A New Lydekkerinid (Amphibia, Temnospondyli) from the Lower Triassic of South Africa: Implications for Evolution of the Early Capitosauroid Cranial Pattern

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A new lydekkerinid (Amphibia, Temnospondyli) from the lower Triassic of South Africa: implications for evolution of the early capitosauroid cranial pattern

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SUMMARY

A new genus and species of lydekkerinid amphibian, *Eolydekkerina magna*, is described from the lower part of the *Lystrosaurus* Assemblage Zone of South Africa. Most distinctions between *Eolydekkerina* and *Lydekkerina* (other than those related to width of interorbital area and structure of choana and squamosal occipital flange) are linked to late growth stages and particularly preorbital elongation of the skull in the former genus. The developmental trends in *Lydekkerina* and the Lydekkerinidae in general are analysed by comparison with the cranial pattern of juvenile rhinesuchids. The evidence suggests that the Lydekkerinidae evolved from more fully developed capitosauroid (rhinesuchid-like) ancestors by gradual truncation of ontogeny in parallel with the acquisition of many advanced features, unknown in the Permian capitosauroids. The composition of the Lydekkerinidae is reviewed, and it is suggested that the family includes six to seven valid genera known from Antarctica, Greenland, India, Russia, South Africa and Tasmania. The smaller, and obviously most paedomorphic forms come from the reptile-dominated assemblages in which *Lystrosaurus* is abundant, whereas the larger ones belong to amphibian-dominated assemblages.

1. INTRODUCTION

The amphibian fauna of the *Lystrosaurus* Assemblage Zone (Middle Beaufort Group) of South Africa is limited in variety, being dominated by the primitive capitosauroid *Lydekkerina* (Broom 1909). The only other relatively common form is a small dissorophoid relic, *Micropholis* (Watson 1913, 1919); other amphibian genera from this assemblage are each known from only single skulls. These are reported to include the disputable lydekkerinid genera *Broomulus* (Broom 1930; Romer 1947), *Putterillia* (Broom 1930) and *Limnoiketes* (Parrington 1948), a relic rhinesuchid, '*Lydekkerina*' *putterilli* (Broom 1930), and a rhytidosteid, *Pneumatostega* (Cosgriff & Zawiskie 1979).

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[The dating of another South African rhytidosteid, the family type genus *Rhytidosteus* (Owen 1884; Watson 1919; Cosgriff 1965) is questionable owing to the unclear record of its locality. The recent attribution of this form to the *Lystrosaurus* zone (Kitching 1978; Cosgriff & Zawiskie 1979) cannot be substantiated with certainty (cf. Shishkin 1994). The provenance of the poorly known trematosaurid '*Trematosaurus*' *kannemeyeri* (Broom 1909; Haughton 1925; Huene 1920) is also open to question. Broom (1909) and Haughton (1925) tentatively placed it in the Upper Beaufort Group, then considered to include the *Procolophon* and *Cynognathus* zones, whereas the catalogue of the South African Museum ascribes it to the *Lystrosaurus* zone.]

Two more genera usually included in this list, the rhinesuchid-related *Uranocentrodon* (van Hoepen 1911, 1915, 1917; Broom 1930; Watson 1962) and the more advanced capitosauroid *Kestrosaurus* (Haughton 1925; Chernin 1978), do not actually come from the *Lystrosaurus* Assemblage Zone. A recent examination of the type localities of both forms has revealed that *Kestrosaurus* is from the lower subzone of the *Cynognathus* Assemblage Zone (Hancox *et al.* 1995), whereas *Uranocentrodon* is most probably from the Upper Permian *Dicynodon* Assemblage Zone (E. M. Latimer, manuscript in preparation).

The fossil record from the lower part of the *Lystrosaurus* Assemblage Zone is of particular interest as the amphibian finds reported from there are very rare (one of them is the type of *Pneumatostega potamia* from Tafelberg, Middelburg, Cape Province) and *Lydekkerina* appears to be absent. For this reason two recent finds from this stratigraphic level made by one of us (JWK) attracted attention. These specimens, both housed in the collections of the Bernard Price Institute for Palaeontological Research, consist of a reasonably well-preserved skull and a separate lower jaw, both from the the Fairydale farm, Bethulie, Free State. Both specimens had been preliminarily identified as *Rhytidosteus*, but further preparation has revealed that the skull belongs to a large lydekkerinid. This paper reports on the significance of the skull. The lower jaw, which is rather poorly preserved, may well belong to the same form.

2. PRESERVATION AND METHODS

The almost complete skull, without a lower jaw, is preserved in a light greenish-grey calcareous siltstone. Ornamentation on the skull roof appears to have been slightly weathered by moving water. The presence of numerous tips of maxillary and palatal teeth, which are broken off from their bases and preserved in a horizontal position in the matrix, suggest that the marginal areas were still covered by soft tissue when buried.

Most skull damage seems to be of postdepositional origin. This includes slight compression of the left cheek, deformation of the left otic notch, asymmetry of the orbits and of the position of both external and internal nares, the matrix-filled crack of the right cheek, and loss of the left jaw articulation, a portion of the right cheek, the tips of both tabulars, and a part of the tooth row of the right premaxilla. The ornamentation surface of the skull roof is eroded along the edge of the premaxillae, as well as the right maxilla and jugal.

Preparation of the skull was undertaken by both mechanical and chemical means. For chemical preparation all exposed bone was coated with diluted glyptal cement before being submerged in a 4% solution by volume of acetic acid for periods of up to 8 h at a time, but with constant monitoring. Between periods of acid immersion the specimen was washed in running water for at least six times the length of acid immersion to remove all acid residue. As a precaution to bone damage by acid the acid was buffered by supersaturating with calcium orthophosphate.

3. REMARKS ON CLASSIFICATION OF CAPITOSAUROIDEA

In the following description of a new lydekkerinid genus, the family Lydekkerinidae is considered to be a member of the Capitosauroidea, which here includes the bulk of the late Permian–Triassic eryopoid descendants. This contrasts with the current practice, which largely follows Romer (1947), who considered these forms in two superfamilies: Rhinesuchoidea and Capitosauroidea (Kuhn 1960; Welles & Cosgriff 1965; Tripathi 1969; Cosgriff 1974; Carroll & Winer 1977; Warren & Hutchinson 1988*a*, *b*). Romer's scheme was intended to express in taxonomic terms the idea of Watson that the posteryopoid temnospondyl radiation falls into two successive grades, Rhachitomi and Stereospondyli. The Lydekkerinidae were included within the former (Watson 1919, 1951). The main point implied by this taxonomic subdivision is that all the advanced forms exhibiting the 'capitosaurid' or *Parotosuchus*-like structural pattern (primarily inclusion of frontals in orbital borders) have inherited it from a common ancestor. This ancestor is presumed to be derived from the Rhinesuchidae; Lydekkerinidae are considered an offshoot of this lineage (cf. Watson 1919, p. 55; Cosgriff 1974, p.70).

In its extreme form this belief is revealed in the survey of the family Capitosauridae (constituting the majority of the Capitosauroidea) by Welles & Cosgriff (1965), who lumped all the forms ever included in this family into three to four genera. Although recent workers consider taxonomic revision of the Capitosauroidea to be necessary (Chernin & Cosgriff 1975; Warren 1980; Cosgriff & DeFauw 1987) the group is generally regarded by them to be monophyletic.

However, there are strong reasons to consider (Watson 1962; Ochev 1966) that the 'capitosaurid' structural pattern was developed more than once in the course of evolution from the rhinesuchoid level. Maryanska & Shishkin (1996) suggested arranging the so-called Capitosauridae into four to five families and presented evidence that at least two of them achieved the *Parotosuchus*-like condition independently. This viewpoint implies that the superfamily Capitosauroidea and family Capitosauridae in the current understanding are artificial units. Consequently the former term cannot reasonably be used other than to

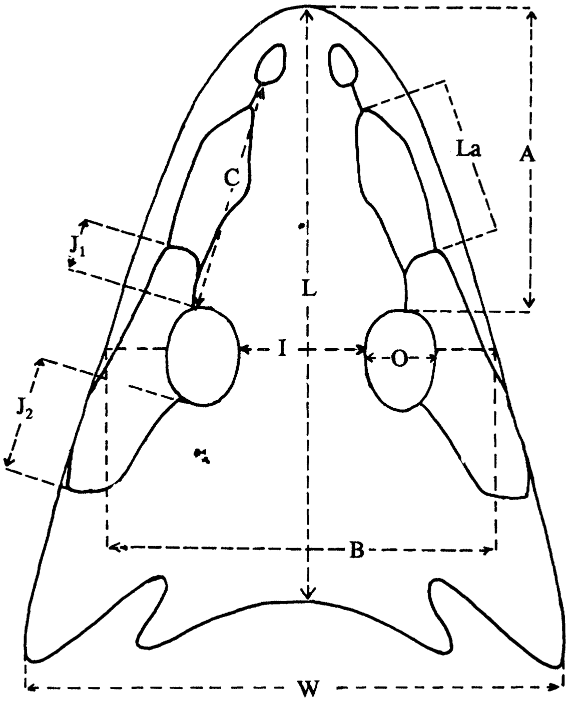

Figure 1. Diagram of skull-roof measurements.

embrace most of the posteryopoid radiation starting from the Rhinesuchidae. In this understanding of the superfamily (or suborder Capitosauroidei) we follow Säve-Söderbergh (1935), Nilsson (1946), Kuhn (1961), Shishkin (1964) and Ochev (1966). The term Rhinesuchoidea is removed from this classification. In our concept of the family Rhinesuchidae we follow Watson (1919; cf. Carroll & Winer 1977) and see no reason for the subdivision of this group into Rhinesuchidae and Uranocentrodontidae as was suggested by Romer (1947). Our observations reveal that the occipital exposure of the opisthotic, considered by Romer (1947) as a main distinction of the rhinesuchids from *Uranocentrodon*, does not actually occur in them.

The measured characters used in the following systematic description and discussion are given in figure 1. Chosen for the analysis are those indexes (other than A/L) that are markedly variable at the generic level in the early capitosauroids and at the same time proved to be not strictly correlated with the preorbital elongation of the skull.

4. SYSTEMATIC PALAEONTOLOGY

Superfamily Capitosauroidea Watson 1919 (nomen transl. ex Capitosauridae Watson 1919).

Diagnosis

Skull with more or less elongate preorbital zone and short orbitopineal zone. Otic notch present. Nares broadly separated. Sensory grooves usually developed to varying degree; supraorbital groove primitively not crossing lachrymal; infraorbital groove with lachrymal flexure. Intertemporal absent. Lachrymal separated from both orbit and naris. Jugal with preorbital projection (except for very paedomorphic forms). Postorbital tends to extend anterolaterally. Parietals with narrowed anterior portions. Prefrontal–postfrontal suture (when present) short. Two occipital condyles. Pterygosquamosal fissure usually absent. Crista obliqua pterygoidei usually developed. Opisthotic not exposed on occiput. Exoccipital bearing conspicuous subotic process. Anterior palatal vacuity from paired to single. Area of pterygoparasphenoid suture elongate and flattened. Parasphenoid body usually with muscular crests. Cultriform process of parasphenoid narrow to moderately broadened. Pterygoid contacts palatine. Continuous palatine–ectopterygoid, parachoanal and interchoanal tooth rows of small uniform teeth present. Ectopterygoid tusks usually absent.

Family Lydekkerinidae Watson 1919

Diagnosis

Small to medium-sized capitosauroids, with orbits close to centre of length of skull roof (A/L close to 0.5). Skull broad (W/L exceeds 0.85; usually more than 0.90). Lateral margins of skull roof convex to nearly straight. Otic notch short and broadly triangular. Cheek border straight in occipital view. Jaw articulation posterior to occipital condyles. Ornamentation fine-pitted. Sensory grooves weakly developed and discontinuous; lachrymal flexure of infraorbital groove gentle or step-shaped rather than Z-shaped. Septomaxilla lacks anteromedial intranarial process. Supratemporal excluded from border of otic notch. Frontoparietal suture more or less transverse. Posterior border of nasal step-shaped. Frontals broadened anteriorly and excluded from orbital borders. Lachrymal long and narrow (La/C not less than 0.70). Preorbital projection of jugal very short, and much shorter than postorbital one. Anterolateral projection of postorbital moderately developed or lacking. Prefrontal not narrowed at orbital rim. Posterior unsupported projections ('horns') of tabulars moderately or weakly developed. Posttemporal fenestrae oval to triangular (not slit-like). Oblique crest of pterygoid shallow, ledge-shaped or absent. Muscular crests of parasphenoid body in line with posterior end of pterygoparasphenoid suture. Subotic process of exoccipital broadly exposed in palatal view and separated by notch from free portion of posterior border of parasphenoid body. No shagreen dentition on vomer and palatine. Anterior palatal fenestra single. Palatine contributes to medial border of choana. Lower jaw with prominent retroarticular process and strictly vertical anterior coronoid.

Comparison

The family differs from Rhinesuchidae (Rhinesuchidae and Uranocentrodontidae *sensu* Romer 1947) in all characters listed except the following: outline of the skull roof; position of the jaw articulation; exclusion of the frontals from the orbital border.

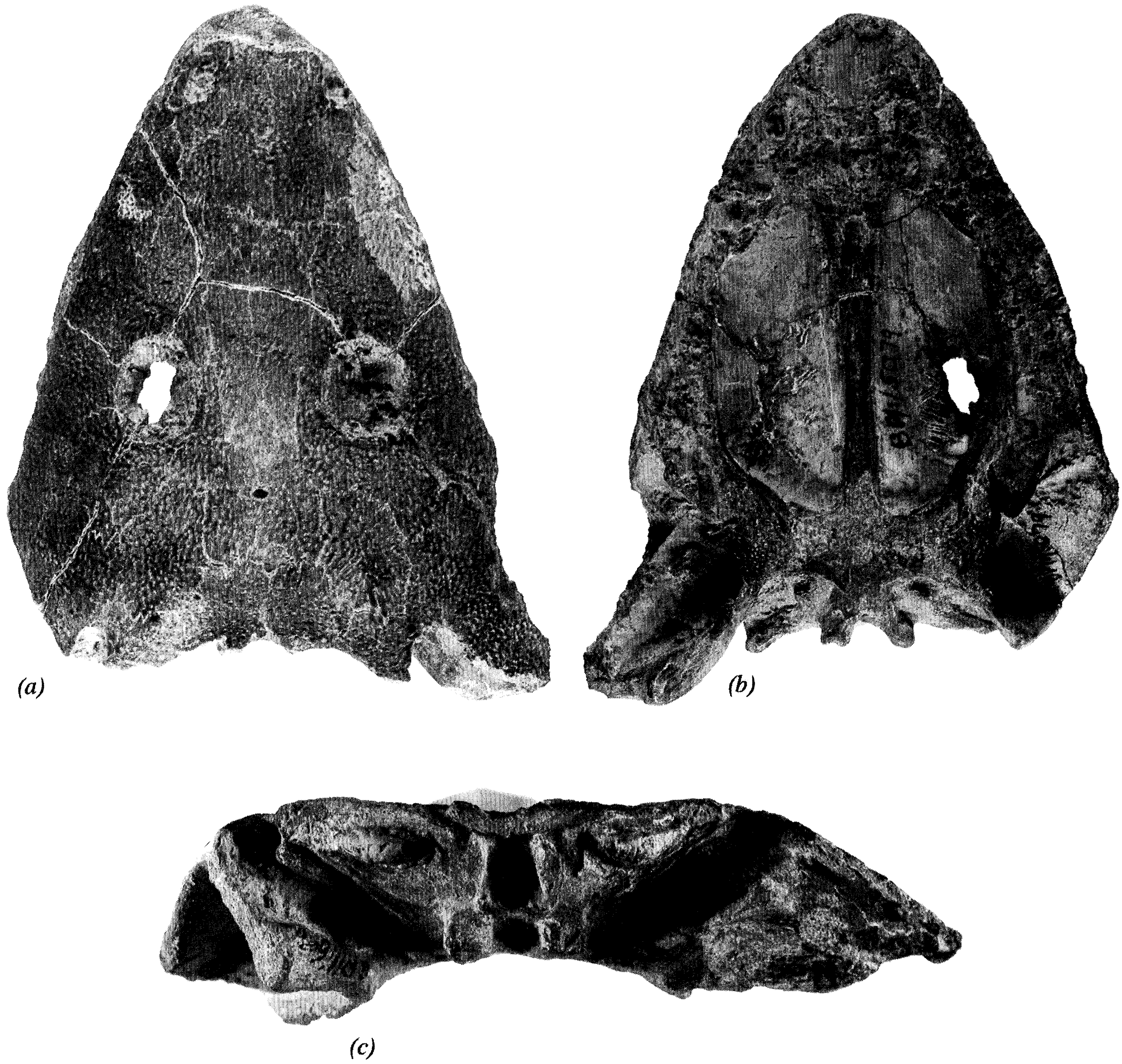

Figure 2. *Eolydekkerina magna* BP/1/5079 holotype, skull: (*a*) dorsal view; (*b*) palatal view; (*c*) occipital view.

