A NEW ICTIDOSUCHID (SCALOPOSAURIA) FROM THE *LYSTROSAURUS*-ZONE

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Abstract

This paper describes a specimen recently discovered in *Lystrosaurus*-zone strata in the Bergville district of Natal. While a contemporary of *Scaloposaurus*, it has retained much of the general structure of the earlier Ictidosuchidae of the *Cistecephalus*-zone and in a few minor respects it shows affinity with the Therocephalia, beyond the characteristics of the infra-order. The specimen consists of a good skull with lower jaw, the whole pectoral girdle with the right fore limb, and a length of anterior vertebral column with ribs; these are figured as preserved. The skull is additionally figured in three views with distortion corrected. The specimen is identified as a new genus and species, belonging to the family Ictidosuchidae of the infra-order Scaloposauria, and the name *Olivieria parringtoni* is proposed.

Introduction

During several visits to some soil erosion dongas on the farm Admiralty Estates in the Oliviershoek Pass between Harrismith in the Orange Free State and Bergville in Natal, Mr J. W. Kitching has extracted a number of interesting Karroo fossils—interesting not only because many have turned out to be new forms, but also from the point of view of their association. One particular donga has yielded several *Lydekkerina* amphibians, thirteen good specimens of *Thrinaxodon*, a *Cyniscops*-like Gorgonopsian not yet described, the scaloposaurid *Tetracynodon darti* described by Sigogneau in 1963, which was discovered about four feet away from and at exactly the same height as the specimen described in this paper. This particular locality is at the very top of the *Lystrosaurus*-zone.

In 1960 the author figured and briefly analysed some scaloposaurian specimens in a paper which dealt mainly with a serially sectioned snout of a therocephalian. At that time the author felt hesitant over the relationship between the ictidosuchids, scaloposaurids and bauriamorphs, and the ictidosuchids were described as if they fall within the range of the Therocephalia. Since then the author has come to the conclusion that the Ictidosuchidae fit in substantially with the scaloposaurid-bauriamorph line, and proposed in 1963 that the whole range be called the Scaloposauria, with the two main subdivisions, the Ictidosuchoidea and the Bauriamorpha. The Ictidosuchoidea includes the two families Ictidosuchidae and Scaloposauridae.

Crompton had earlier (1955) proposed that *Ictidosuchoides intermedius* be transferred to the genus *Ictidosuchops*. This entails a transfer from the family Ictidosuchidae to the family Scaloposauridae. In 1960 the author agreed, at least as far as some described specimens of *Ictidosuchoides intermedius* are con-

cerned, to the generic transfer, but felt reserved over the implications of a family transfer.

In the light of the new specimen described in this paper, it is proposed that the genus *Ictidosuchops* be transferred to the family Ictidosuchidae.

Olivieria parringtoni gen. et sp. nov.
(Figures 49 and 50)

Type. Complete skull and anterior portion of skeleton (Field No. 3849/Museum No. 379) discovered in 1963 by Mr J. W. Kitching very high in *Lystrosaurus*-zone beds on the farm Admiralty Estates in the Oliviershoek pass between Harrismith and Bergville.

General. The specimen is named generically after the significant locality, and specifically after Dr F. R. Parrington who, at the moment of writing, is in the process of describing a very similar specimen which Mr J. W. Kitching also recovered from *Lystrosaurus*-zone beds. It is unlikely that we are describing two specimens which may turn out to be of the same genus and species, because the two localities are substantially different and some 400 miles apart.

Diagnosis. Slightly smaller than *Ictidosuchoides longiceps* and slightly larger than *Ictidosuchops intermedius*. In general structure and proportions it agrees better with the latter, but it has the complete postorbital bars of the former as is also the case in *Ictidosuchus*. Dentary very straight; coronoid processes not curved up as much as in these two genera, and ending more squarely. Outer face of the dentary characterised by a strong ridge extending from what can be recognised as an "articular angle" to beyond half the length of the dentary. Anterior free margins of the nasals deeply concave and generally at a sharp angle to the midline. Nasals constricted in the middle and expanded posteriorly. Frontals form little of the dorsal borders of the orbits. Dental formula i5 : c3 : pc3 for the upper jaw and i4 : c1 : pc4 for the lower jaw (six incisors in the upper jaw is more characteristic for the Ictidosuchidae). The highly reduced postcanine series is taken as the most significant characteristic of generic diagnostic value. Parietal crest narrow; pineal large. Elementary secondary palate widely open.

