

THE CONSTITUTION OF THE THECODONTIA.

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ABSTRACT.

The Thecodontia (Trias) are the key-order for all Mesozoic Archosauria. They have been divided into three suborders: Phytosauria, Pelycosimia, Pseudosuchia. From new South American genera and from a revision of *Stagonolepis* from Elgin the author recognized that the Stagonolepidae do not belong to the Phytosauria, but to the Pseudosuchia. Further the Stagonolepidae are the nearest relatives of the Pelycosimia, they form the bridge between Pelycosimia and other Pseudosuchia. Consequently but two suborders constitute the Thecodontia: Phytosauria and Pseudosuchia. This is shown by a seemingly more natural system than before.

Recently the author had again an opportunity to deal with the Thecodonts during his study of some good material he collected in southern Brazil a few years ago. Not only the new forms, but also several of the known genera were restudied. The general results are given here. The author has a strong impression that his present conception of the order is much more natural and simple than it seemed to be in the former shape. This order at the same time is the key-order for the later Mesozoic Archosaurians.

First, definitions are given of the single groups which have been described and afterwards they will be valued.

PHYTOSAURIA.

Long snout formed by praemaxillae. Praemaxilla with posterior border resting upon maxilla. Nares in most primitive forms quite or partly in front of praeorbit; choanae in such forms about the middle of the length of the maxillae (especially *Mesorhinus* of Middle Bunter); in all more advanced forms the external and internal narial openings lie far backward from snout. Nasals short and small. Supratemporal opening in advanced forms at and even below posterior edge of dorsal roof of skull. No supratemporal. Postpalatal opening very small except in *Mesorhinus*. In all advanced forms neural part of skull much shortened, also base of skull very much so (not much in *Mesorhinus*).

Twenty-five praesacral vertebrae (*Machacroprosopus*); two sacrals. Cervicals short. Coracoid not perforated, but anterior border broadly incurved. Scapula slender. Interclavicle dagger-like. Acetabulum closed. Posterior spine of ilium much larger than anterior. Pubis short and broad.

Ischium also distally broad. Ulna with olecranon. Digits 1-4 increasing in length, 5th shorter, stronger, and directed more laterally. Femur with slight fourth trochanter in high position. Fibula with distal end broader than proximal, with strong muscular attachment above midlength. Fibulare with process. Abdominal ribs present. Heavy dermal scutes, in some cases long, narrow plates in transverse double rows, in other cases the scutes are more scale-like in shape.

Occurring from Middle Bunter up to the Rhaetic, only in the northern hemisphere.

PELYCOSIMIA.

Praemaxilla medium size or small, its posterior process resting upon maxilla. Nasal long and narrow. Nares at the end of the snout, internal openings large and on anterior end of palate (between anterior extremities of the maxillae). Postpalatal openings of normal size. Distal end of quadrate directed backward. No supratemporal. Supratemporal opening normally on dorsal roof of skull. Neural part of skull and skull base not shortened. In oldest form, teeth also on the pterygoid. Jaw teeth in oldest form acrodont, but even there the premature teeth are thecodont; all other Thecodonts have thecodont teeth.

Two sacrals. In oldest form, long cervical vertebrae, but except for this, they are short. Coracoid perforated. Acetabulum closed. Pubis short and broad, directed downward. Ischium broad. Femur nearly the shape of Paleozoic forms, but bridging over to the Phytosaurs. Three elements in proximal row of tarsus. Fibulare with process. Abdominal ribs present. Dermal scutes not known.

Lowest to Middle Trias in South Africa and Central Asia.

STAGONOLEPIDAE.

Praemaxilla small with long posterior process resting upon maxilla. Nasal long and narrow. Nares at the end of snout. Internal narial openings large and on anterior part of the palate (between the middle of the maxillae). Postpalatal opening of normal size. Distal end of quadrate directed more or less backward. No supratemporal. Supratemporal opening normally in dorsal roof of skull. Neural part of skull and base of skull not shortened.