The lydekkerinid distinctions assessed as derived in relation to Rhinesuchidae include: (1) short preorbital division of skull; (2) long lachrymal; (3) reduced preorbital projecton of jugal; (4) anterior broadening of frontals; (5) step-shaped posterior border of nasal; (6) short and broad otic notches; (7) reduction or loss of crista obliqua pterygoidei; (8) presence of vental basicranial notches ((1–7) and possibly (8) considered to be paedomorphic); (9) flattened cheek; (10) exclusion of supratemporal from otic notch; (11) presence of unsupported tabular horns; (12) lack of intranarial process of septomaxilla; (13) extention of basicranial sutures up to muscular crests of parasphenoid body; (14) single large anterior palatal vacuity; (15) spread of palatine along medial border of choana; (16) loss of shagreen on palatine and vomer; (17) development of retroarticular process of lower jaw. Derived (and paedomorphic?) may be also broad ventral exposure of subotic process of exoccipital (18).

Distinctions of the Lydekkerinidae from the advanced capitosauroid families (Capitosauridae Watson 1919, Cyclotosauridae Shishkin 1964, Stenotosauridae Heyler 1969, Paracyclotosauridae Ochev 1966 and (?)Mastodonsauridae Watson 1919) (the latter may be a capitosauroid derivative rather than a member of the superfamily; cf. also Milner 1990)) include: paedomorphic characters listed above as (1–5), (7), (18); step-shaped (not Z-shaped) lachrymal flexure; presence of septomaxilla; exclusion of frontals from orbital margins; and (as compared with lineages other than Cyclotosauridae) lack of marked trend toward anterolateral growth of postorbital. Of these characters, only those designated as paedomorphic are derived.

Genus *Eolydekkerina* gen. nov.

Etymology

Name refers to the ancestral position of this genus relative to *Lydekkerina* Broom.

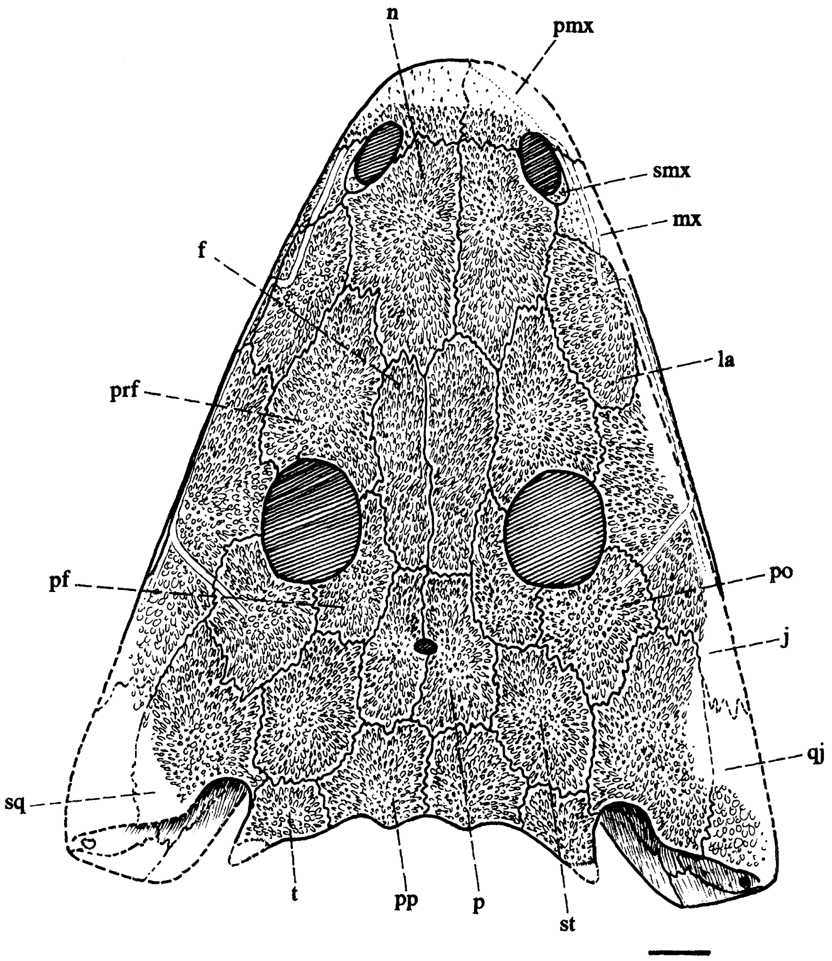

Figure 3. *Eolydekkerina magna* holotype, skull dorsal view. Scale bar, 10 mm.

Diagnosis

Large lydekkerinid with skull length along midline exceeding 130 mm; lateral margins of skull almost straight; preorbital elongation exceeds that of all other lydekkerinids (A/L = 0.54); orbits broadly separated (O/I = 0.72); skull roof with median longitudinal depression and shallow preorbital step; orbital margins elevated; ornamentation of skull roof with poorly developed zone of intensive growth in area of frontonasal contact; supraorbital and jugal sensory grooves not developed; infraorbital groove extending from external nares to jugal ossification centre and giving off postorbital branch; lachrymal flexure of infraorbital groove step-shaped; premaxilla and nasal elongated; postorbital with marked anterolateral projection; ascending lamina of pterygoid has shallow crista obliqua and contacts occipital flange of squamosal; tympanic crest of squamosal subvertical in position; tabular forms two-thirds of roof of posttemporal fenestra; ventral exposure of parasphenoid cultriform process with rounded anterior end and does not reach level of anterior margin of interpterygoid fenestra; choanae pear-shaped with convergent anterior ends; pterygoid body ornamented; shagreen fields on anterior half of parasphenoid body, most of processus cultriformis and along medial side of anterior (palatal) branches of pterygoids; anterior palatal vacuity rounded, its posterior part indented on both sides; transverse interchoanal tooth row straight; no ectopterygoid tusks; maxillary and premaxillary tooth rows overlap slightly; teeth in them only moderately compressed in cross section.

Comparison

The new form differs from *Lydekkerina* Broom in: larger size; prominent preorbital elongation (A/L 0.54 instead of 0.40–0.48 in *Lydekkerina*) involving premaxilla and nasal; broadly separated orbits; shorter lachrymal; more prominent projection from postorbital bone; subvertical position of tympanic crest of squamosal; rounded anterior palatal vacuity; pear-shaped and obliquely orientated choanae; rounded and more posteriorly situated anterior end of processus cultriformis; interchoanal teeth arranged in transverse row. Distinctions from *Chomatobatrachus* Cosgriff and *Luzocephalus* Shishkin include: presence of oblique crest of pterygoid, shape of choanae and interchoanal tooth row, and position of this tooth row close to anterior palatal vacuity. (Some other distinctive characters figured or described for the type of *Chomatobatrachus*, such as position of the muscular basicranial pockets on the exoccipitals and the short nasals (Cosgriff 1974, p. 48, fig. 31), seem to be the result of misinterpretation). Besides, the new genus differs from *Luzocephalus* in lacking its most distinctive characters (large orbitopineal distance, postorbital without anterolateral projection, pterygosquamosal fissure, vomeropalatine contact lateral to choana). Distinctions from *Broomulus* Romer include nearly straight lateral borders of skull, elongation of preorbital area, presence of unsupported tabular horns, shape of choanae.

Eolydekkerina magna sp. nov.

Etymology

The name refers to the large size of the type skull relative to most other lydekkerinids.

Holotype

Specimen BP/1/5079: Almost complete skull without lower jaw.

Type locality

Fairydale Farm, Bethulie, Free State, South Africa.

Horizon

Middle Beaufort Group, lower part of *Lystrosaurus* Assemblage Zone.

Diagnosis

As for genus.

5. MORPHOLOGICAL DESCRIPTION

(*a*) *Skull roof* (figures 2, 3, 4; table 1)

The skull is broadly triangular with a rounded anterior tip. Because of the elongation of the facial region (A/L 0.54; cf. table 1) the skull is closer to the typical capitosauroid pattern than to that of other lydekkerinids. The relative skull breadth (W/L 0.91) corresponds to the lower limit known in *Lydekkerina*. There is a marked preorbital step in lateral view as in *Lydekkerina* (figure 4; cf. Parrington 1948, figs. 2, 5B). The sagittal depression is deepest between the orbits and disappears towards the parietals. The orbits are rather small and broadly separated (O/I 0.72) showing a condition intermediate between that in *Lydekkerina* and *Chomatobatrachus* (0.85–1.20) on one hand and *Luzocephalus* (*ca.* 0.42) on the other. The pineal foramen is close to the level of the orbits. The infraorbital sensory groove (only one visible) is very narrow and preserved mostly on the left side; on the right side only its postorbital branch is preserved. The lachrymal flexure formed by this groove is step-shaped.

The interrelationships and particular features of most bones of the skull roof show the typical lydekkerinid pattern (figure 3). In particular, the characteristics of the nasal, frontal, postorbital and frontoparietal suture as listed in the diagnosis of the family are readily seen. The nasal and premaxilla are much longer than in *Lydekkerina* as a result of more intensive preorbital growth (figures 3, 7*a*). In the proportions of these two bones *Eolydekkerina* is much more similar to *Luzocephalus*. The lachrymal is relatively short (La/C = 0.68–0.70), the postorbital projection spreads rather far anteriorly along the orbital rim so that the contribution of the jugal to the orbital rim is reduced to the extent comparable to that of *Broomulus* (figure 9; cf. Broom 1930, fig. 10). The jugal projects rather far in front of the orbit. The occipital border of each postparietal bears a short posterior projection similar to that shown in some individuals of *Lydekkerina huxleyi* (NMQR 3182; BP/1/2672a; cf. figure 7*a*) and known also in the type of '*Parotosuchus*' *rewanensis* from the Lower Triassic of Australia (Warren 1980, fig. 12, p. 27).

(*b*) *Occiput* (figure 5)

In occipital view the cheek part of the skull roof is sloped at an angle of about 45° and has a straight outline as in other lydekkerinids including *Chomatobatrachus* (Cosgriff 1974, fig. 2), *Luzocephalus* (Shishkin 1980, fig. 2*b*), *Broomulus* (authors' personal observations) and the adult *Lydekkerina* (more than 15 specimens examined; cf. figure 7*c*).

The quadrate ramus of the pterygoid bears posteriorly a crista obliqua (Bystrow & Efremov 1940), which ascends very gradually towards the quadrate. Unlike its homologue in rhinesuchids and the advanced capitosauroids, which forms a deep blade-shaped vertical lamina ('otic flange' of Watson 1962) ascending to the area of the otic notch, the crista obliqua of *Eolydekkerina* is a stout ridge. It is step-like in cross section and extends slightly less than half-way up the quadrate ramus of the pterygoid. Its upper surface, corresponding to the groove between the quadrate ramus and the blade-shaped lamina in other capitosauroids ('stapedial groove' Watson 1962), is flat rather than grooved. The crista obliqua marks the lower limit of the tympanic cavity and underlay the ligamentous process of the stapes, which extended to the quadrate and the hyoid (Shishkin 1973; Westoll 1943). In our opinion the crista obliqua corresponds to the crista posterior, which is situated on the level of the palate in a number of brachyopoids and some other temnospondyls (Shishkin 1973, figs 3, 15, 25). In *Eolydekkerina* the ridge under discussion is transitional between the crista posterior and the typical crista obliqua, in both its position and its structure. In these respects it is very similar to the crista obliqua of juvenile individuals of the non-lydekkerinid capitosauroids, both rhinesuchids (type of '*Lydekkerina*' *kitchingi* BP/1/214), and more advanced Triassic forms like the type of '*Benthosuchus*' *madagascarensis* (Lehman 1961, plate IVB).

The distal (posterolateral) end of the crista obliqua has a buttressed eroded surface, which most probably includes a portion of the quadrate and corresponds with the tubercle (tuberculum supratrochleare, Bystrow & Efremov 1940; tuberculum hyoideus, Shishkin 1973; 'boss', Watson 1962) known in the same position in many labyrinthodonts and diadectids.

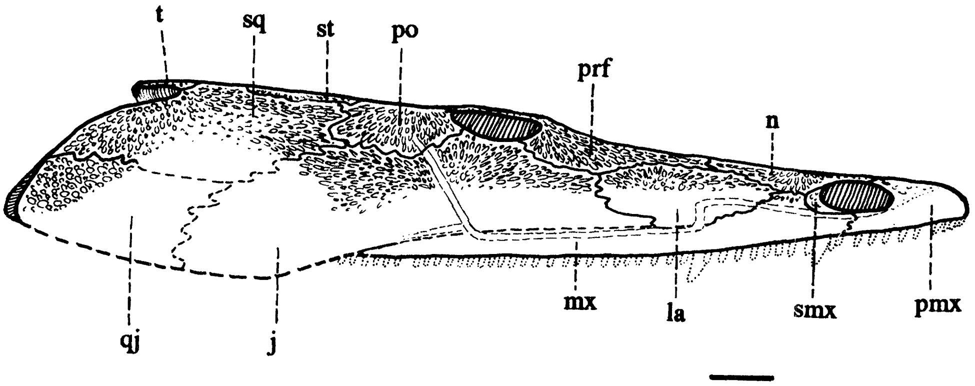

Figure 4. *Eolydekkerina magna* holotype, skull lateral view. Scale bar, 10 mm.

This structure obviously served as an attachment for the stapedial ligament and the hyoid, and has been reported in *Lydekkerina* (Parrington 1948, fig. 6c). The upper part of the quadrate ramus of the pterygoid, above the crista obliqua, forms the lamina ascendens, which contacts the occipital flange of the squamosal over its entire length on the occiput.