Measurements. In the following table the measurements of the present specimen are compared with the average of the three best specimens of *Ictidosuchops intermedius* in the collection of the Bernard Price Institute (Nos. 267, 268, 343—see table I, Brink, 1960), and the average of the three specimens of *Ictidosuchoides longiceps* (see table II, Brink, 1960), the only specimens at hand of which dimensions are adequately known (all measurements in millimeters).

	Present specimen	*I. intermedius*	*I. longiceps*
Length of skull to occipital condyle . .	102	103	139
Length to pineal foramen	74	78	107
Length of snout to anterior borders of orbits	49	52	70
Maximum breadth of skull	66	64	79
Minimum breadth of snout	27	22	27
Interorbital width	21	18	20?
Tip of snout to interpterygoid fossa . .	70?	67	88
Distance occupied by upper incisors	14	12	17
Distance occupied by three upper canines	12	9	11
Distance occupied by three upper postcanines	8	—	—
Distance across pterygoid processes	37?	35	41
Distance between palatal ridges of palatines	13	7	15
Narrowest parietal constriction . .	10	12	10

Description

The *basioccipital* is not exposed in the present specimen.

The *exoccipitals* are covered by the two halves of the pro-atlas and could not be exposed. In figure 49C they are illustrated according to indirect deduction, guided by conditions in *Ictidosuchops intermedius* (Crompton 1955) and *Tetracynodon darti* (Sigogneau 1963), but proportionally according to the surrounding structures. They would appear to be shorter in their dorso-lateral extensions either side of the foramen magnum.

The *supraoccipital* is basically the same as in *Ictidosuchops*, *Ictidosuchoides*, *Tetracynodon* and *Bauria*, but there are differences in detail. On the whole it is broad and low and the present specimen shows more clearly that it is covered dorsally by the interparietal. Laterally, too, it is well overlapped by the tabulars. It differs from *Ictidosuchops* in that it does not contribute substantially to the dorsal borders of the posttemporal fossae, the condition being more like that in *Ictidosuchoides* and *Tetracynodon*. In *Bauria* (Brink 1963) it contributes more substantially to the medial margins of these fossae. It differs from *Tetracynodon* in surface sculpture, and corresponds further with *Ictidosuchoides* in the slight sign of a median ridge. This ridge is more conspicuous in *Ictidosuchops*. There is a good fusion between the supraoccipital and opisthotics, as in *Ictidosuchoides*, unlike the more delicate contacts of *Ictidosuchops* and *Tetracynodon*.

The *opisthotics* seem to agree with both *Ictidosuchops* and *Ictidosuchoides*. In the former the contact with the supraoccipital is more delicate and in the latter the processes themselves are more delicate. In *Tetracynodon* the paroccipital