Twenty-five praesacral vertebrae and two sacrals. Cervical vertebrae short. Coracoid perforated. Scapula slender. In-

terclavicle dagger-shape. Clavicles rather weak. Acetabulum closed. Pubis longer than wide. Ischium with distal peduncle not broadened. Femur reminds one of that in *Pelycosimia*. Fibula with strong prominence above middle. Two elements in proximal row of tarsus. Fibulare with process. Perforation in intermedium. Metatarsal V hammer-shaped and shorter than the preceding ones (*Chirotherium*). Abdominal ribs present. Armor in cases full and heavy (*Stagonolepis*, *Desmatosuchus*) with long and narrow transverse plates in double rows on back, in other cases (*Prestosuchus*) incomplete; double rows of dorsal, paramedian scale-like scutes on back.

Middle Trias to lower Upper Trias, Europe, North and South America, East Africa, India.

OTHER PSEUDOSUCHIA.

Small praemaxilla with posterior process resting upon maxilla. Nasal long and narrow. Nares at the snout. Internal narial openings large and on anterior part of palate (between the middle of the maxillae). Postpalatal opening of normal size. Quadrate movably articulated with squamosal. No supratemporal. Supratemporal opening normal. Neural skull and base of skull not shortened.

Mostly 25 praesacral vertebrae and two sacrals, except for instance in *Scleromochlus* four sacrals, of which the two anterior ones are specialized dorsals, in front of those are still 25 praesacrals, the last sacral is the heaviest, showing that the third and fourth are the original sacrals. Coracoid perforated. Scapula slender or broad. Interclavicle dagger-shaped. Acetabulum closed. Pubis broad or narrow and elongated, directed downward. Ischium distally widened or with peduncle. Extremities more or less slender. Fifth digit in manus and pes shortened, stout, and directed laterally. Abdominal ribs present. Armor differing in weight or nearly or quite missing.

Middle to Upper Trias, Europe, North America, South Africa.

The essentials of the foregoing definitions would be: *Phytosaurs*: Long snout formed by praemaxillae. Narial openings far backward; choanae the same. Neural skull shortened. Coracoid not perforated, but upper border with wide incision. *Pelycosimia*: Small praemaxilla. Narial opening at end of snout; choanae in anterior part of palate. Neural skull not

shortened. Coracoid perforated. Three tarsals in proximal row. *Stagonolepidae*: Small praemaxilla. Narial opening at end of snout; choanae in anterior part of palate. Neural skull not shortened. Coracoid perforated. Ischium and pubis

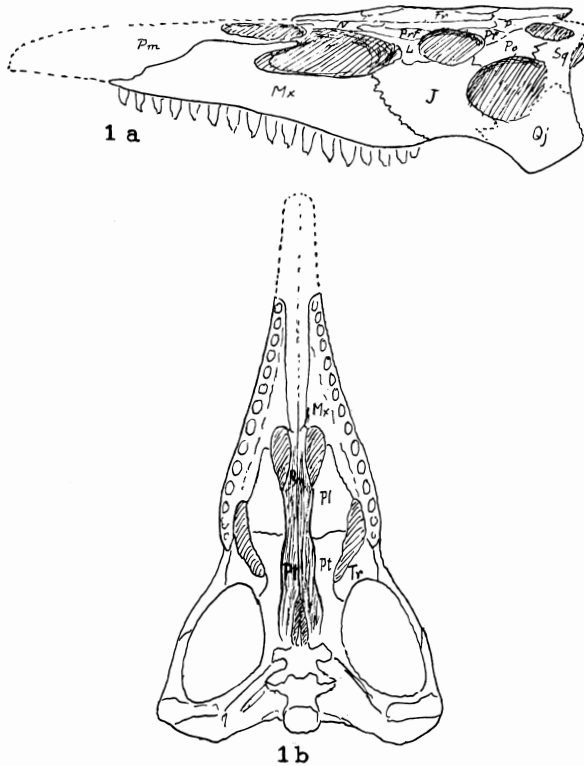


Fig. 1. *Mesorhinus*, the most primitive Phytosaur; a, side view; b, palatal view. Fr, frontal; J, jugal; L, lacrymal; Mx, maxilla; N, nasal; P, parietal; Pf, postfrontal; Pl, palatine; Pm, praemaxilla; Po, postorbital; Prf, prefrontal; Pt, pterygoid; Pv, prevomer; Qj, quadratojugal; Sq, squamosal; Tr, transverse; about 1/5 natural size. (From Jaekel.)