The occipital surface of the cheek is divided by a sharp subvertical ridge of the occipital flange of the squamosal (crista tympanica), which abuts ventrally against the tuberculum hyoideum and dorsally reaches the posterior end of the lateral margin of the otic notch. The triangular medial area between the crista tympanica, the crista obliqua pterygoidei, and the paroccipital bar of the occiput is concave, pointed towards the hyoid tubercle, and formed the anterolateral wall of the tympanic cavity. The outline of this wall shows that the cavity wedged out posteroventrolaterally towards the jaw articulation along the hyostapedial connection.

The occipital area lateral to the crista tympanica and the tuberculum hyoideum faces posterodorsally and served for the origin of the depressor mandibulae muscle. The lateral portion of the occipital flange of the squamosal belonging to this area contacts both the occipital flange of the quadratojugal and the dorsomedial projection of the quadrate. The flange of the quadratojugal bears a paraquadrate foramen immediately above the lateral portion of the quadrate condyle. The occipital exposure of the quadrate includes the smooth anteromedial projection (contacting the pterygoid and forming a buttress with it as described above) and a narrow strip of the posteriormost part of the condylar surface.

The central portion of the occiput is similar in structure to that in other lydekkerinids and more advanced capitosauroids. The posttemporal fenestrae are rather deep in contrast to the slit-like openings of rhinesuchids. The paroccipital bar (formed by processes from the tabular and exoccipital without the opisthotic between them) slopes obliquely, is rod-shaped, and lacks the lateral flattened projection.

The tabular forms at least two-thirds of the roof and floor of the posttemporal fenestra. The free tabular 'horns' overhanging the paroccipital processes are broken off and were probably moderately developed as in *Lydekkerina*. The occipital condyles are poorly preserved and formed entirely by the exoccipitals. Between the condyles the basioccipital ossification is notched dorsally for the notochord and not separated from the condyles. The exoccipital forms the standard set of processes known in the late temnospondyls. In occipital view these include the poorly developed processus lamellosus separating the foramen magnum from the supraoccipital area, the processus submedullaris separating the notochordal notch from the foramen magnum, the dorsal process meeting the postparietal, and the very short paroccipital process completely surrounding the vagus foramen. On the left side this foramen is seen to continue into the horizontal groove directed to the suture with the tabular. On the right side the exit of the vagus nerve is represented by two smaller foramina. Below the vagus foramen is the hypoglossal foramen. One more process of the exoccipital (processus suboticus) is indistinctly separated from the paroccipital process and, as in all lydekkerinids, is seen in palatal view. The posterolateral portions of the parasphenoid body are exposed in occipital view as small elevated triangular areas with the apexes pointing dorsolaterally. Each of these areas is abutted laterally by a similarly elevated area of the pterygoid body. The dorsal point of the contact between these two bones provides the insertion for the pointed anteroventral process of the stapedial footplate (processus ventralis of Shishkin 1973, 1975) and corresponds to the crista parafenestralis of the Triassic trematosaurids (Säve-Söderbergh 1936). The parasphenoid component of this area corresponds to the posterolateral end of the crista parapterygoidea (Bystrow & Efremov 1940), a paired ridge marking, in most temnospondyls, the anterior border of the otic capsule on the dorsal side of the parasphenoid body.

The stapes is preserved very close to its natural position. On the left side it extends close to the paroccipital bar of the tabular; on the right side it is slightly shifted towards the middle of the otic notch. The anterior end of its broadened footplate (processus ventralis) contacts the pterygoparasphenoid elevation as described above. The remainder of the footplate (processus vestibularis, Shishkin 1973, 1975), which faced the fenestra ovalis of the otic capsule, rests on the subotic process of the exoccipital. Immediately above the footplate the stapes is perforated by the stapedial foramen. The occipital surface of the stapes is gently

Table 1. *Comparison of skull roof indices in* Lydekkerina huxleyi (*samples of juvenile and adult individuals*) *and* Eolydekkerina magna (*holotype*)

All measurements are from originals except those for BMNH R6850 and AMNH 9799, taken from photographs. For explanation of abbreviations of measurements, see figure 1.

	Lyd BP/1 4683	*Lyd* SAM 3604	*Lyd* NMQR 1428	*Lyd* BP/1 4249	*Lyd* TvM 183	*Lyd* BP/1 4319	*Lyd* BP/1 3223	*Lyd* NMQR 3182	*Lyd* NMQR 1431	Lyd BMNH R6850	*Lim* UMZC T214	*Lyd* AMNH 9799	*Lyd* BP/1 4336	*Lyd* SAM K1121	Lyd NMQR 1435	*Lyd* NMQR 1432	*Lyd* SAM K1421	*Eolyd* BP/1 5079
L (mm)	55	49	55	54	77	80	72	68	65.5	65.5	55	75.6	91	80	72	59	80	133
A/L	0.44	0.39	0.40	0.41	0.48	0.41	0.44	0.44	0.46	0.46	0.43	0.48	0.47	0.46	0.44	0.39	0.45	0.54
O/I	0.88	1.35	1.12	1	1.18	*ca.* 1	*ca.* 1	1.08	1.0	0.77	0.90	0.80	1.0	1.16	1.0	0.96	0.85	0.72
O/B	0.22	—	0.23	0.26	0.25	0.22	0.18	0.23	0.22	0.21	0.24	0.22 0.21	0.22	—	0.22	0.25	0.22	0.19
La/C	0.91	—	—	—	0.79	0.78	0.76	0.80	0.74	0.90	0.75	0.81	0.87	—	—	—	0.84	0.68 0.70
J1/J2	0	—	—	—	0.20	0.25	0	0.25	0.24	0	0.25	0.24	0	—	—	—	—	0.50
J1/C	0	—	—	—	0.12	0.20	0	0.15	0.16	0	0.23	0.19	0	—	—	—	—	0.22 0.18

grooved along its length and faces posteroventrolaterally.

Comparison of this pattern of the occipital surface with that of *Lydekkerina* shows their very close similarity. The only distinctions we were able to detect in *Lydekkerina* relate to a more gentle slope of the tympanic crest of the squamosal, a more marked concavity along the dorsal surface of the crista obliqua pterygoidei, and the clear predominance of the quadrate in the formation of the hyoid buttress (figures 5, 7*c*). Both principal ridges bordering the tympanic cavity, the crista obliqua and crista tympanica, have been found in all of the more than 20 specimens of *Lydekkerina* examined for this study (cf. figure 7*c*). The ridges were also clearly figured by Watson (1919, fig. 4), the ridge termed crista tympanica here being briefly commented upon (Watson 1919, p. 14). The crista obliqua was also figured (although not described) by Parrington (1948, fig. 6B) in the type of *Limnoiketes*, which is considered by us to be a young individual of *Lydekkerina*. This is puzzling, as recent researchers (Cosgriff 1974; Milner 1990; Warren & Black 1985) all consider a crista obliqua to be absent in *Lydekkerina* and use this as a basis for their conclusions on the taxonomic position of the Lydekkerinidae. The crista obliqua and the tuberculum hyoideum were actually shown to be lacking in *Chomatobatrachus* (Cosgriff 1974) and *Luzocephalus* (Shishkin 1980), but this is not the case in *Lydekkerina* and *Eolydekkerina*.

The tympanic crest of the squamosal in *Eolydekkerina* and *Lydekkerina* (beginning at about the midlength of the squamosal occipital flange) is much more lateral in position than in *Luzocephalus*, where this crest begins in front of the tabular (Shishkin 1980, fig 2b). In the non–lydekkerinid capitosauroids the tympanic crest is situated very close to the squamosal–quadratojugal suture (and is particularly sharp in rhinesuchids). Its position is strictly correlated with the extent of the lateral border of the otic notch, which in fact forms a continuation of the tympanic crest. The longer the otic notch, the more lateral is the position of the tympanic crest.

With respect to the contact of the lamina ascendens pterygoidei with the squamosal flange, the condition in *Eolydekkerina* is consistent with that in *Lydekkerina* and *Chomatobatrachus*. In *Luzocephalus* the structures mentioned are separated by a broad fissura pterygosquamosa. A partial separation of the structures is also shown by Parrington (1948, fig. 6B) for '*Limnoiketes*' and ascribed by him to the juvenile condition of the specimen.

Finally it should be mentioned that the lack of occipital exposure of the opisthotic found in *Eolydekkerina* is shared by all other lydekkerinids (and capitosauroids in general) including *Lydekkerina* (figure 7*c*). The restorations of this exposure in *Lydekkerina* made by Broili & Schroeder (1937, figs 2, 3) and by Parrington (1948, fig. 1b, p. 429) are based on the description of Watson (1919).

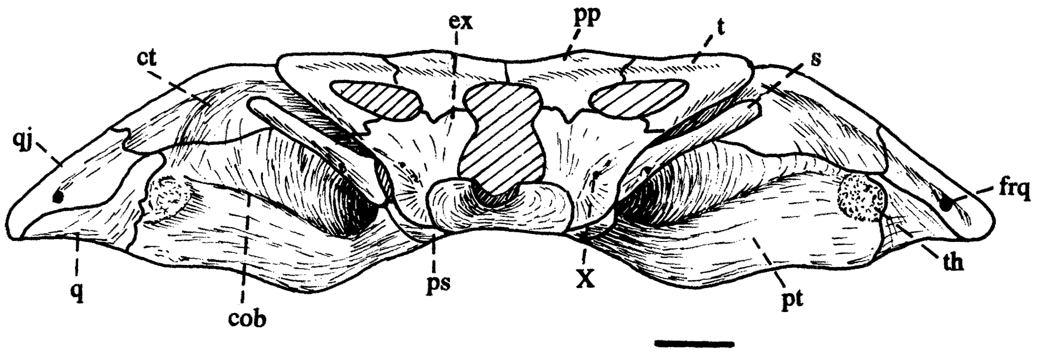

Figure 5. *Eolydekkerina magna* holotype, skull occipital view. Scale bar, 10 mm.

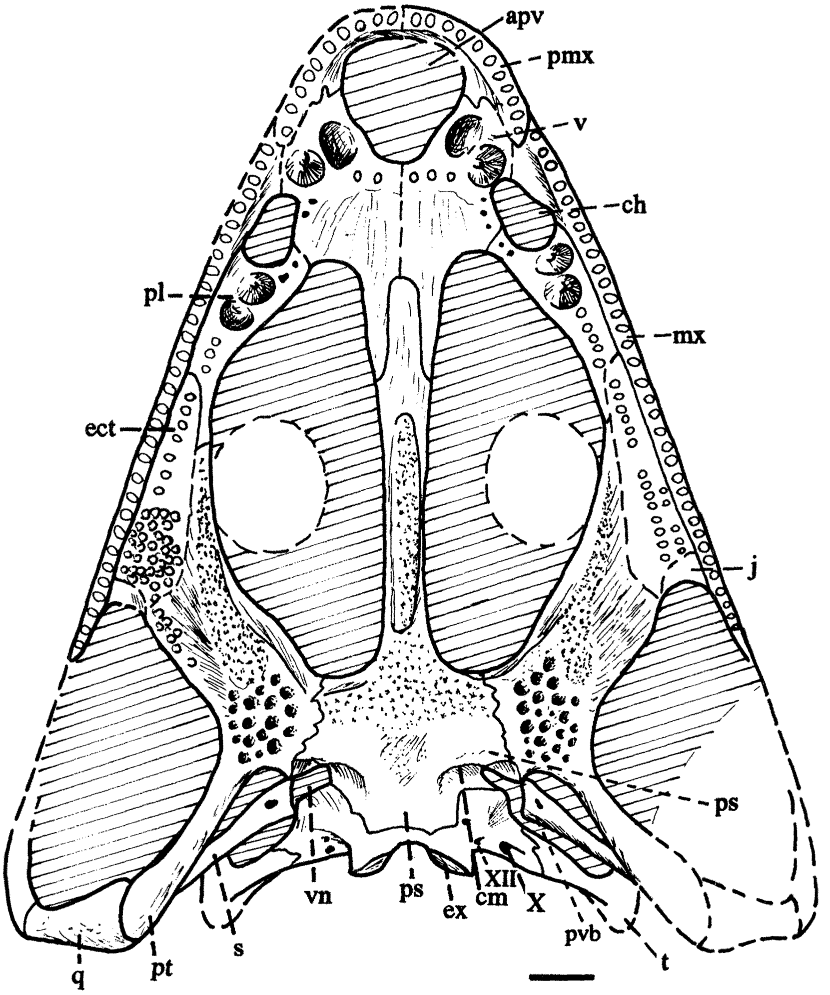

Figure 6. *Eolydekkerina magna* holotype, skull palatal view. Scale bar, 10 mm.

(*c*) ***Palate*** (**figure 6**)

The structure of the palate resembles that of *Chomatobatrachus* (cf. Cosgriff 1974, figs 32, 33). Both have moderately elongated interpterygoid fenestrae (intermediate in length between those of *Luzocephalus* and *Lydekkerina*) and a subcircular anterior palatal vacuity with its anterior border positioned very close to the premaxillary tooth row.

The anterolateral margin of the interpterygoid vacuities in *Eolydekkerina* has a slight indentation caused by the development of the palatine tusk pair, as in *Luzocephalus* and *Chomatobatrachus*. In *Lydekkerina* this indentation has been previously figured only in the type of '*Limnoiketes*' (Parrington 1948) but we have found it in many specimens examined (figure 7*b*). The choanae in *Eolydekkerina* are different from those of all other lydekkerinids in being pear-shaped rather than oval. The parasphenoid body is rather broad with the ventral surface being transversely concave. Posterior to the pterygoparasphenoid sutures the parasphenoid body tapers and forms a pair of obliquely orientated crests indicating the anteromedial boundaries of shallow muscular pockets. The surface of the pockets is

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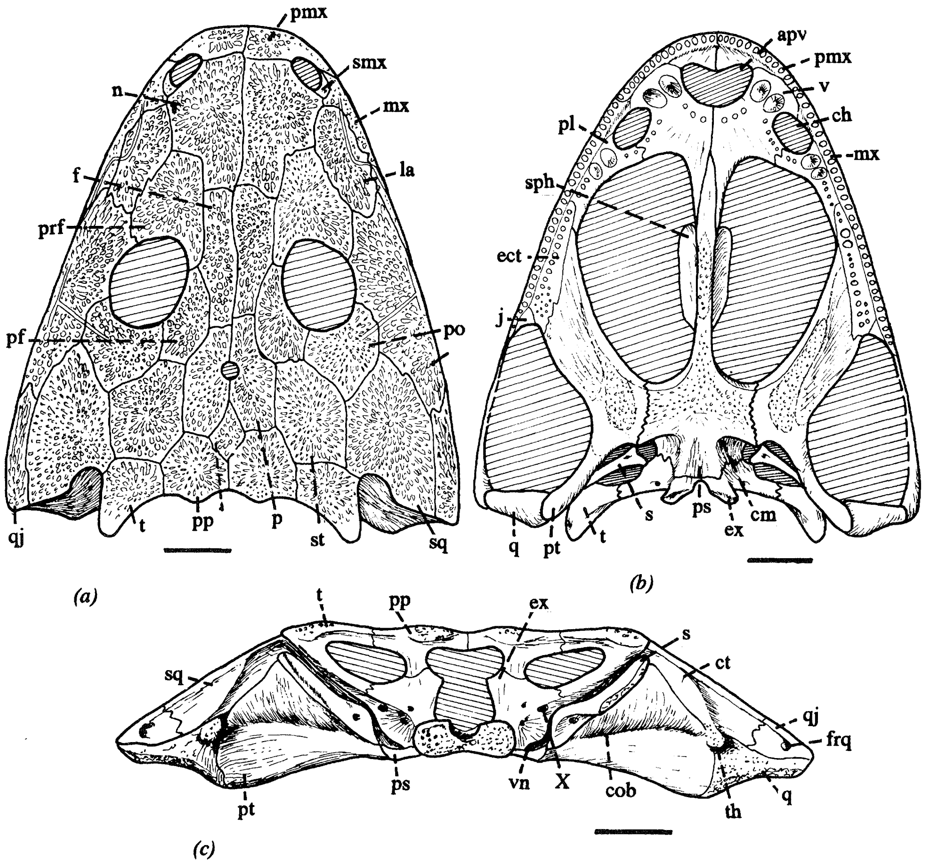

Figure 7. *Lydekkerina huxleyi* skull (mainly after BP/1/5082b and NMQR 3182): (*a*) dorsal view; (*b*) palatal view; (*c*) occipital view. Note the presence of an interparietal in (*a*), a variation found in BP/1/5082b. Scale bar, 10 mm.

concave and passes posterodorsolaterally onto the side walls of the exoccipital, as in rhinesuchids (Watson 1962). At the posterolateral margin of the left pocket the parasphenoid body sends off a small pointed process, which contacts the medial part of the subotic process of the exoccipital. The same structure on the opposite side of the palate is not as clearly visible.