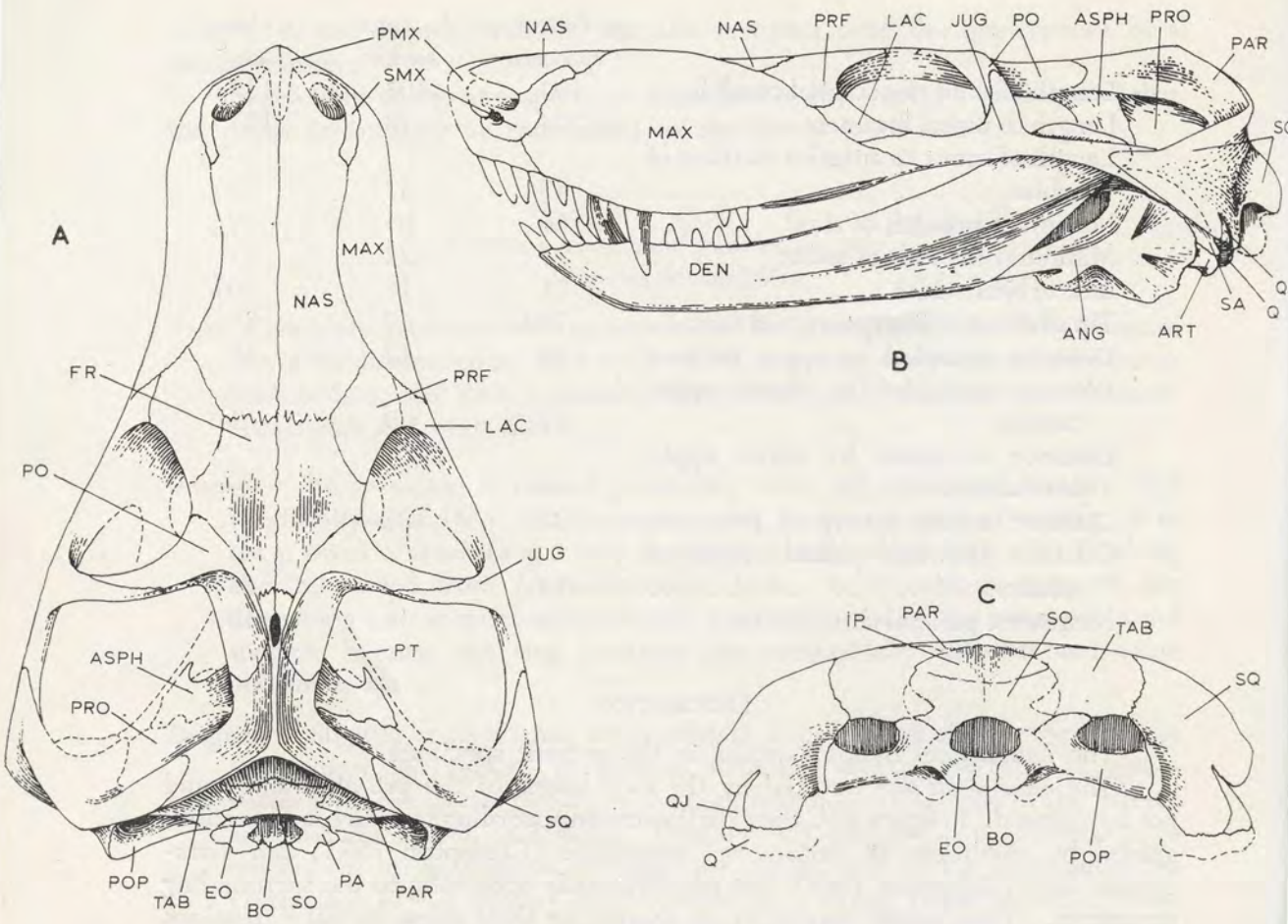

Figure 49

A—Dorsal; B—Side and C—Posterior views of the skull of *Olivieria parringtoni* gen. et sp. nov., half natural size.

Abbreviations: Ang—angular; art—articular; asph—alisphenoid; bo—basioccipital; den—dentary; eo—exoccipital; fr—frontal; ip—interparietal; jug—jugal; lac—lachrymal; max—maxillary; nas—nasal; pa—proatlas; par—parietal; pmx—premaxillary; po—postorbital; pop—paroccipital process; prf—prefrontal; pro—prootic; pt—pterygoid; q—quarate; qj—quadratojugal; sa—surangular; smx—septomaxillary; so—supraoccipital; sq—squamosal; tab—tabular.

processes are shorter. The lateral blunt ends of these processes abut boldly against prominent flanges of the squamosals, as is the case in *Ictidosuchoides* and *Bauria*. This condition is not portrayed in the illustrations of *Ictidosuchops* (Crompton, op. cit.) and *Tetracynodon* (Sigogneau, op. cit.).