specialized as in certain Archosauria. Two tarsals in proximal row. *Other Pseudosuchia*: Small praemaxilla. Narial openings at end of snout; choanae in anterior part of palate. Quadrate movable. Neural skull not shortened. Number of praesacral and sacral vertebrae can be enlarged. Coracoid perforated, in some cases specialization of girdles and extremities. Two tarsals in proximal row.

From the sense of these definitions it becomes clear, that the

Phytosaurs are a group by themselves and the three other units form the other half of the Thecodonts. So the order includes but two main groups, the Phytosauria and the Pseudosuchia.

The Stagonolepidae are not part of the Phytosauria, but

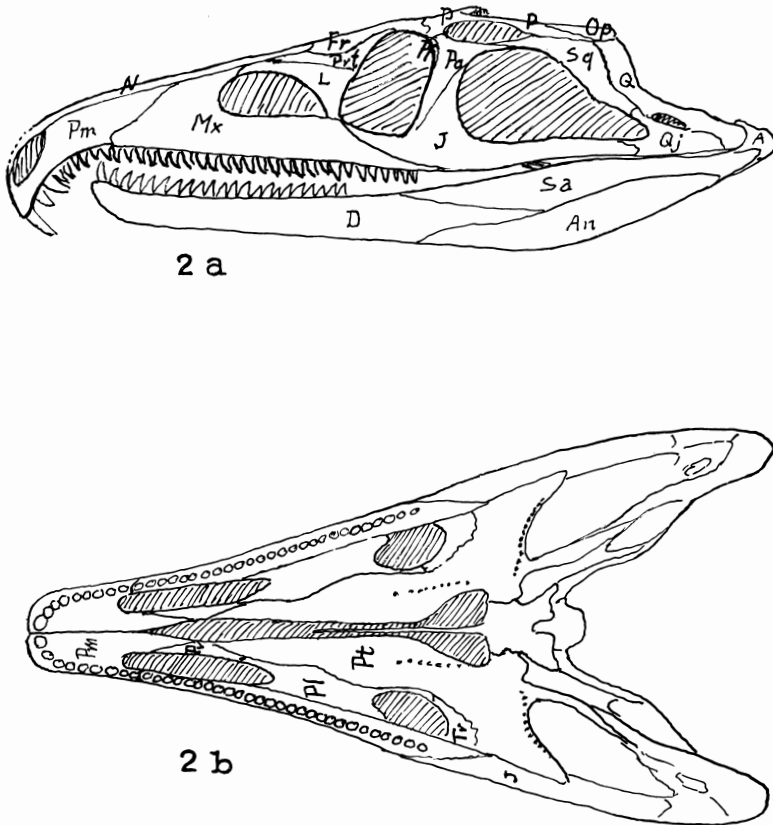


Fig. 2. *Chasmatosaurus*, the most primitive Pelycosimian; a, side view; b, palatal view. A, articular; An, angular; D, dentary; Op, opisthotic; Q, quadrate; Sa, surangular; other lettering as in Fig. 1; about 1/5 natural size. (From Broili and Schroeder.)

they form one and the same group with the Pelycosimia. The oldest Pelycosimian, *Chasmatosaurus*, is even little older than the first Phytosaurian, *Mesorhinus*. The Pelycosimia are the stem group of the Thecodontia. This the author has only recognized during his study of the South American Stagonolepids and in consequence of the revision of other Pseudosuchia; the descriptions and results of this study are in press