At the posterior end of the pterygoid–parasphenoid suture, lateral to the muscular pockets, the posterior borders of these bones together form a broad pointed projection described above as a homologue of the crista parafenestralis. This in fact belongs more to the occipital than the palatal surface of the pterygo-parasphenoid complex. It is visible from the ventral side only because the occipital surface of the projection slopes posterodorsally.

The same structure is present (and partly seen from the palate) in *Lydekkerina* (figure 7*b*, *c*). Watson (1919) described it as a palatal 'lappet' of the parasphenoid, giving attachment to the stapes, whereas Parrington (1948) concluded that this projection actually belongs to the pterygoid. Our observations indicate that, as in *Eolydekkerina*, the projection includes both bones.

The parasphenoid component of this projection in *Eolydekkerina* is separated posteriorly from the subotic process of the exoccipital by a deep transverse notch. This stucture has been found in all *Lydekkerina* specimens examined for this study (figure 7*b*) and also identified from previously published figures of the skull of *Lydekkerina* (Watson 1919, fig. 6; Broili & Schroeder 1937, fig. 2; Parrington 1948, fig. 1B), *Chomatobatrachus* (Cosgriff 1974, fig. 32) and *Luzocephalus* (Shishkin 1980, fig. 1*b*). This notch was first described by Warren (1980) as a possibly derived character in '*Parotosuchus*' *gunganj* (Lower Triassic of Australia) where it forms a ventral exposure of the groove that continues dorsally behind the parapterygoid crest of the parasphenoid body. Warren believed that a similar structure in *Lydekkerina* did not correspond to this notch, and belonged to the lateral rather than the ventral side of the parasphenoid. This assumption, however, is not correct. The notch in *Lydekkerina*, *Eolydekkerina* and all other lydekkerinids occupies exactly the same position between the parasphenoid and the subotic process of the exoccipital, as in a number of advanced capitosauroids such as the Australian '*Parotosuchus*' or the European *Wetlugasaurus* (PIN 1277/1; 3200/277).

The position of this notch, immediately in front of the exoccipital, is suggestive that it is a ventral remnant of the embryonic fissura metotica, which separates the otic capsule from the occipital arch in vertebrates. This structure is partly retained in the Paleozoic palaeoniscoids and crossopterygians (Jarvik 1954). If our interpretation is correct, the ventral notch in lydekkerinids is a primitive character. Its non-functional (rudimentary) nature can be evidenced by its total lack on the right side of the *Lydekkerina* skull BP/1/5082B.

The anterior division of the parasphenoid (processus cultriformis) in *Eolydekkerina* is flattened at the base and anteriorly, whereas the narrower central portion is slightly elevated. The anterior end, bordered by the posterior processes of the vomers, has a rounded outline and does not reach the level of the anterior margin of the interpterygoid vacuities. The anterior half of the parasphenoid body and the posterior two-thirds of the processus cultriformis are covered by shagreen dentition. The shagreen field does not extend backwards along the sutures with the pterygoids, in contrast to rhinesuchids. On the processus cultriformis the shagreen dentition covers the elevated middle part and comes to a point anteriorly.

The pterygoid is very similar to that of *Lydekkerina* in the proportions of its palatal and quadrate branches. It is uncertain whether the pterygoid reaches the palatine bone; the position of their contact as well as that of the ectopterygoid–pterygoid suture shown in figure 6 are conjectural. Most of the pterygoid body is covered by rounded or elongated pits resembling the ornamentation of the skull roof.

Anterolaterally this ornamentation is replaced by shagreen dentition, which forms a zone narrowing along the medial border of the palatal pterygoid branch. Lateral to this belt the surface of the palatal branch has faint and poorly preserved longitudinal striations, which are considered to be an anterior continuation of the ornamented area. A small field of shagreen dentition composed of larger teeth is present on the anterolateral part of the right palatal pterygoid branch, close to the anterior end of the subtemporal fossa.

Most of the outline of the ectopterygoid can be only indirectly defined on the basis of its tooth row and the border of the pterygoid shagreen field. A notable feature is the difference in the dentition on the left and right ectopterygoids. The posterior half of the right ectopterygoid is covered by a densely packed field of large shagreen teeth, thus preventing the row of ectopterygoid teeth from extending backwards to the subtemporal fossa. By contrast the left ectopterygoid lacks shagreen and has a continuous row of teeth over its entire length. An additional row consisting of five to six small teeth is present on the posterior part of the ectopterygoid lateral to the main row.

The palatine does not show any noteworthy characters. Both of the palatine tusks are present on the left side, and on the right is one tusk and a replacing pit behind it. The palatine–ectopterygoid dentition on the left side includes at least 20 small teeth behind the palatine tusk pair. With the present state of preparation only the tips of these teeth can be seen. The palatal part of this row seems to have only five to six teeth. No ectopterygoid tusks are present.

The vomer forms three processes: the broadest anterior one accommodating the tusk pair, and those contacting the palatine and parasphenoid, respectively. The bridge formed by the vomer-palatine contact bears the parachoanal row of four to six small teeth, interrupted in the middle. The suture between these bones is not visible but probably crosses the gap in the tooth row, as in *Chomatobatrachus*. The suture of the vomer with the premaxilla is traceable for most of its extent on the left side of the skull. Anteriorly it reaches the anterior palatal vacuity halfway along its length. A straight transverse row of the interchoanal teeth (two on the right, three on the left) is present immediately behind the anterior palatal vacuity.

The palatal surface of the premaxilla is limited mainly to the tooth-bearing margin and has only a narrow palatal shelf lateral to the anterior palatal vacuity. The posterolateral end of the premaxilla is slightly overlapped by the maxilla so that the neighbouring pair of teeth of both bones are in line with each other. The premaxillary tooth row, preserved only on the left side, has 10–11 teeth.

The maxilla is broadened along the lateral side of the choana and has more than 25 teeth, which decrease in size towards the posterior end. The posteriormost five to six teeth lie behind the anterior margin of the subtemporal fossa. Anteriorly the maxilla forms the lateral choanal margin, as in most lydekkerinids and other temnospondyls. The maxillary and premaxillary teeth are moderately compressed in cross section.

In palatal view the exoccipital exhibits the base of the occipital condyles and the subotic process, which is not clearly differentiated from the paroccipital process. The condyles are damaged and bridged by a narrow portion of the basioccipital ossification, which does not form a separate element. The subotic process is broad, flattened and almost entirely exposed on the palatal side, as in all lydekkerinids. This contrasts markedly with the condition in rhinesuchids and advanced capitosauroids, where the subotic process has a more pronounced lateral wall. The anterior rim of the subotic process in *Eolydekkerina* contacts the lateral pointed projection of the parasphenoid body medially and is separated from it laterally by a ventral notch, as described above. The base of the subotic process in front of the occipital condyle bears a small foramen for the nutritive blood vessel, which is more clearly seen on the left side of the skull.

The condylar surface of the preserved right quadrate is broad on the medial side, as is common in temnospondyls. The suture with the preserved remnant of the quadratojugal could not be determined.

The posteroventrolateral surface of the stapes is exposed and can also be seen in occipital view. It is longitudinally grooved and pierced by a stapedial foramen, as described above. The posterior part of the stapedial footplate (processus vestibularis) is situated just above the lateral border of the exoccipital subotic process, as seen on the right side of the skull.

A comparison of the palatal structures of *Eolydekkerina* with those of *Lydekkerina* shows their close similarity (figures 6, 7*b*). The main characters of the parasphenoid body are the same in both forms, including the shape of the muscular pockets and their position relative to the ventral notches. In some individuals of *Lydekkerina* (e.g. NMQR 1435) the parasphenoid body has lateral projections as in *Eolydekkerina*.

The dentition in both forms is also similar. Shagreen fields on the parasphenoid and pterygoid have the same shape and extent in both forms, although *Lydekkerina* has some variations (for example, a pterygoid completely covered by shagreen dentition, as seen in SAM K1121). The ornamentation pattern of the pterygoid is also the same.

The variations in the ectopterygoid dentition seen in *Lydekkerina* are particularly noteworthy, as they include the variants seen on both sides of the *Eolydekkerina* holotype. In specimen BP/1/2672a the posterior end of the left ectopterygoid has a short additional tooth row (similar to that described in *Eolydekkerina*); the left ectopterygoid of the same specimen has a shagreen field arranged in three or four irregular rows (figure 7*b*).

Apart from these similarities the scope of variations in *Lydekkerina* includes a number of other variants approaching the *Eolydekkerina* condition. The anterior palatal vacuity, which is normally kidney-shaped in *Lydekkerina*, is more rounded (heart-shaped or triradiate) in specimens BP/1/4225, 4336 and SAMK 1121.

The anterior end of the palatal exposure of the cultriform process (normally wedge-shaped in *Lydekkerina*) has a rounded outline in specimens BP/1/4225, 4317 and NMQR 1434. The position of this end, well behind the anterior limit of the interpterygoid vacuities (as found in *Eolydekkerina*), occurs only rarely in *Lydekkerina* but nevertheless is present in one small individual, NMQR 1428. Finally, the trend towards the straight transverse arrangement of the interchoanal tooth row seen in *Eolydekkerina* was found in specimens BP/1/4336 and NMQR 1432. On the other hand, the pear-shaped outline of choanae present in *Eolydekkerina* was not seen in any *Lydekkerina* specimens examined.

In other lydekkerinids the palatal structure differs significantly from the *Eolydekkerina* pattern, or is not sufficiently well known to permit comparison. In *Chomatobatrachus* the interchoanal tooth row is deeply curved and positioned far behind the anterior palatal vacuity. The shagreen dentitition was not found at all, and the muscular pockets of the basicranial region are described as belonging to the exoccipitals (Cosgriff 1974). However, the former of these characters could be an artefact of preservation (as is probably also the case for the *Lydekkerina* specimen described by Parrington (1948)) whereas the latter seems to be doubtful (cf. Cosgriff 1974, fig. 32). One more distinction of uncertain importance is the presence of ectopterygoid tusks in the type of *Chomatobatrachus*. This may simply be a variation, which is also not uncommon in *Lydekkerina* (BP/1/2672a; figure 7*b*).

In *Luzocephalus* shagreen dentition covers most of the palatal branch of the pterygoid (as far as it is preserved), whereas on the parasphenoid it is limited to a small area at the base of the processus cultriformis. The interchoanal tooth row is concave and positioned far posterior to the anterior palatal vacuity, as in *Chomatobatrachus*. Other distinctions from *Eolydekkerina* with reference to the palate include the shape of the choana and the presence of a vomer–palatine contact on the lateral side of the choana.

6. DISCUSSION

From the above description it is evident that *Eolydekkerina* is close to the Australian *Chomatobatrachus* as regards the skull proportions and especially the shape of the palatal vacuities. However, in morphology it is most similar to the South African *Lydekkerina*, which occurs stratigraphically slightly higher in the *Lystrosaurus* Assemblage Zone. Except for the difference in size, interorbital distance and the position of the squamosal tympanic crest, most distinctions between *Eolydekkerina* and *Lydekkerina* are confined to the preorbital part of the skull; it can be assumed that these are caused by the elongation of the snout in *Eolydekkerina*. This assumption is clearly illustrated by the elongation of the premaxilla and nasal in *Eolydekkerina* and possibly by the relative shortness of the lachrymal.

With regard to the palatal structures, the same explanation may well prove to be true for the shape of the anterior palatal vacuity and especially that of the interchoanal tooth row, both characters showing variations in *Lydekkerina* toward the condition in *Eolydekkerina*. For the latter character the phylogenetic parallel (with reverse temporal succession) is provided by the evolution of the Capitosauridae. In this lineage the smaller *Wetlugasaurus*, which has a curved interchoanal tooth row, is succeeded by the much larger *Parotosuchus*, which has a longer snout combined with the transverse arrangement of the interchoanal teeth (cf. Bystrow & Efremov 1940, figs 84, 86; Welles & Cosgriff 1965, figs 21, 38e). The same trend is seen in the evolution from *Benthosuchus* to the Heylerosauridae (Bystrow & Efremov 1940, figs 4, 16; Kamphausen 1989, fig. 4).

The above assumption cannot, however, be supported for the difference in the shape of the choana and in the position of the anterior end of the cultriform process relative to the anterior end of the interpterygoid vacuities. For the latter character the phylogenetic trend in capitosaurids is the same as that of the *Eolydekkerina*–*Lydekkerina* temporal succession. This means that the position of the anterior end of the cultriform process in front of the interpterygoid vacuity in *Lydekkerina* corresponds to the advanced condition in Capitosauridae and thus cannot be attributed to the shortness of the preorbital area. Nevertheless, in summation, characters controlled by preorbital growth appear to dominate the distinctions of *Eolydekkerina* from *Lydekkerina*.

Intensive preorbital growth is a well-known feature of late ontogenetic allometric changes in many temnospondyls (Bystrow 1935; Shishkin 1973; Boy 1988; Warren & Hutchinson 1988*a*); it could be suggested that *Lydekkerina* and *Eolydekkerina* are just two developmental stages of the same form. This would seem to be consistent with the difference in their size and with some other juvenile characters recognizable in *Lydekkerina* (such as the very common variation towards retention of the anterior position of the pineal foramen on the parietals (BP/1/2672a; cf. Shishkin 1973)).

This assumption, however, cannot be accepted.

There are various lines of evidence that suggest that *Lydekkerina* is the fully grown paedomorphic form.

