeny would be:

Class Reptilia.
- Subclass Anapsida.
  - Order Cotylosauria.
  - Order Testudinata.
- Subclass Synapsida.
  - Order Pelycosauria.
  - Order Therapsida.
- Subclass Parapsida.
  - Infraclass Araeoscelidia (possibly including the Trilophosauridae).
  - Infraclass Synaptosauria (doubtful relationships).
  - Infraclass Ichthyopterygia (doubtful position).
- Subclass Diapsida.
  - Two or more temporal fenestrae (lost in Squamata).
  - Infraclass Lepidosauria, Haeckel 1868 (=Tocosauria, Haeckel 1870, partim).
    - Primitively with two temporal fenestrae, no antorbital vacuity, and a supratemporal bone; tabulare absent; laterosphenoids reduced or absent; pineal foramen usually present.
    - Superorder Protorosauria, Huxley 1871 (=Eosuchia+Trachelosauria, and Protorosauria of Williston, partim). Quadrate usually fixed; usually with a supratemporal bone; a quadratojugal.
      - Order Prolacertiformes (=Eosuchia, s.s., Broom 1914, Haughton 1929, Huene 1926b Protorosauridae;=Prolacertilia, partim, Huene 1940).
        - Nares terminal, a lower temporal arch. Includes: Protorosauridae, Saurosternidae (=Younginidae), Tangasauridae.
      - Order Trachelosauria (Broili and Fischer 1917; Peyer 1937).
        - Tanystrophaeidae.
        - Nares dorsal; apparently no lower temporal arch.
      - Order Thalattosauria (position uncertain).
        - Limbs in the form of paddles, palate narrow, teeth acrodont.

Order Acrosauria (position doubtful, cf. Broili 1926).
Pleurosauridae.

Superorder Rhynchocephalia.

Quadrate fixed; a quadratojugal; no separate supratemporal bone.

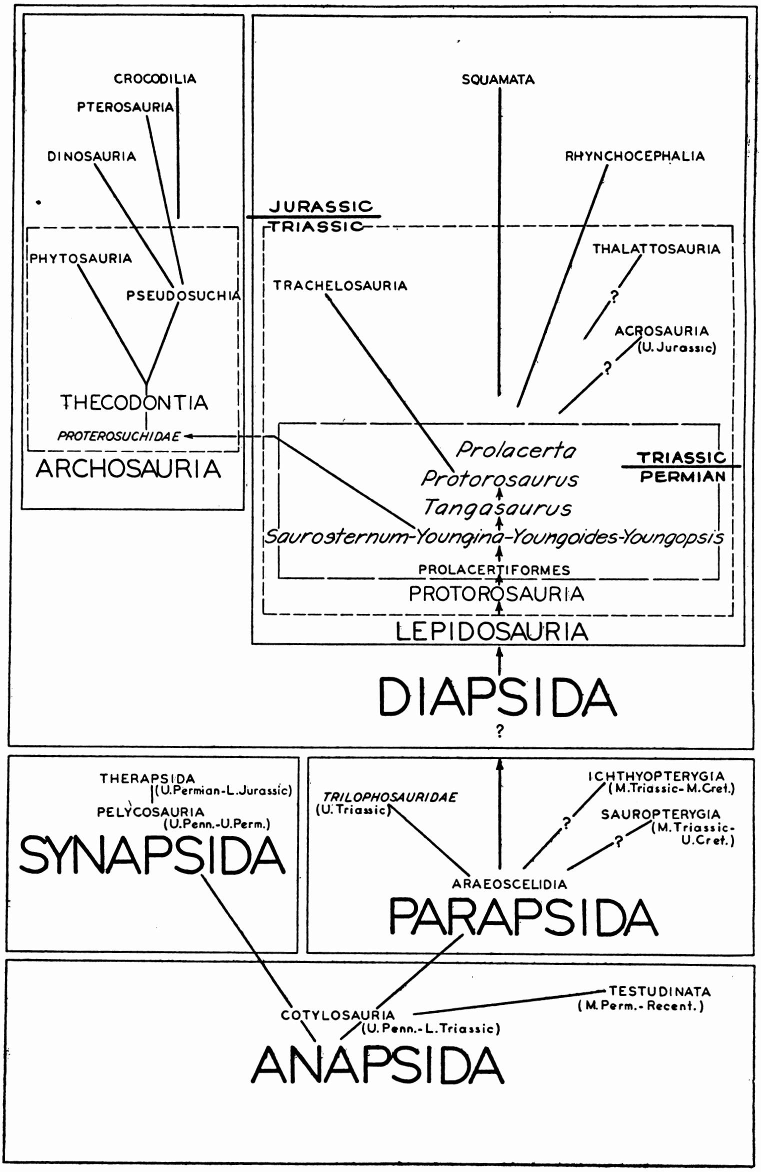

Fig. 12. Phylogeny and relationships of the Protorosauria.

Superorder Squamata.

Streptostylic quadrate; no ossified quadratojugal, supratemporal commonly present.

Infraclass Archosauria.

Primitively with two temporal fenestrae and an antorbital vacuity; supratemporal absent; tabulare (or supratemporal?) present in Phytosauria; laterosphenoids extensive; pineal foramen usually absent.

Superorder Thecodontia.

Order Pseudosuchia.

Superfamily Aëtosauroidea.

Superfamily Proterosuchoidea.

Order Phytosauria.

Superorder Crocodilia.

Superorder Dinosauria.

Superorder Pterosauria.

AGE RELATIONS AND DISTRIBUTION.

The *Lystrosaurus* zone in the Karroo Series of South Africa has usually been considered as Lower Triassic in age. Elements of the fauna of this zone are widespread (Huene 1940a). *Lystrosaurus* and *Chasmatosaurus* occur together in Central Asia (Sinkiang) as well as in South Africa. Dr. Philipp Yuan, who collected the Asiatic material, has told me of a small, undescribed skull which was being studied by Dr. Ting-pong Koh. This specimen was taken to Munich and is mentioned by Huene as "gen. et sp. nov. Prolacertiliorum," indicating its resemblances to *Prolacerta.*

A combination of three "South African" elements in the Lower Triassic or Upper Permian of Central Asia would be noteworthy. An extreme western occurrence of *Lystrosaurus*, is at Orenburg province, in the southern Urals, 45 km. southeast of the town of Orenburg on the Donguz River in beds of "continental Lower Triassic," (Efremov 1938). Forms similar to *Chasmatosaurus* are reported in beds farther west in Russia (Huene 1940b). *Lystrosaurus* has also been somewhat doubtfully identified from India.

Absence of the *Lystrosaurus* fauna from Western Europe makes it probable that a hiatus, presumably the Uralian seaway, traversed European Russia from north to south and prevented the land faunas from mingling during this time. Some land or shallow water connections between Africa and Central Asia were evidently maintained across the Tethys.

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