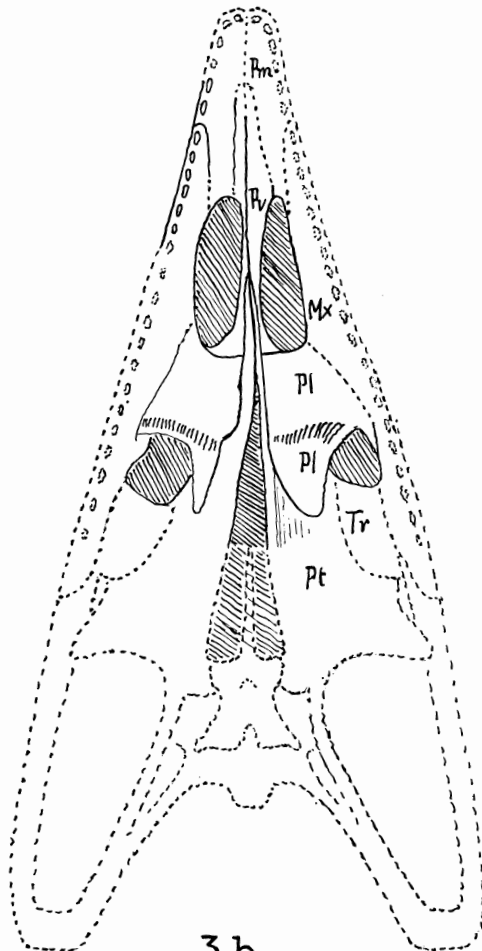
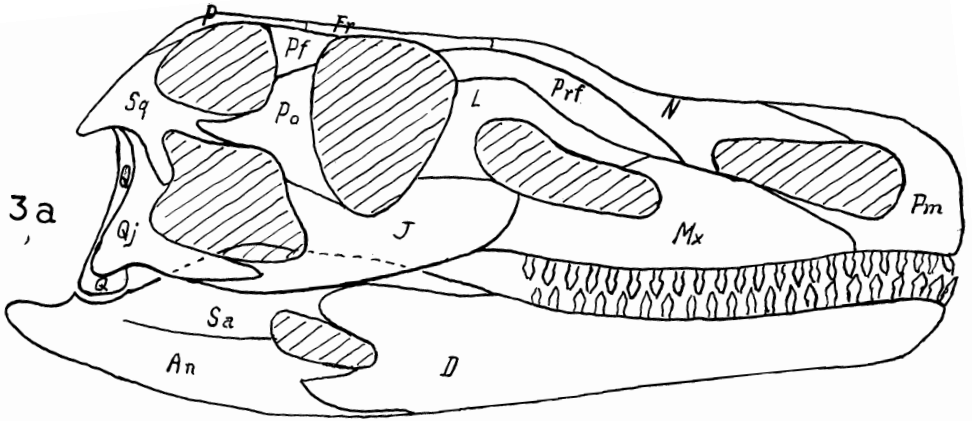


Fig. 3. *Stagonolepis* (restoration); a, side view; b, palatal view; lettering as in Figs. 1 and 2.

now ("Die fossilen Reptilien des südamerikanischen Gondwanalandes etc." Printed by F. Heine, Tübingen, in U. S. A. to be had from Stechert and Co., New York).

Here some illustrations are given to show the above mentioned conditions. For the Phytosaurs, *Mesorhinus* from the Middle Bunter of Germany has been chosen as the oldest representative; the size of the praemaxilla is not known, but