(*a*) ***Paedomorphic status of* Lydekkerina *and developmental trends in Lydekkerinidae***

(i) *Evidence from mode of burial and structural pattern*

Lydekkerina is known from many localitites throughout the large geographic area of the *Lystrosaurus* Assemblage Zone (Kitching 1978); among the more than 200 specimens collected so far, the overwhelming majority have a skull length of 60–80 mm (cf. Parrington 1948). Thus as regards size and the most important morphological characters (see description) the generic pattern is rather stable. In principle, larvae of the same age can be trapped and buried together at specific localities, but it is unlikely that the same taphonomic bias would apply for the entire area of distribution. On average, preservation of the fossil record tends to favour the most common and long-term events rather than ephemeral ones such as transitional ontogenetic stages. For example, in Palaeozoic branchiosaur-like temnospondyls, those known only from juvenile individuals usually prove to be neotenous or paedomorphic (Boy 1972).

The paedomorphic nature of *Lydekkerina* is also proved by the following adult cranial characters. Ornamentation of dermal bones shows only slight or no evidence of local intensive growth, a feature not present in temnospondyl juveniles (Boy 1974; Bystrow 1935). Other features suggesting maturity are weakly developed sensory grooves and extensive development of endocranial ossifications (cf. Boy 1974). Many specimens have an ossified sphenethmoid (figure 7*b*; see also Broili & Schroeder 1937) and in some specimens (NMQR 3182; BP/1/4336; 2762a) the epipterygoid and otic elements are also ossified. *Lydekkerina* thus represents a combination of juvenile and mature characters, substantiating the above conclusion of its paedomorphic status.

This evidence suggests that *Lydekkerina* evolved from a more fully developed (non- or less paedomorphic) *Eolydekkerina*-like ancestor. This is in accordance with both their main morphological distinctions and their respective stratigraphic positions.

(ii) *Evidence from comparative studies*

Additional evidence that the cranial pattern of *Lydekkerina* is paedomorphic can be obtained in two ways. First, there should be indications that at least some trends in the growth changes in *Lydekkerina* conform to differences between this genus and *Eolydekkerina*. Secondly, it is necessary to show that distinctions of *Lydekkerina* from a more fully developed lydekkerinid pattern are paralleled by the juvenile characters of some closely related capitosauroid group. This can be done by comparison of *Lydekkerina* with immature rhinesuchid specimens.

Analysis of growth changes in Lydekkerina: The sample of *Lydekkerina huxleyi* available for comparison permits an analysis of skull-roof characters only. Of these, measurable characters that are different in *Lydekkerina* and *Eolydekkerina* are: the degree of preorbital elongation (A/L); the relative length of the lachrymal (La/C); the extent of preorbital projection of the jugal (J1/J2, J1/C); and the relative width of the orbits (O/I, O/B).

The sample studied is too small to reveal in detail the correlation between the increase of size and morphological change. Hence this analysis is confined to comparing a group of smaller specimens (49–55 mm midline skull length) to the rest of the sample (skull length 58–90 mm). Of the smaller specimens, the extent of the lachrymal and jugal can be determined (and measured) in only one specimen (BP/1/4683).

As seen from table 1, the preorbital elongation of the skull in most specimens of the smaller group of individuals corresponds to, or is even lower than, the minimum value found in the larger sample (A/L 0.39–0.41 and 0.41–0.48 in the two groups, respectively). Only one small specimen (BP/1/4683) falls within the average of the 'larger' range with A/L = 0.44. For *Eolydekkerina* A/L = 0.54. This comparison shows a uniform trend from the youngest *Lydekkerina* individuals towards the condition in the fully developed *Eolydekkerina*.

The lachrymal in the only small specimen where it can be seen is fairly long and occupies 0.91 of the orbitonarial length (La/C index). This is close to the lower part of the range of this index in the larger sample (0.90–0.74). *Eolydekkerina* exceeds the 'normal' *Lydekkerina* condition with a La/C value of 0.68 and 0.70 for the different sides of the skull.

The growth transformation of the jugal is also quite obvious. Specimen BP/1/4683 of the smaller group has practically no preorbital projection of the jugal, so both indexes used to estimate this character (J1/J2, J1/C) give a value of 0. This is also not uncommon for the larger individuals, but in general the antorbital/postorbital projection ratio (J1/J2) ranges from 0 to 0.30. The growth of the anterior jugal projection with respect to the orbitonarial distance (J1/C) has almost the same range (0–0.24). In *Eolydekkerina* the former index is much higher (0.50) whereas the latter does not exceed the range in *Lydekkerina* (0.18 and 0.22, for different sides of the skull).

The orbital width : interorbital distance ratio (O/I) does not exibit as marked a trend in the growth of *Lydekkerina*. In the younger group only the smallest specimen (SAM 3604), with a skull length of 49 mm, shows unusually large relative orbital width, which can be expected in a juvenile (O/I = 1.35). The rest of the smaller specimens shows a broad scope of variation (1.0–0.88), which nearly corresponds to the range of most of the normal sample (O/I = 1.27–0.8). The only exception in this sample is specimen R6850, which has a very broad interorbital distance (O/I = 0.77). In *Eolydekkerina* this value is even less (O.72).

The O/B ratio shows *Eolydekkerina* (O/B = 0.19) and adult *Lydekkerina* (O/B = 0.25–0.18) having similar values, which are somewhat lower than those of younger *Lydekkerina* individuals (O/B = 0.26–0.22). This reflects the relative reduction of the orbit size with growth, a feature well known in the ontogeny of temnospondyls, but also shows that in this parameter *Lydekkerina* corresponds to the normal adult lydekkerinid condition.

The comparison demonstrates that, at least for some measureable characters (A/L, La/C, J1/J2, and to some extent O/I and O/B), the growth changes in *Lydekkerina* have the same trends as seen from comparison of this genus with *Eolydekkerina*. This substantiates the conclusion that the differences between *Eolydekkerina* and adult *Lydekkerina* arose phylogenetically by the removal of definitive ancestral (*Eolydekkerina*) stages for some characters.

Similarly it can be demonstrated that if the morphological trend seen from a comparison of *Lydekkerina* with *Eolydekkerina* were continued it would imply the transition to the rhinesuchid pattern (see below).

Comparison of lydekkerinid patterns with rhinesuchid ontogeny: Numerous rhinesuchid juveniles discovered by one of us (JWK) at a single locality on the Beeldhouersfontein farm, Murraysburg, situated in the *Cistecephalus* Zone, enabled this study. About 60 small individuals with an average skull length of 50–65 mm (Kitching 1978) were found in a mudstone lens cut into coarser surrounding siltstone and overlain by a sandstone layer. This burial preservation is unique for the Lower Beaufort. It appears that the fossil-bearing sediments were probably deposited in an ephemeral pool in which mass death of the young individuals occurred, possibly as a result of drought or oxygen deficiency caused by overheating of the water.

As suggested by Kitching (1978), these individuals (figure 8*a*) are most probably the early growth stages of some rhinesuchid similar to *Muchocephalus muchos* specimen BP/1/213 (Watson 1962) known from the overlying *Dicynodon* Assemblage Zone on the neighbouring farm, Ringsfontein. This is supported by two lines of evidence.

(1) No temnospondyls other than rhinesuchids have ever been recorded in the *Cistecephalus* and *Dicynodon* (*Daptocephalus*) Assemblage Zones (Kitching 1978). Taking this into account, the unusual accumulation of numerous conspecific individuals of small size can be more easily explained by the mass death of rhinesuchid juveniles rather than the occurrence of a totally new form.

(2) Morphological evidence from the specimens reveals their juvenile nature. Apart from their small size (5–10 times smaller than normal adult rhinesuchid skulls) they also demonstrate relatively large orbits and a pineal foramen positioned anteriorly on the parietals, usually in front of their ossification centres, as is common for temnospondyl larvae and neotenic forms (Shishkin 1973; Boy 1974). The ossification centre of the prefrontal is situated in its anterior half, as in juveniles; in some specimens a zone of weakness is present between the cheek and skull roof table (judging by an isolated skull table BP/1/2942b); and the position of the posterior table border is in line with the quadrates (BP/1/3705 & 2931). These characters are not present in adult rhinesuchids but could be expected in their juveniles.

On the other hand the individuals under discussion appear to have undergone metamorphosis, as no branchial denticles were found and all skull roof elements are well ossified and joined by sutures. Ornamentation of the skull roof (pits in the central areas of bones and grooving around the periphery) is typical for postmetamorphic stages. In some cases (BP/1/2942a), pitted ornamentation occupies most of the bone surfaces, as in adult rhinesuchids.

Examination of rhinesuchid cranial material from various South African institutions (Bernard Price Institute, Geological Survey, National Museum, Rubidge Collection, South African Museum, Transvaal Museum) shows that the lydekkerinid skull roof pattern differs from that of the adult rhinesuchid in the following characters.

1. Preorbital part of skull roof short (A/L about 0.5).
2. Otic notch short and posteriorly broadened.
3. Supraorbital sensory grooves usually absent or weakly developed.
4. Supratemporal excluded from otic notch.
5. Lachrymal long (La/C usually not less than 0.7).
6. Preorbital projection of jugal much less than postorbital one (J1/J2 not more than 0.5).
7. Anterior ends of frontal broad.
8. Prefrontal does not narrow posteriorly.
9. Posterior margin of nasal is step-shaped owing to truncation of anterior end of prefrontal.
10. Anterolateral projection of postorbital weakly or moderately developed.

If the *Lydekkerina* skull-roof pattern corresponds to the juvenile stage of the typical (ancestral) lydekkerinid life cycle, as suggested above, then comparison of this pattern with that of rhinesuchids could be in accordance with von Baer's Law. One would thus expect differences in cranial morphology between *Lydekkerina* and rhinesuchid juveniles to be much less than those between adult rhinesuchids and (fully grown) lydekkerinids. The following data fit this expectation.

In examining the rhinesuchid juveniles (table 2) the same procedure was followed as for *Lydekkerina*. Measurements of the smallest skull (50 mm midline length) were compared with the rest of the sample (55–65 mm); two larger rhinesuchid specimens (BP/1/213, 214) ranging in size from 84 to 236 mm in the midline skull length (figure 8*b*, *c*), were also included in the comparison. These two are also from the Ringsfontein farm, Murraysburg, from the same horizon as *Muchocephalus*. The smaller of these skulls (specimen BP/1/214) was previously described as '*Lydekkerina*' *kitchingi* Broom; the larger (BP/1/213) is the holotype of *Muchocephalus muchos* Watson (Broom 1950; Watson 1962) (for comments on validity of these taxa see Kitching 1978).

As seen from a comparison of tables 1 and 2, the relative length of the preorbital area (A/L) of the juvenile rhinesuchid skull roof (0.43–0.46) is of the same order as that of adult *Lydekkerina* (0.41–0.48). However, in the type of '*Lydekkerina*' *kitchingi*, which is intermediate in size between the discussed juveniles and fully grown rhinesuchids, this index (0.50) is greater than that of the top of the *Lydekkerina* range, and in the fully grown *Muchocephalus* (236 mm) it is even higher (0.55). This indicates accelerated growth of the antorbital area with age.

Ontogenetic reduction of the lachrymal is reflected by the change of the La/C index. In rhinesuchid

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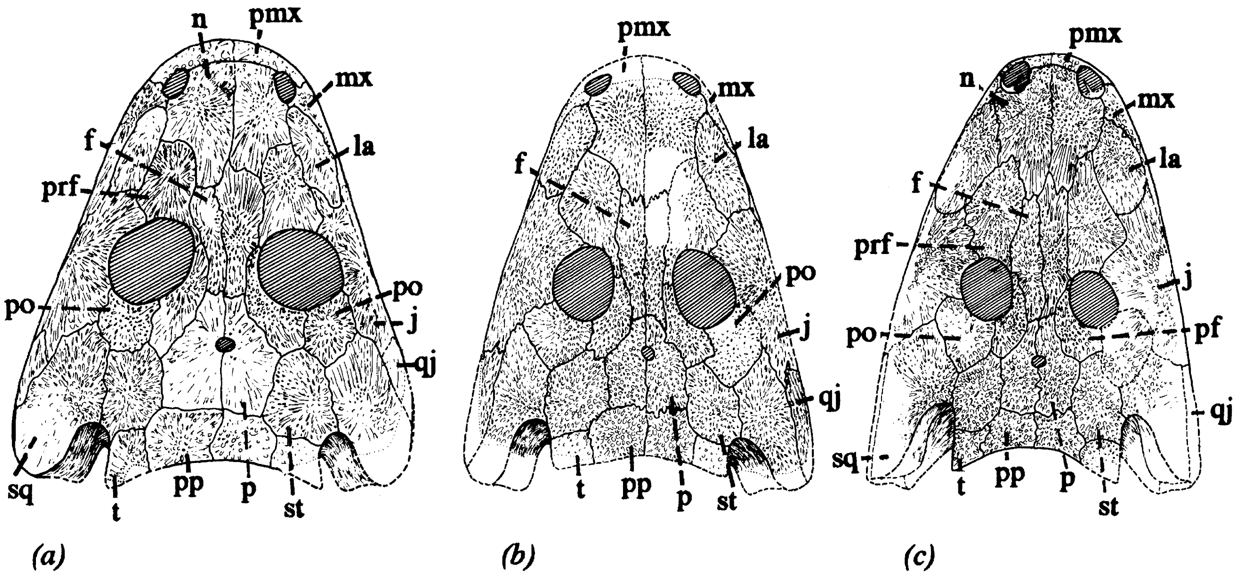

Figure 8. Rhinesuchid growth series in dorsal view: (*a*) juvenile (unnamed) BP/1/3705 skull; (*b*) semi-grown stage (presumed late juvenile of *Muchocephalus muchos* known as the type of '*Lydekkerina*' *kitchingi*) BP/1/214; (*c*) adult (type of *Muchocephalus muchos*) BP/1/213. Not to scale.

Table 2. *Comparison of skull roof indices in juvenile, semi-grown and adult rhinesuchids*

Specimens 1–8, hitherto undescribed rhinesuchid juveniles from Beeldhouersfontein, Murraysburg district (*Cistecephalus* Assemblage Zone); 9, type of '*Lydekkerina*' *kitchingi* (Broom 1950); 10, type of *Muchocephalus muchos* (Watson 1962), both 9 and 10 from Ringsfontein, Murraysburg district, C.P. (*Dicynodon* Assemblage Zone).

	specimen and specimen numbers									
	1 BP/1 3075	2 BP/1 2931	3 BP/1 3079	4 BP/1 3070	5 BP/1 2942A	6 BP/1 2958	7 BP/1 2941	8 BP/1 2965	9 BP/1 214	10 BP/1 213
A/L	0.46	0.43	—	—	—	—	—	—	0.50	0.55
O/I	1.21	1.0	1.23	1.15	1.44	1.2	1.2	1.22	1.0	0.8
O/B	0.25	0.23	0.23	0.24	0.26	0.22	0.26	0.24	0.21	0.18
La/C	0.76–0.86	0.75	—	—	0.75	—	0.65	0.65	0.63	0.65
J1/J2	0.5–0.36	0.71	0.35	0.63–0.68	0.30–0.37	0.43	—	0.45	0.63	1.7–2.0
J1/C	0.23–0.26	0.26–0.31	0.17	0.31	—	—	0.23	0.24	0.23	0.29
L	55 mm	56 mm	*ca.* 60 mm	*ca.* 60 mm	60–65 mm	65 mm	*ca.* 65 mm	*ca.* 62 mm	84 mm	236 mm

juveniles the lachrymal is still relatively long (La/C = 0.86 and 0.76) on both sides of the smallest specimen (BP/1/3705) and 0.75–0.65 for the rest of the sample. These figures indicate that the degree of lachrymal reduction in rhinesuchids is somewhat larger than in *Lydekkerina* (La/C ranges from 0.91 to 0.75). Lachrymal reduction is emphasized in further development of rhinesuchids (from semi-grown juveniles to adults) where the La/C index is reduced to 0.65 (table 2). In other rhinesuchids examined, but not included in this comparison, La/C decreases to 0.55.