The *prootics* are not exposed. In figure 49A they are merely indicatedas lying in the space behind the alisphenoids.

The *tabulars* differ reasonably from the condition depicted for *Ictidosuchops* and *Tetracynodon*. In specimen No. 344 of *Ictidosuchoides longiceps* (Brink 1960)

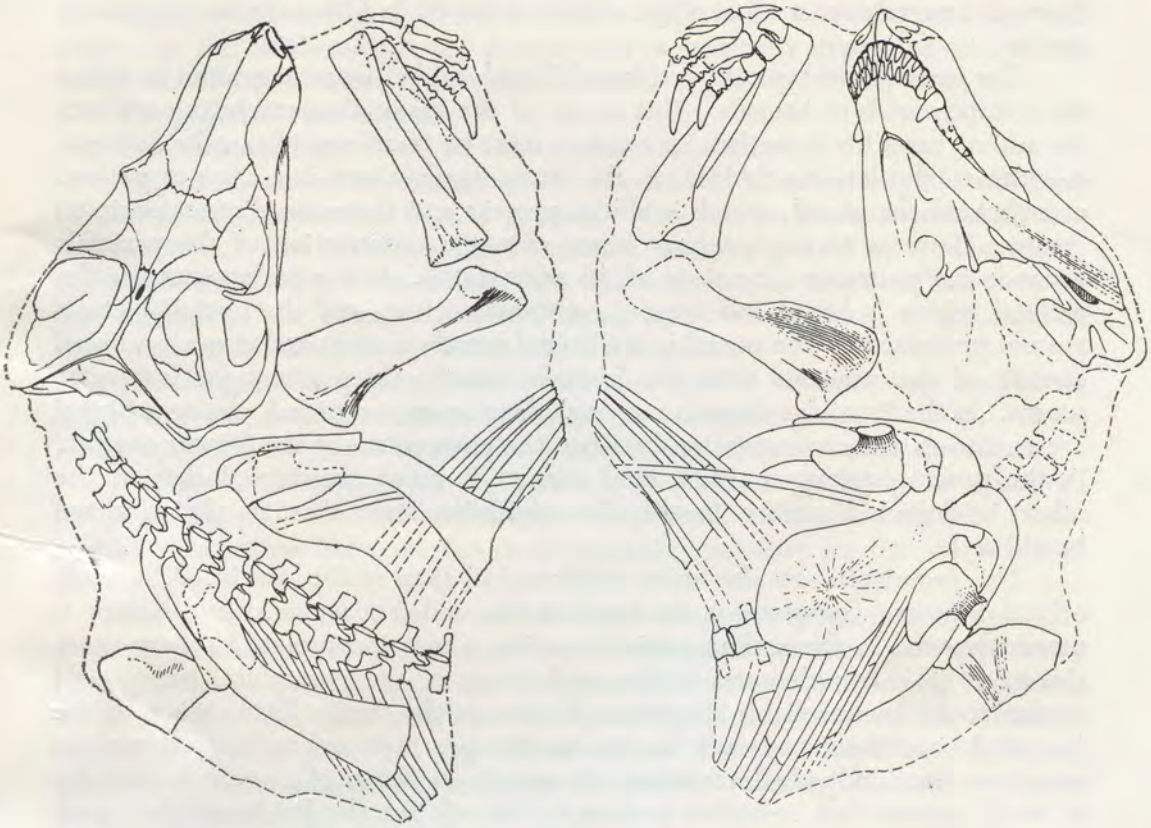

Figure 50
Left: Dorsal view and right: Ventral view of the specimen of *Olivera parringtoni*, gen. et sp nov., as preserved. Half natural size.

the regions of the tabulars are damaged, but there seems to be a marked correspondence. The tabulars reach inward above the interparietal, shortly below the crests formed by the parietals. The tabulars also send extensions inward across the supraoccipital, in the direction of the dorsal border of the foramen magnum. They form the dorsal borders of the posttemporal fossae and do not extend farther laterally than the lateral borders of these fossae. In this respect there is a marked contrast with *Bauria*. The surfaces are smooth where the tabulars meet the squamosals, as in *Ictidosuchoides*, and unlike *Tetracynodon*, *Ictidosuchops*, and especially *Bauria*, where medial edges of the external auditory meatus valleys are carried farther up. As in the ictidosuchids and unlike the typical scaloposaurids and baurids, the squamosals, rather than the tabulars, form the lateral borders of the posttemporal fossae.