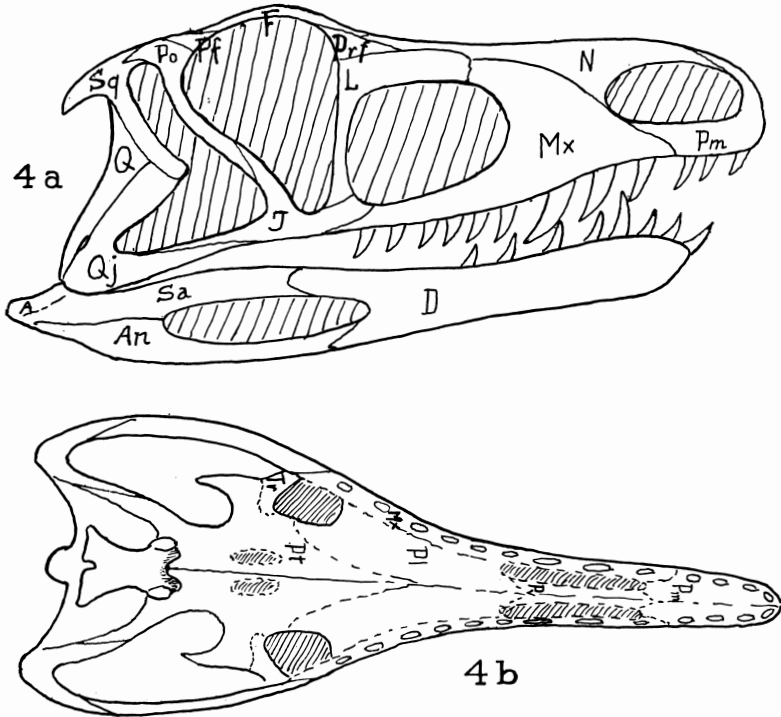


FIG. 4. *Ornithosuchus* (from E. T. Newton, altered); a, side view; b, palatal view; lettering as in Figs. 1 and 2; about 5/6 natural size.

the narial openings are visible (Fig. 1). The Pelycosimian, *Chasmatosaurus*, is still older as it comes from the lowest part of the Lystrosaurus zone (= Bunter) of South Africa (Fig. 2). Its praemaxilla is intermediate between that of a Phytosaur and that of an ordinary Pseudosuchian. But another Pelycosimian, *Erythrosuchus* (from the lower part of the Cynognathus zone = Middle Trias) has quite a small and short praemaxilla. The third is *Stagonolepis* from the Stagonolepis sandstone (probably lowest Upper Trias) of Elgin in

Scotland, from which I made this restoration (Fig. 3); though it is mainly from Huxley's type specimen, other specimens have been used; in the palate all unbroken lines are taken from observation of the specimen and the rest has been adapted from the restoration of the side view for which several specimens have been used. Out of the other Pseudosuchians, *Ornithosuchus* has been taken (from the same beds and place as *Stagonolepis*) (Fig. 4); in the side view the sutures have been put in. They are not in any way doubtful. In the palate a part is not visible in the type and had to be reconstructed. A significant error is hardly possible. The choanae must be far forward. Dotted sutures have been put in where they are not visible in the type. In the posterior part of the palate a pair of paramedian gaps in the pterygoid are visible in the type (although indicated by dotted lines in the figure) and I am doubtful whether they could have been caused during preparation, because the same thing occurs in specimen XXI of the *Aëtosaurus* group (at Stuttgart); probably this is just a gap or a thin place in the pterygoids.

According to the writer's present view the constitution of the Thecodonts is as follows:

ORDER THECODONTIA.

I. Suborder Phytosauria.

I.a. Family Mesorhinidae.

Mesorhinus.

I.b. Family Angistorhinidae.

Promystriosuchus.

Angistorhinus.

Angistorhinopsis.

I.c. Family Phytosauridae.

Phytosaurus (= *Belodon*, *Nicrosaurus*,
Palaeoconus, *Lophoprosopus*).

Mystriosuchus.

Clepsysaurus (= *Eurydorus*, *Palaeoconus*,
Suchoprion).

Rutiodon (= *Rhytidodon*, *Omosaurus*,
Compsosaurus).

Typothorax vide Camp.

Machaeroprosopus (= *Metarhinus*, *Hetero-*
dontosuchus, *Pseudopalatus*).

Palaeorhinus.

Leptosuchus.

Brachysuchus.

II. Suborder Pseudosuchia.

II,a. Superfamily Pelycosimioidea.

II,a,1. Family Proterosuchidae.