These data demonstrate that, although the La/C value of *Eolydekkerina* (0.7–0.68) is well above the developmental stage represented by the adult *Lydekkerina*, it is still within the range of rhinesuchid juveniles. This is because the degree of lachrymal reduction in adult lydekkerinids is considerably smaller than in rhinesuchids.

Tables 1 and 2 show a sharp difference in the design of the jugal in rhinesuchids and lydekkerinids. Data on rhinesuchid development implies that the lydekkerinid jugal pattern (J1/J2 = 0–0.25) probably corresponds to the earliest postmetamorphic stages of rhinesuchids, even younger than those available for our examination. The smallest rhinesuchid juvenile studied (BP/1/3705) already has a J1/J2 value of 0.36 and 0.50 on opposite sides, whereas the rest of the juvenile sample ranges from 0.30 to 0.70. During later development towards the semi- and fully grown stages, the relative length of the anterior projection of the jugal increases substantially (J1/J2 = 1.0–2.0). In *Eolydekkerina* (J1/J2 = 0.50) the anterior projection of the jugal is much longer than in *Lydekkerina* but still corresponds to the average of the range of juvenile rhinesuchids.

It thus appears that ontogenetic remodelling of the jugal was retarded and truncated in the Lydekkerinidae in general, whereas in the ontogeny of the deeply paedomorphic *Lydekkerina* it was almost negligible.

The size of the orbits relative to interorbital distance (O/I) in rhinesuchid juveniles (1.44–1) is larger than in *Lydekkerina* (1.35–0.77 including the youngest individuals). In this respect the condition in *Lydekkerina* is more adult. In the semi-adult rhinesuchid ('*Lydekkerina* *kitchingi*') this value is 1.0 whereas in fully grown rhinesuchids it ranges from 0.80 in specimen BP/1/213 to 0.60 in specimens not included in this study. *Eolydekkerina* (O/I = 0.72) falls within the range of adult rhinesuchids, thus also having smaller and wider separated orbits.

With respect to the O/B index, the rate of changes in rhinesuchid ontogeny is comparable to that in Lydekkerinidae. Both rhinesuchid juveniles (table 2) and the smallest *Lydekkerina* specimens (table 1) have the same O/B range, 0.26–0.22. In adult *Lydekkerina* and *Eolydekkerina* the range of O/B (0.25–0.18) is close to that of the semi-grown and adult rhinesuchids from Ringsfontein, Murraysburg. In sum, both parameters characterizing the relative size of orbits do not reveal important differences between the lydekkerinid and rhinesuchid development.

Examination of ontogenetic trends of non-measurable characters listed above as separating lydekkerinids from rhinesuchids shows that most of the characters actually occur in rhinesuchid juveniles. The following characters (when preserved) are present in all the specimens from Beeldhouersfontein: broadening of the anterior end of the frontal; lack of posterior narrowing of the prefrontal; rudimentary or absent anterior projection of postorbital; and a broad otic notch. In addition, the step-like posterior border of the nasal was found in two of the four specimens in which this area is preserved.

The typical (adult) rhinesuchid condition for all the characters listed first appears as late as the semi-adult stage represented by specimen BP/1/214 from Ringsfontein. On the other hand at least one rhinesuchid character (inclusion of supratemporal in the otic notch border) is found in all the stages examined. To some extent the same may be true for the presence of the well-developed supraorbital sensory groove that occurs in many adult rhinesuchids and is present in the juvenile specimen BP/1/2942a (the only specimen in which the surface of the preorbital region is sufficiently well preserved).

The early developmental stages of rhinesuchids thus have many characters that are considered diagnostic for lydekkerinids. These include the shape of the frontal, prefrontal, nasal and postorbital bones, and also the relative length of the lachrymal and the short preorbital projection of the jugal. This implies that the Lydekkerinidae evolved from the more fully developed capitosauroid ancestors by gradual truncation of ontogeny and loss of some ancestral characters (cf. Milner 1990).

This process was combined with the acquisition of many advanced characters unknown in the Permian capitosauroids. These include exclusion of the supratemporal from the otic notch, development of unsupported tabular horns, the position of the muscular crests of the parasphenoid body in line with the posterior end of the pterygoparasphenoid sutures, spread forward of the palatine along the medial choanal border, unpaired anterior palatal vacuity and loss of vomer–palatine shagreen dentition. The presence of these characters in all lydekkerinids provides evidence that they were acquired very early in lydekkerinid evolution and probably inherited from a common ancestor. By contrast, the degree and pattern of paedomorphic change is variable among the different genera. For example, *Eolydekkerina* is more juvenile-like than *Luzocephalus* in possessing the preorbital step and the sagittal depression of the skull roof, but is more mature in lacking the pterygosquamosal fissure, which is retained by *Luzocephalus*. The paedomorphic trends culminate in *Lydekkerina*, which is comparable with the earliest rhinesuchid juveniles in size, the shortness of the preorbital region, and the structure and proportions of the jugal and lachrymal.

This accounts for the striking similarity in the skull roof of *Lydekkerina* and juvenile rhinesuchids, which may be confusing for taxonomic analysis. The best example of this is provided by the description of the semi-grown rhinesuchid skull from Ringsfontein as *Lydekkerina* ('*L*'. *kitchingi*) (Broom 1950).

7. COMPOSITION OF LYDEKKERINIDAE

(*a*) *Structure of family*

The above description of *Eolydekkerina*, which appears to be the ancestor of *Lydekkerina* and also had a more complete ontogeny, now removes the break between the latter genus and the larger lydekkerinids *Chomatobatrachus* and *Luzocephalus*. These two genera have been included in the separate family Luzocephalidae Shishkin (Warren & Hutchinson 1988*a*; Milner 1990; cf. Milner 1991). The family was proposed (Shishkin 1980) because *Luzocephalus* had a number of characters that separate it from the rest of the Lydekkerinidae. These primarily include open pterygosquamosal fissure, long orbitopineal distance, and double contact between the palatine and vomer (for more details see p. 1656). As clearly implied by figure 11, the subfamily Luzocephalinae could be retained for this genus, but for the present we prefer to consider the Lydekkerinidae as a family without any subdivisions.

(*b*) *Survey of lydekkerinid genera*

(i) *Chomatobatrachus and Luzocephalus*

There is thus no doubt about the lydekkerinid status of *Luzocephalus* (a type species *L. blomi* Shishkin from the Vokhmian Horizon of Northern Russia, and a group of species from the Wordy Creek Formation, Greenland, all probably synonomous with *L. kochi* (Säve-Söderbergh 1935; Shishkin 1980)). The same is the case for the type of *Chomatobatrachus* (*C. halei*) Cosgriff from the Kokatea Formation of Tasmania (Cosgriff 1974). However, the lower jaw assigned to this genus (Cosgriff 1974, figs 41, 42) most probably belongs to a rhytidosteoid, judging from the structure of its glenoid portion (Warren & Black 1985) and the coronoid series (Shishkin 1994).

(ii) *Cryobatrachus*

Cryobatrachus (*C. kitchingi*) Colbert & Cosgriff from the Lower Fremouw Formation of Antarctica is known mainly from the holotype, a small incomplete skull roof (46 mm midline length) seen from the ventral side

(Colbert & Cosgriff 1974; Cosgriff & Hammer 1984). Distinctive characters of this form include the narrowness of the skull, the short interorbital distance, and the long otic notch deeply incising the squamosal. The holotype exhibits a number of lydekkerinid characters such as a shortened preorbital region, as restored by Colbert and Cosgriff (1974, figs 14, 15A), the lack of a preorbital projection of the jugal, the long lachrymal, and the postorbital not projecting laterally. However, as was shown above, all these characters can be expected in any small early capitosauroid individual regardless of its family affinities. In view of this, the only specific evidence to attribute the holotype to the Lydekkerinidae remains the alleged presence of the septomaxilla as figured by Colbert and Cosgriff. This element is unknown in capitosauroids other than the Rhinesuchidae and Lydekkerinidae; but assignment of the specimen to the former is precluded by the condition of its supratemporal which does not border on the otic notch. An additional argument is that the dermal ornamentation seen on many referred fragments is *Lydekkerina*-like (i.e. the bones are fine-pitted without the grooving along the periphery). The inclusion of *Cryobatrachus* in the Lydekkerinidae thus appears to be justified until arguments to the contrary are revealed. This solution is also consistent with the provenance of the holotype, which has a tetrapod assemblage equivalent to that of the *Lystrosaurus* Assemblage Zone.

(iii) *Indobenthosuchus*

Some poorly known lydekkerinids occur in the Upper Panchet Series of the Damodar Valley in India. The holotype of *Lydekkerina panchetensis* (Tripathi 1969), found in association with several *Lystrosaurus* skulls, comprises a weathered and incomplete skull roof with a calculated length of about 100 mm. As in the South African lydekkerinids, a sagittal depression of the skull roof is present. This form is distinctive for its very short preorbital region ($A/L = 0.39$, as calculated from the restoration by Tripathi (1969, fig. 1), and the lachrymal extending far backwards beyond the anterior orbital border. Unusual for lydekkerinids are the pointed anterior ends of the parietals and frontals (cf. Tripathi 1969, p. 19, fig. 1). Doubtful features of the original restoration are the long pointed prefrontal occupying most of the orbitonarial distance, reduction of nasals, and the lachrymal reaching up to the nostrils. This form may well be a lydekkerinid and is possibly congeneric with *Indobenthosuchus panchetensis*.

Indobenthosuchus (*I. panchetensis* Tripathi) is from the same horizon as *Lydekkerina panchetensis*, but at another locality. It is known from a single badly damaged and weathered skull about 100 mm in length. A suggestion of its benthosuchid affinities (Tripathi 1969, p. 22) is not supported by evidence of any particular resemblances with this group. The presence of a Z-shaped curve of the lachrymal flexure of the infraorbital sensory groove mentioned in the diagnosis is at variance with the accompanying figure, which shows this flexure to be step-like, as in lydekkerinids (Tripathi 1969, p. 22, fig. 2). The skull outline (Tripathi 1969, Pl. II, figs 1, 4), the lack of the preorbital jugal projection, the shape of the anterior palatal vacuity, and the pattern of the palatal dentition are consistent with the condition in *Lydekkerina*. The orbits, as restored, are well in front of the middle of the skull roof so that the relative length of the preorbital (A/L) appears to be only 0.36, rather close to the type of *L. panchetensis*. The synonymy of both taxa seems likely. One more specimen ascribed to *Indobenthosuchus panchetensis* is a lower jaw from the type locality that shows shagreen dentition in the posterior part of the coronoid series. This is also not at variance with the *Lydekkerina* pattern. Synonymy of *Indobenthosuchus* with *Lydekkerina* is not ruled out, but this is difficult to access without more complete material of the Indian form.

Five more Gondwanan forms that have in the past been listed among lydekkerinids and are each known from only a single skull are '*Lydekkerina*' *putterilli*, *Putterillia*, *Broomulus*, *Limnoiketes* and *Deltacephalus*. None of these have been re-examined in detail since their original description, except for *Deltacephalus* (Hewison 1996). The first three forms were only briefly inspected by Cosgriff (1984, p. 35), who assigned them to *Lydekkerina huxleyi*. In the present study all these taxa are for the first time re-evaluated together. Apart from *Deltacephalus* all of them are from the Middle Beaufort Group (*Lystrosaurus* Assemblage Zone) of South Africa and were collected from the Harrismith district (an area that has also produced most known specimens of *Lydekkerina* (Kitching 1978)). Re-assessment of the systematic position of these forms is given below.

(iv) *Lydekkerina*

This genus certainly includes the forms described as *Limnoiketes* and *Putterillia*. According to the senior author (personal observation), the most peculiar characters of the type of *Limnoiketes paludinatans* (UMZC T214) are: (1) the short interorbital distance, (2) the curved and steeply sloped occipital outline of the cheek, and (3) the lack of an interorbital depression.

Points (1) and (2) are the juvenile characters found by us in other smaller individuals of *Lydekkerina huxleyi*; (3) is most probably an individual variation. It may be further noted that the marked pterygoid flange present on the palate of the holotype of *Limnoiketes* is also developed to almost the same extent in some individuals of *Lydekkerina* (BP/1/4317; BP/1/4336). Likewise, from measurements analysed in this paper *Limnoiketes* also cannot be distinguished from *Lydekkerina huxleyi* and is very similar to specimen BP/1/4319, which is much larger in size (table 1). There is also nothing in Parrington's (1948) description that justifies generic separation. Parrington's conclusion that *Limnoiketes* is an 'immature animal' whose 'adult size would not have been very great' (Parrington 1948, p. 440) implies again that the fully grown stage of this form would most likely correspond to *Lydekkerina*. We consider the specimen in question as a juvenile of *Lydekkerina huxleyi*.

Two specimens of *Putterillia* (*P. platyceps* Broom 1930) have been described: the skull TM 168 referred to as the holotype, and the paratype TM 88, comprising a poorly preserved dermal shoulder girdle and lower jaw of an individual smaller than the holotype. In the erection of the genus Broom (1930, fig. 9B) relied mostly on the shoulder girdle, as it was considered to differ from that of *Lydekkerina* because of its great width and long median contact between the clavicles. We confirm the presence of the latter character but the same is present in some specimens that are undoubtedly *Lydekkerina huxleyi* (e.g. BP/1/4336). We consider that the holotype of *Putterillia* also belongs to the same form. The skull roof of this specimen is not prepared; the few details of the skull roof shown by Broom (1930, fig. 7) actually pertain to its ventral side and are consistent with the pattern seen in *L. huxleyi*.

The distinguishing characters listed by Broom for the type of *Putterillia* pertain mainly to the palate and are: wide snout; parasphenoid body (shown to be unusually wide and short) toothless and widely articulated with the exoccipitals; pterygoid also sutured with latter bone. Our examination did not confirm the presence of any of these characters. The snout is not as robust as restored by Broom (1930, fig. 7). What is figured as parasphenoid body is in fact only the smooth posterior part of this structure. The rest, which is tooth-bearing in *Lydekkerina*, is not preserved. The area of the parasphenoid–exoccipital contact resembles that of *Lydekkerina* in showing a broad ventral exposure of the exoccipital subotic process and a ventral notch in front of it. The pterygoid–exoccipital contact mentioned by Broom does not exist. The pterygoid shagreen field shown by Broom to cover the entire palatal branch of this bone actually wedges out anteriorly and is here replaced with ornamentation ridges as in *L. huxleyi* (figure 7*b*; see also Broili & Schroeder 1937, fig. 2). It is thus evident that *Putterillia platyceps* Broom is a junior synonym of *Lydekkerina huxleyi* (Lydekker 1889), as suggested by Cosgriff (1984).