The *interparietal* is broader and lower than in *Ictidosuchops*, and it tapers to left and right to points below the upper medial projections of the tabulars. In straight posterior view the parietals are barely visible above its dorsal margin.

There is a prominent median ridge. The conditions in *Ictidosuchoides* are exactly similar.

The *parietals* are typically ictidosuchid and unlike the arrangement in either the scaloposaurids or baurids. This is one of the many characteristics on which the author bases his view that *Ictidosuchops* must be transferred from the Scaloposauridae to the Ictidosuchidae. In the latter family there is a distinct parietal crest behind the pineal, which is always present, and there are distinct occipital crests. There is to a greater or lesser extent a constriction of the parietals between the posterior extensions of the postorbitals. In the Scaloposauridae the parietal region is broad and smooth, without a crest, and the occipital crests are not prominent. The pineal is small (and mostly absent) and there is a broad contact of the parietals with the frontals, mostly along a straight transverse suture. In the Bauriidae there is a strongly fused crest, no pineal, strong occipital crests, and extreme constriction between the postorbitals at the frontal contact. In the present specimen this frontal contact is more constricted than in the other ictidosuchids, more in the therocephalian style than in the advanced baurid style.

The *postorbitals* are also more ictidosuchid than scaloposaurid. The postorbital bars are complete as in *Ictidosuchoides* and *Ictidosuchus*. *Ictidosuchops* is more advanced in the scaloposaurid direction where incomplete bars are more the rule. The completeness or incompleteness of the postorbital bars would appear to be an unreliable diagnostic feature at the family level; some of the recorded conditions may even be due to damage. It is not unlikely that there may have been individual variation. However, in terms of present knowledge it would appear that complete arcades is the rule for the Ictidosuchidae, with incomplete arcades the exception, while the reverse is the case in the Scaloposauridae. In the Bauriidae the arcades are more definitely open.

In the present specimen ridges are carried across the postorbitals from the parietal crest and outward along the posterior margins of the arcades. Although slight indications of these can be seen in some *Ictidosuchops* specimens, the rule is a condition more like that of the scaloposaurids. In this feature, and the strength of the arcades, the present specimen displays an extra affinity with the Therocephalia.

The *frontals* are reasonably normal for an ictidosuchid. They do not contribute as substantially to the dorsal borders of the orbits. In this respect there is also some affinity with the Therocephalia, where the contribution is exceptionally small. In the present specimen the dorsal orbital border is a sharp edge, as in *Ictidosuchoides* and the Therocephalia in general. In *Ictidosuchops* it inclines to become rounded as in the scaloposaurids. In *Bauria* it is also a sharp edge.

The fronto-parietal suture is shorter transversely, because of the narrower crest. This is also more reminiscent of the condition in the Therocephalia. In the ictidosuchids this region is generally broader, and it is even broader in the scaloposaurids, while the in the bauriids, taking *Bauria* as the classic example, it is narrow.

Each parietal is depressed and a rather conspicuous crest is formed between them. In the ictidosuchids the frontal area is generally depressed and in the scaloposaurids it is mostly smoothly convex.

The *prefrontals* are normal.

The *lachrymals* are low, and short antero-posteriorly.

The *nasals* are more constricted in the middle of their lengths, and they expand more posteriorly, than is generally the case in the scaloposaurids and ictidosuchids. This is also a therocephalian feature, shared by *Ictidosuchoides;* in *Ictidosuchops* the condition is more like that in the scaloposaurids. The anterior free margins of the nasals are more concave and more inclined to the midline than in any of the other forms in the whole infra-order.