Chasmatosaurus.
Proterosuchus.

II,a,2. Family Erythrosuchidae.

Erythrosuchus.

II,a,3. Family Stagonolepidae.

II,a,3,a. Subfamily Stagonolepinae.

Stagonolepis.

II,a,3,b. Subfamily Desmotosuchinae.

Desmotosuchus.
Acompsosaurus.
?Hoplitosaurus.

II,a,3,c. Subfamily Episcoposaurinae.

Episcoposaurus.
?Stegomus.

II,a,3,d. Subfamily Rausuchinae.

Rausuchus.
Prestosuchus.

II,a,3,e. ?Subfamily.

Procerosuchus.

II,b. Family Euparkeriidae.

Euparkeria.
Browniella.

II,c. Family Aëtosauridae.

Aëtosaurus.
Dyoplax.

II,d. ?Family.

Erpetosuchus.

II,e. Family Ornithosuchidae.

Ornithosuchus.
Saltoposuchus.

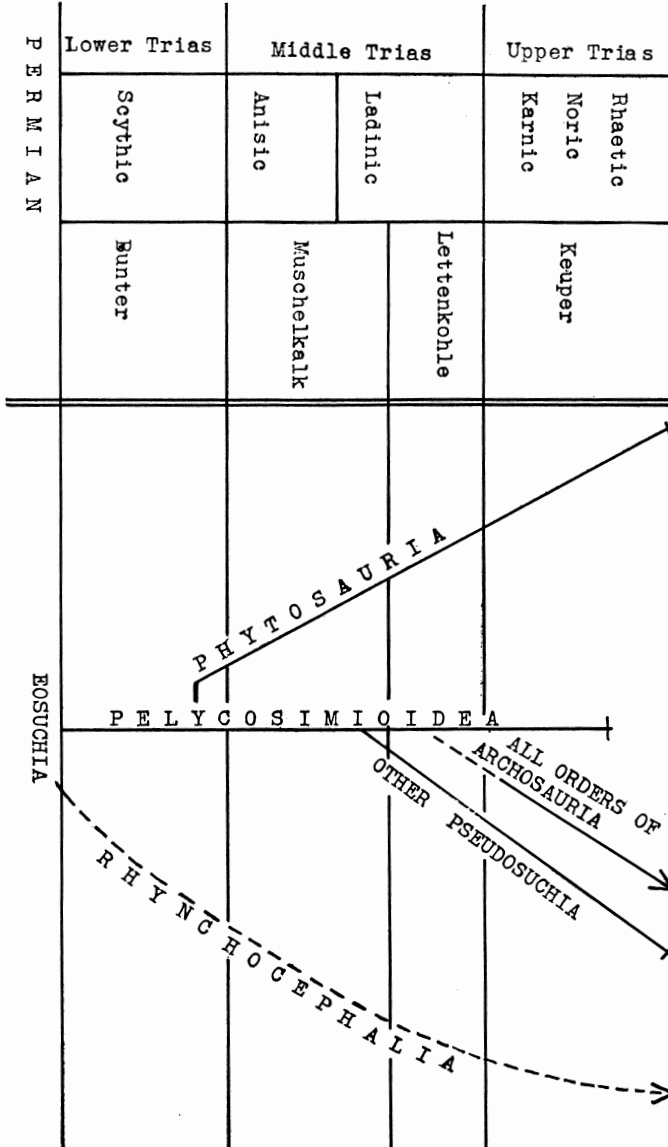
II,f. Family Stegomosuchidae.

Stegomosuchus.

II,g. Family Scleromochlidae.

Scleromochlus.

The scheme of evolution of this order would be the following one:



As shown elsewhere the order of the Thecodonts gives rise to all of the Mesozoic Archosauria (Cope): Saurischia, Pterosauria, Ornithischia, Crocodilia, and Aves.

The Thecodontia and the Rhynchocephalia come from the same root, the Eosuchia of Permian age (South Africa).

A brief list of the most important literature:

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TÜBINGEN, GERMANY.