(v) *Broomulus* (*figure* 9)

Broomulus (Romer 1947) was proposed as a new generic name for the type of *Lydekkerina dutoiti* Broom (1930). The holotype (MGM 4285) is a broad skull (midline length of 84 mm) associated with a lower jaw and the anterior portion of the vertebral column. The right side of the skull roof is badly distorted, particularly in the postorbital region, and the facial region is not completely prepared. Broom (1930, fig. 10) described the skull roof very briefly and provided a generalized figure based on the sutural arrangement of the left side of the skull. He did not exclude generic separation of this form but considered that the palate must be prepared before this can be done.

Romer's (1947) account is based entirely on Broom's data and points out the shortening of the face and the unusual breadth of the skull as a diagnostic feature of the genus. Among other characters shown on Broom's figure and stressed by Romer, the most peculiar are the extension of the lachrymal right up to the narial border, and the postorbital–parietal sutural contact, which is typical of ichthyostegids but very uncommon in temnospondyls. Romer suggested that the specimen may be generically identical to the type of *Putterillia platyceps*. Some authors (Parrington 1948; Swinton 1956; Carroll & Winer 1977) recognized *Broomulus* as a valid lydekkerinid genus. Cosgriff (1974) considered it *incertae sedis* but later (Cosgriff 1984) attributed it to *Lydekkerina huxleyi*. In Milner's (1990) review of the temnospondyl genera it is not mentioned at all. Swinton (1956) thought this genus to be very close to *Deltacephalus* (see below).

Reinvestigation and additional preparation of the type of *Broomulus* has led to an improved restoration of the skull roof (figure 9). The parietal–postorbital contact is not present; the lachrymal was obviously separated from the narial border by the septomaxilla, which is now lost. The position of this bone is indicated by the posterolateral pointed projection of the left external naris.

The specimen exhibits a remarkable anomaly in the arrangement of the preorbital bones of the right side: the prefrontal is strongly reduced and much of its normal anterior extent is taken up by the enlarged nasal; whether the right lachrymal is developed at all is not certain, as most of its presumed area is still covered by matrix. This asymmetry is certainly not caused by the posthumous displacement of bones on the right side of the skull, as all of its preorbital region is preserved intact.

The specimen closely conforms to the lydekkerinid pattern in the following aspects.

1. Preorbital region short (A/L = 0.46).
2. Lachrymal occupies most of orbitonarial distance (La/C = 0.84).
3. Preorbital projection of jugal is short and far exceeded by postorbital one (J1/J2 = 0.24).
4. Nasal has step-like posterior border.
5. Frontals broadened and not pointed anteriorly.
6. Anterior parts of parietals not narrowed or pointed at their ends.
7. Pineal foramen lies in the anterior half of the parietals, as is very common in *Lydekkerina*.
8. Sensory grooves not developed.
9. Otic notch broad.
10. Broad ventral exposure of subotic process of the exoccipital and presence of notch between it and the parasphenoid.
11. Palatal dentition pattern similar to that in *Lydekkerina*.

Although most of these characters (1–7, 9) have been shown in this paper to be features common to juveniles of early capitosauroids, their presence in the type of *Broomulus* can hardly be ascribed to its immaturity as this specimen is rather large in comparison to the average *Lydekkerina* and shows an ossified sphenethmoid.

Generic separation of the specimen seems to be well justified. Apart from the very great width of the skull, the most important features precluding it from *Lydekkerina* are as follows.

1. Ornamentation even more finely pitted than in *Lydekkerina* with pit walls being much thinner and lacking 'knots' at their points of junction. In contrast to *Lydekkerina*, radiate grooving is well developed around the pitted fields of all the bones.
2. Orbits small and round.

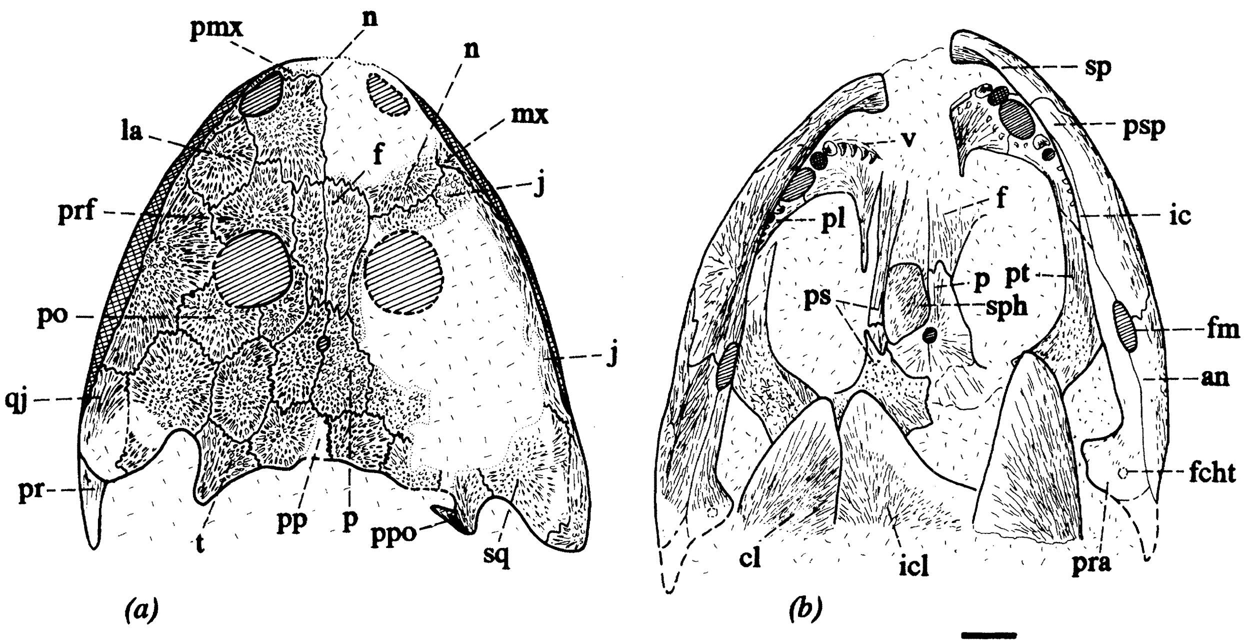

Figure 9. *Broomulus dutoiti* MGM 4285, holotype skull: (*a*) dorsal view; (*b*) palatal view. Scale bar, 10 mm.

3. Anterolateral projection of postorbital bone rather conspicuous.
4. Lachrymal very broad and removed far forward from orbit.
5. The poorly preserved articulation area of the lower jaw shows the shallow retroarticular process, which is much longer than in *Lydekkerina* and devoid of the ascending surangular projection that occurs in this genus.
6. Tabulars lack the unsupported posterior projection.

The last character, combined with the broad skull, anterior position of the orbit, and long retroarticular process of the lower jaw, bears some resemblance to the Chigutisauridae. However, both the lydekkerinid type of basis cranii and the very deep processus hamatus of the lower jaw make the capitosauroid affinity of *Broomulus* unquestionable. All this reinforces the conclusion that *Broomulus* is a valid lydekkerinid genus.

Apart from the lydekkerinids known as formal taxa, some indeterminate fragments from the Sanga do Cabral Formation (lowermost Triassic) of Brazil have also been ascribed to the Lydekkerinidae (Lavina and Barberena 1985, Fig. 3–4). This identification is based entirely on the ornamentation pattern and cannot be confirmed with certainty.

(*c*) *Non-lydekkerinid taxa formerly assigned to Lydekkerinidae*

The following three forms are removed from the Lydekkerinidae.

(i) ‘*Lydekkerina*’ *putterilli*

The type (TM 184) of ‘*Lydekkerina*’ *putterilli* Broom (1930) is the posterior part of a rather large skull with an estimated total midline length of 110–115 mm, consisting of a well-preserved dorsal and palatal surface and a small portion of the occiput. Part of the right half of the skull-roof table is missing. The quadrate regions are not prepared. Broom (1930), who described only the dorsal side of this skull, provisionally attributed it to *Lydekkerina* but noted that it may belong to a separate related genus.

Published distinctions from *L. huxleyi* include: (1) large size; (2) much coarser sculpturing of bones; (3) interorbital distance considerably less than diameter of orbit; (4) parietals extend further forward; (5) jugal much wider posteriorly; (6) supratemporal forms a part of otic notch border.

Three more distinctive characters not mentioned in Broom’s description but readily seen from his figure (Broom 1930, fig. 6) are: (7) anterior ends of parietals strongly narrowed and sharply pointed; (8) anterolateral projection of postorbital very broad; (9) paroccipital process of tabular projecting backwards from tabular horn and visible in dorsal view. Characters (6) and (9) link ‘*Lydekkerina*’ *putterilli* with rhinesuchids; (2) and (8) are shared by both rhinesuchids and most of the advanced capitosauroids. This is inconsistent with Cosgriff’s (1984) conclusion that ‘*L.*’ *putterilli* is a synonym of *L. huxleyi*.

Proceeding from the position of the supratemporal (character (6)), Parrington (1948) suggested that ‘*L.*’ *putterilli* may be a juvenile of *Uranocentrodon*. This interpretation (cf. Cosgriff 1974; Colbert & Cosgriff 1974; Kitching 1978) is based on the current assumption that *Uranocentrodon* comes from the *Lystrosaurus* Assemblage Zone. Recent field work has shown that *Uranocentrodon* appears to be from the *Dicynodon* Assemblage Zone. Therefore the status of ‘*L.*’ *putterilli* needs to be explained in another way.

Re-examination of the holotype confirms the presence of all the characters listed above except for (5) (hence Broom’s interpretation of the skull roof needs to be improved slightly). This means that the specimen is undoubtedly a rhinesuchid. In addition, the occipital surface has a typical rhinesuchid pattern (the parocciptial bar is oriented almost parallel to the upper border of the posttemporal fenestra, is flattened anteroposteriorly and curved downwards on its lateral tip; the posttemporal fenestra is slit-like and partly roofed by the postparietal and tabular occipital flanges).

The parasphenoid body, seen on the palatal surface, further demonstrates the typical rhinesuchid condition in having the muscular cristae situated behind the posterior end of the pterygoparasphenoid suture. However, in contrast to that of Permian rhinesuchids, it has a very long middle portion between the structures mentioned above, with the lateral sides gently concave rather than deeply notched. This character, along with the shape of the parietal (see above) and small size of the skull, provides a basis for generic separation of this form within the Rhinesuchidae.

(ii) *Deltacephalus whitei (figure 10)*

Deltacephalus (*D. whitei*) Swinton from the Middle Sakamena Group, Madagascar, is known only by the holotype skull (BMNH R 6695), which is about 50 mm in length and preserved as a natural mould in a concretion. Once placed in the Lydekkerinidae, mainly on the basis of skull proportions (Swinton 1956; Carroll & Winer 1977), this form has been long considered to be of uncertain taxonomic affinities (Cosgriff 1974; Milner 1990). More recently Hewison (1996) places it again in the Lydekkerinidae. By contrast, Maryanska & Shishkin (1996) united this genus with other coeval Madagascan capitosauroids in the newly established family Deltacephalidae, presumed to be one of the capitosaurid-like lineages advanced over the lydekkerinid level.

Excellent diagrams of the *Deltacephalus* type skull presented by Hewison (1996) are in accord with our figure 10 in all those points which, to our opinion, preclude this genus from being placed in the Lydekkerinidae (characters (1–7), see below). On the other hand, neither of two characters of the type skull stressed in Hewison's account as the evidence to the contrary is specific for Lydekkerinidae. One of them, the shortness of the snout region, as agreed by the author himself, is a well-known juvenile capitosauroid character that does not point to any particular family if taken separately. The preorbital index reported for *Deltacephalus* (A/L = 0.44) is actually very close to what is seen in the juvenile advanced capitosauroid known as the type of '*Benthosuchus*' *madagascarensis* (0.47 to our estimation; cf. Lehman 1961, Pl. IV A). Another stressed character, the well-developed dermal ornamentation of pterygoids, is more typical for advanced capitosauroids than for lydekkerinids.

Two more features mentioned by Hewison (1996) as distinctions of the Lydekkerinidae from Capitosauridae and described (although not emphasized) by him for *Deltacephalus* are the lack of confluence of the muscular crests of the parasphenoid and the presence of stapedial 'lappets' in the former family. However, a broad disconnection of muscular crests is a very common variation in the capitosaurid *Wetlugasaurus*, and the pterygoparasphenoid elevation giving the rest for the stapes occurs in both the early Triassic Capitosauridae and their trematosauroid derivatives. This elevation is usually not exhibited in palatal view (in contrast to 'lappet' in *Lydekkerina*); the same applies to *Deltacephalus* as seen from palatal restorations in this (figure 10) and Hewison's papers.

Recent re-examination of the type of *Deltacephalus* by Shishkin confirmed the assignment of this genus to the advanced capitosauroids and permitted a new interpretation of the cranial morphology (figure 10*a*, *b*). The main characters linking *Deltacephalus* with advanced capitosauroids and separating it from lydekkerinids are as follows.

1. Lachrymal flexure of infraorbital sensory groove (taken by Swinton (1956, figure 1) for a portion of the lachrymal-maxillary suture) is Z-shaped.
2. Lachrymal short (La/C = 0.56–0.63).
3. No sign of septomaxilla detected.
4. Frontals pointed and not broadened anteriorly.
5. Preorbital projection of jugal, albeit much shorter than the postorbital one, rather prominent (J1/C = 0.27) for such a small (probably juvenile) individual.
6. Preorbital sensory grooves well developed.
7. Parasphenoid body shows the radiate pattern of shagreen dentition, similar to that in the Madagascan '*Wetlugasaurus milloti*' (Lehman 1961, pl. XIV, B) and unknown in lydekkerinids.

All this supports the conclusion that *Deltacephalus* is closely related to the other Middle Sakamena capitosauroids. Morphologically it appears similar to the type of '*Benthosuchus*' *madagascarensis* (photographs in Lehman (1961, pl. IV A,B), in contrast to the reconstructions by Lehman (1961, figure 4) and Warren & Hutchinson (1988*b*, figure 1), which is a juvenile individual of comparable size and shows all the dermal-roof characters listed above. The lack of a frontal contact on the orbital rim in *Deltacephalus* is not considered to be a very important difference as far as the Madagascan forms are concerned. Judging by published photographs of the Madagascan '*Benthosuchus*' and '*Wetlugasaurus*' (both designated as '*Parotosuchus*' by Warren & Hutchinson (1988*b*)) the inclusion of the frontal on the orbital rim is caused in these by a gradual wedging out of the opposing ends of the pre- and postfrontal rather than by a clearly defined lateral projection from the frontal as in the advanced *Parotosuchus*-like forms. As a result there is no clear demarcation between the presence or absence of the frontal on the orbital rim.

Former attempts to ascribe the Madagascan capitosauroids to the above-mentioned European genera (Lehman 1961; Warren & Hutchinson 1988*b*) are not justified (Maryanska & Shishkin 1996) and hence the only valid name ever proposed for any of these forms is *Deltacephalus* Swinton. For this reason the family specifically uniting them must be Deltacephalidae.