The *septomaxillaries* penetrate deeply and broadly between the maxillaries and nasals, and these extensions terminate in conspicuous square ends. These bones are fairly large and contribute much to the surfaces below the nares.

The *premaxillaries* carry 5 teeth each. The internarial bridge is damaged, but it clearly projected forward with a sharp bend. There are signs of a substantial penetration between the nasals dorsally, contrary to the condition in *Ictidosuchops*.

The *maxillaries* carry two small anterior canines, a large canine, and only three postcanine teeth. The maxillary dentition is perhaps this specimen's most distinctive generic diagnostic feature. Otherwise the maxillary is normal for this family. The palate could not be exposed properly, the lower jaw obstructing the anterior region, but the indications are that the elementary secondary palate is in the ictidosuchid condition, not properly closing with the vomer as in the scaloposaurids.

The *transverse* bones are not properly exposed.

The *jugals* are delicate, as is typical of the ictidosuchids and scaloposaurids. They contribute to the postorbital arches, which is more an ictidosuchid than a scaloposaurid feature.

The *squamosals* overlap the jugals more broadly than in the ictidosuchids, more in the therocephalian style. In the infra-order Scaloposauria delicate extensions of the squamosals reach forward more dorsally to the jugals, but in the present specimen the broader squamosal contributions to the zygomatic arches lie more laterally. The bulk of the squamosals show in posterior view, where the whole surfaces form broad and shallow external auditory meatus valleys. Medially, on the posterior face, the squamosals pass smoothly over to the tabulars, but lower down they form bold projections curving back and abutting against the blunt ends of the paroccipital processes. Their lower margins are excavated in two places either side to accommodate the roots of the quadrates and quadratojugals. On the side of the temporal fossae the dorsal processes reach normally inward to join the parietal flanges. The lower prootic processes are not exposed.

The *quadratojugals* and *quadrates* are unsatisfactorily displayed, but enough can be seen to conclude that the arrangement is in line with *Ictidosuchops*. The

quadratojugal can be seen in side view. It penetrates upward, wedgelike, into a deep notch in the squamosal. The quadrate is inserted more anteriorly in the squamosal, so that its foot-piece cannot be seen in posterior view.

The *stapes* could not be exposed.

The *vomer* is exposed only posteriorly, between the palatines. The median keel in this region is continuous with a median interpterygoid keel.

The *palatines* are sufficiently exposed to indicate an arrangement not different from *Ictidosuchops* or *Ictidosuchoides*. At this level the elementary secondary palate is still very widely open.

The *pterygoids* form more of a median keel than a restricted bulge between them. Either side of this keel, on the borders of the suborbital fossae, the pterygoids form small but very conspicuous ventrally projecting processes. In other related forms these are only slight prominences on longitudinal ridges. The suborbital vacuities are large. The pterygoid processes are vaguely exposed and their relationship with the transverse bones cannot be seen, the lower jaw making detailed preparation difficult. More posteriorly a hyoid bone obstructs the region of the interpterygoid fossa which could consequently not be exposed. The quadrate processes are also too deeply buried in matrix and obstructed by other structures to be successfully excavated.

The right *alisphenoid* is exposed. It is high, narrow, and lies far back, as is typical of the ictidosuchids. Its anterior free margin is deeply concave. Its posterior margin is not sufficiently exposed to show its relationship to the prootic.

The *orbitosphenoid* and *parasphenoid* bones could not be exposed.

The lower jaw is in a good condition, but the more important structural details are obscured by the fact that it is in intimate articulation with the skull.

The *dentary* carries 4 incisors, one canine, and 4 postcanine teeth. It forms a reasonably sharp chin, more conspicuous in ventral view than in side view. The delicate, thin, elongated *splenials* reach to the symphysis, to which they contribute.

The dentaries are reasonably straight, with somewhat square coronoid processes. A strong ridge extends from what can be recognised as an articular angle for a long distance forward along the lateral face. The *angular* bone is well preserved and displayed externally on the left side. Its interesting sculpture is accurately portrayed in figure 49B. The other lower jaw bones are not satisfactorily exposed.

Discussion

The present specimen belongs to the family Ictidosuchidae. Its nearest allies are *Ictidosuchoides*, *Ictidosuchus*, *Ictidosuchops*, and other forms which may, on closer investigation, be found to be more at home in this family than in the Scaloposauridae. Although a much later form—a contemporary of *Scaloposaurus* and *Tetracynodon*—it is not conspicuously more advanced in the direction of this

family, compared with its earlier relatives. In fact, in some details it is less advanced than its own relatives, and in these features somewhat reminiscent of the Therocephalia.

Ictidosuchops is here regarded not as a member of the family Scaloposauridae but of the Ictidosuchidae. In terms of structure and chronology it is more closely related to *Ictidosuchoides* and *Ictidosuchus* than to any of the more typical scaloposaurids.

The author favours the inclusion of all ictidosuchid-bauriamorph forms under the Infra-order Scaloposauria, which can be split into two superfamilies, the earlier Ictidosuchoidea and the later Bauriamorpha. The Ictidosuchoidea in turn contains at least the two families Ictidosuchidae and Scaloposauridae, while the Bauriamorpha contains at least the family Bauriidae. These three families can be distinguished as follows:

Ictidosuchidae	*Scaloposauridae*	*Bauriidae*
Generally *Endothiodon-Cistecephalus*-zone forms, to *Lystrosaurus*-zone by exception. (Middle to late Permian)	Generally *Lystrosaurus-zone* (Late Permian to early Triassic).	Mostly *Cynognathus*-zone (Middle Triassic).
Secondary palate elementary and still wide open.	Elementary secondary palate closing.	Secondary palate closed. (Maxillaries only).
Pineal present and large.	Pineal disappearing in some.	Pineal absent.
Postorbital bars still closed in some.	Postorbital bars mostly open.	Postorbital bars open.
Dentition simple, multiple canines.	Dentition simple, multiple canines.	Single canines, molariform postcanines.
Fronto-parietal region constricted.	Fronto-parietal region broad.	Fronto-parietal region constricted.
Parietal region crested.	Parietal region broad and rounded.	Parietal region crested.
Definite occipital crests.	Inconspicuous occipital crests.	Definite occipital crests.
Sharp dorsal orbital borders.	Rounded dorsal orbital borders.	Sharp dorsal orbital borders.

The infra-order Scaloposauria can be distinguished from the infra-order Therocephalia on the following grounds:

(1) Postorbital bars delicate to incomplete.

(2) Zygomatic arches delicate.

(3) Frontals form substantial portions of dorsal orbital borders.
(4) Alisphenoids somewhat primitive.
(5) Suborbital fossae large.
(6) Interpterygoid fossa present and generally large.
(7) Dentaries weakly developed posteriorly.
(8) Posttemporal fossae large.
(9) Nasals generally not much constricted, or expanded posteriorly.
(10) Parietal crest not as thin and high, absent in one family.
(11) Greater number of postcanine teeth.
(12) Different multiple canine arrangement.

The Scaloposauria is nevertheless more closely related to the Therocephalia than to other infra-orders, on the following grounds:

(1) The frontals contribute to the dorsal orbital borders.
(2) There is no contact between the lachrymals and nasals.
(3) The zygomatic arches are weak.
(4) The post-dentary bones are in a very similar condition.
(5) The dentaries are in the same stage of development.
(6) The elementary secondary palate can be brought into relationship.
(7) The occipital condyle is characteristically trilobed.
(8) The dentitions are reasonably related.

The present specimen, although chronologically a contemporary of the more typical scaloposaurids, has a slight therocephalian affinity in the reduced postcanines, the constricted nasals, the strong postorbital bars, the large pineal, the stronger contribution of the squamosals to the zygomatic arches and the lesser contribution which the frontals make to the dorsal orbital borders.

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