(iii) '*Lydekkerina*' *kitchingi*

For the sake of completeness of this survey the Permian '*Lydekkerina*' *kitchingi* Broom (1950) should be mentioned. The holotype is a semi-adult rhinesuchid whose adult is most probably *Muchocephalus muchos*

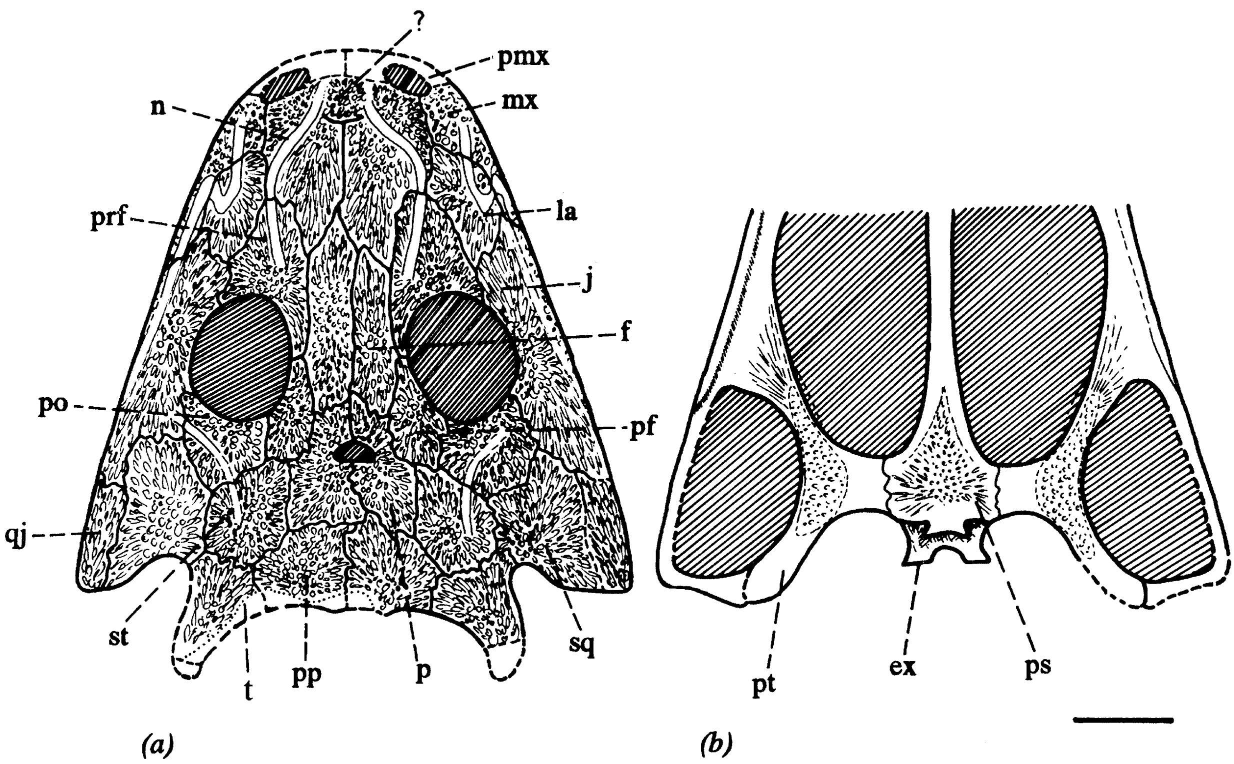

Figure 10. *Deltacephalus whitei*. Holotype R6695, skull: (*a*) dorsal view; (*b*) posterior part of palatal view. Scale bar, 10 mm.

(Watson 1962) from the same locality (Kitching 1978) (see above).

8. COMMENTS ON LYDEKKERINID INTERRELATIONSHIPS

The above survey is intended simply to outline the content of the Lydekkerinidae rather than be a comprehensive analysis of the interrelationships of lydekkerinid genera. However, available data (both gathered in this account and known from the literature) provides a basis for preliminary conclusions concerning patterns of the lydekkerinid diversification.

A summary of differential diagnoses of the principal lydekkerinid genera is given below, in which these taxa are characterized by comparison with *Eolydekkerina*. Each character included in the comparison of the different genera is marked with the same number in the case of each genus. For the character states thought to be primitive, the numbers have the suffix 'a'; for derived states the suffixes are 'b' and 'c'.

The suggested polarization of characters is underlain by the concept, advocated above, that lydekkerinid structural patterns are mostly paedomorphic and derived from the more fully developed 'archetype', which is very close to the *Eolydekkerina* pattern. This implies that such traits as the parabolic outline of the skull (1b), short preorbital region (2b), strong reduction of the preorbital projection of the jugal (10b), and lack of the crista obliqua pterygoidei (14b) (manifested in mosaic way in some of the genera), or the kidney-shaped anterior palatal vacuity (17b) seen in *Lydekkerina* are actually derived states acquired by phyletic truncation of the ontogeny. Based on this assumption, only very few characters of *Eolydekkerina*, such as the shape of the choanae (19b) and the interchoanal tooth row (21b), could be ascribed with a reasonable confidence as an autapomorphy. For some characters, primarily the depth of the palatal vault (16), the polarity remains uncertain.

Suggested relationships of the lydekkerinid genera discussed are illustrated by a cladogram (figure 11). The most evident implication from this cladogram is the striking divergence between *Luzocephalus* and the Gondwanan genera, with the former showing a great number of autapomorphies (both paedomorphic and non-paedomorphic) that are unknown among the other Lydekkerinidae and even the capitosauroids in general (4b, 8c, 12b, 15b, 20b, 23b).

Within the Gondwanan radiation, *Chomatobatrachus* is close to *Eolydekkerina* and seems to differ from the latter only by the lack of its specializations and by a few paedomorphic changes (14b and possibly 25b). *Lydekkerina* is simply a juvenilized variant of the *Eolydekkerina* pattern, as discussed above. Another paedomorphic offshoot of the same pattern is represented by *Broomulus*.

Diagnoses of principal lydekkerinid genera (as compared with *Eolydekkerina*) are as follows.

Eolydekkerina gen. nov.
(1a) Skull relatively large (more than 100 mm long), subtriangular, with nearly straight lateral margins.
(2a) Midline length of skull exceeding width.
(3a) Preorbital part of skull moderately elongate, with A/L about 0.50.
(4a) Postorbital zone of growth not expressed (orbito-pineal distance not exceeding 0.3 of median orbito-occipital distance).

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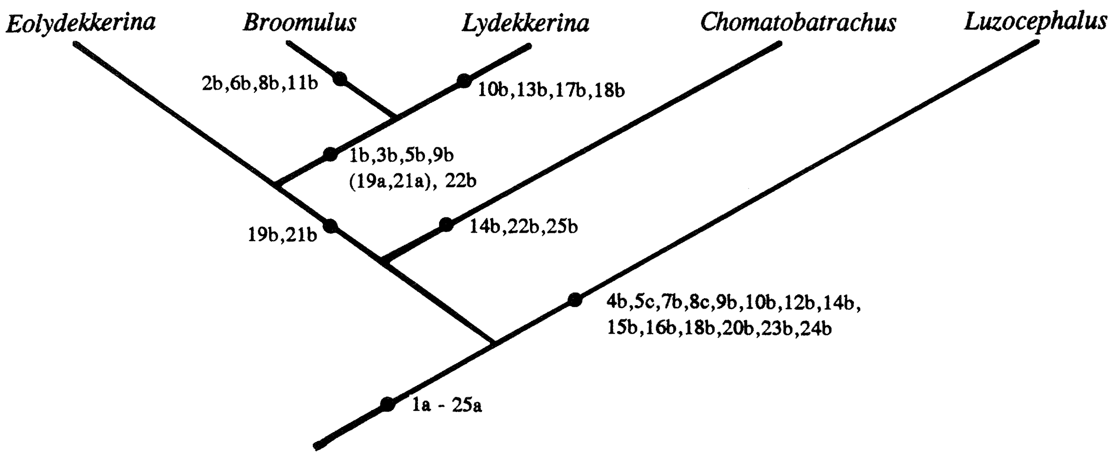

Figure 11. Cladogram of relationships of principal lydekkerinid genera. (Numbered characters as in text. Primitive characters shown in square brackets presumed to reappear owing to paedomorphosis.)

(5a) Orbits broadly separated (O/I about 0.70).
(6a) Dermal ornamentation finely pitted, bearing knots at points of junction of pit walls, without radiate grooving around the pitted fields.
(7a) Supraorbital sensory grooves absent.
(8a) Lachrymal flexure of infraorbital groove step-shaped.
(9a) Lachrymal moderately short relative to orbitonarial distance (La/C about 0.70).
(10a) Preorbital projection of jugal well detectable (J1/C about 0.20).
(11a) Tabular horns projecting behind paroccipital processes.
(12a) Occipital edge of squamosal S-shaped.
(13a) Tympanic ridge of squamosal deeply curved, subvertical in its distal part.
(14a) Crista obliqua pterygoidei shallow, ledge-shaped.
(15a) Pterygosquamosal fissure absent.
(16a) Palate flattened.
(17a) Anterior palatal vacuity rounded (nearly heart-shaped).
(18a) Anterior palatal vacuity immediately bordered by premaxillary tooth row.
(19b) Choanae pear-shaped.
(20a) Palatine not contacting vomer lateral to choana.
(21b) Interchoanal vomerine tooth row straight.
(22a) Palatal exposure of parasphenoid cultriform process does not reach the level of anterior limit of interpterygoid vacuities.
(23a) Muscular crests of parasphenoid body well developed.
(24a) Shagreen field on parasphenoid body extending laterally up to sutures with pterygoids.
(25a) No ectopterygoid tusks.

Chomatobatrachus Cosgriff
(14b) Crista obliqua pterygoidei absent.
(19a) Choanae oval.
(21a) Interchoanal vomerine tooth row arched.
(22b) Anterior limits of interpterygoid vacuities and palatal exposure of parasphenoid cultriform process at the same transverse level.
(25b) Ectopterygoid tusks present.

Lydekkerina Broom (adult)
(1b) Skull small (usually up to 80 mm long), parabolic in outline.
(3b) Preorbital part of skull short, with A/L from 0.40 to 0.48.
(5b) Orbits rather closely positioned, with O/L from 1.2 to 0.8.
(9b) Lachrymal long, with La/C from 0.75 to 0.90.
(10b) Preorbital projection of jugal from moderately expressed to lacking (J1/C from about 0.25 to 0).
(13b) Tympanic ridge of squamosal nearly straight, with shallow distal slope.
(17b) Anterior palatal vacuity kidney-shaped.
(18b) Anterior palatal vacuity bordered anteriorly by premaxillary palatal shelf.
(19a) Choanae oval.
(21a) Interchoanal vomerine tooth row arched.
(22b) Anterior limit of palatal exposure of parasphenoid cultriform process in line with, or extending in front of the anterior limit of interpterygoid vacuities.

Broomulus Romer
(1b) Skull relatively small (about 85 mm long), parabolic, with convex side margins.
(2b) Midline length of skull less than width.
(3b) Preorbital part of skull short, with A/L about 0.45.
(5b) Orbits closely positioned (O/I about 0.90).
(6b) Dermal ornamentation without knots on pit walls, showing zones of radiate grooving around the pitted fields on ossification centres.
(8b) Infraorbital groove absent (as well as other sensory grooves).
(9b) Lachrymal long (La/C about 0.85).
(19a) Choanae oval.
(11b) Tabular horns not projecting behind paroccipital processes.
(21a) Interchoanal vomerine tooth row arched.
(22b) Anterior limits of interpterygoid vacuities and palatal exposure of parasphenoid cultriform process at the same transverse level.

Luzocephalus Shishkin
(4b) Postorbital zone of growth present (orbitopineal

distance approaching 0.50 of median orbito-occipital distance).
(5c) Orbits widely separated (O/I about 0.45).
(7b) Supraorbital sensory grooves present.
(8c) Lachrymal flexure of infraorbital groove smoothed out to S-shaped bend.
(9b) Lachrymal fairly long (La/C 0.90).
(10b) Preorbital projection of jugal absent.
(12b) Occipital edge of squamosal nearly straight.
(14b) Crista obliqua pterygoidei absent.
(15b) Continuous pterygosquamosal fissure present.
(16b) Palate deeply vaulted.
(18b) Anterior palatal vacuity bordered anteriorly by premaxillary palatal shelf.
(19a) Choanae oval.
(20b) Palatine contacting vomer lateral of choana.
(21a) Interchoanal vomerine tooth row arched.
(23b) Muscular crests of parasphenoid body absent.
(24b) Shagreen field on parasphenoid body confined to median part of bone.

9. CONCLUSION

The family Lydekkerinidae is thus considered to include six to seven valid genera. It is remarkable that those genera represented by small and obviously paedomorphic individuals, such as the South African *Lydekkerina* and the Antarctic *Cryobatrachus*, come from reptile-dominated assemblages in which *Lystrosaurus* is abundant. In contrast, the largest forms, such as *Luzocephalus* from Russia and Greenland, and *Chomatobatrachus* from Tasmania (holotype skull 106 mm in length, but some referred fragments come from much larger specimens (Cosgriff 1974, p. 52; Colbert & Cosgriff 1974, p. 21)), belong to amphibian-dominated assemblages in which *Lystrosaurus* is absent or extremely rare. The Indian *Indobenthosuchus* ('*Lydekkerina*' *panchetensis*) is intermediate in size. This appears to be consistent with the composition of the assemblage from which it comes: the Panchet fauna includes an abundance of both amphibians and *Lystrosaurus*.

Eolydekkerina, which is one of the larger forms, seems to be an exception to this rule as it comes from the reptile-dominated *Lystrosaurus* Assemblage Zone of South Africa. The lower part of the zone, which produces this form, also contains the procolophonid *Owenetta*, the archosaur *Proterosuchus* and the therapsids *Lystrosaurus*, *Moschorhinus*, *Galesaurus* and *Ictidosuchops*.

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APPENDIX 1. *Institutional abbreviations*

AMNH: American Museum of Natural History, New York, U.S.A.

BMNH R: Natural History Museum, London, U.K.

BP/1/: Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, R.S.A.

MGM: MacGregor Museum, Kimberley, R.S.A.

NMQR: National Museum, Bloemfontein, R.S.A.

PIN: Palaeontological Institute, Academy of Science, Moscow, Russia.

SAM: South African Museum, Cape Town, R.S.A.
UMZC T: University Museum of Zoology, (tetrapod collection), Cambridge, U.K.
TM: Transvaal Museum, Pretoria, R.S.A.

APPENDIX 2. *Abbreviations used in figures*

A: snout length, tip to line across anterior margin of orbits
an: angular
apv: anterior palatal vacuity
B: width of skull across orbit centres
C: orbitonarial distance
cob: oblique crest of pterygoid (=crista obliqua pterygoidei)
ch: choana
cl: clavicle
cm: muscular crest of parasphenoid body (= crista muscularis pterygoidei)
ct: tympanic crest of squamosal (= crista tympanica squamosi)
ect: ectopterygoid
ex: exoccipital
f: frontal
fcht: chorda tympani foramen
fm: meckelian foramen
frq: paraquadrate foramen
I: interorbital distance
ic: intercoronoid
icl: interclavicle
ip: interparietal
j: jugal
J_1: preorbital extent of jugal measured along lateral border of skull (figure 1)
J_2: postorbital extent of jugal measured along lateral border of skull (figure 1)
L: midline length of skull roof
la: lachrymal (lachrymal length in figure 1)
mx: maxilla
n: nasal
O: width (the shortest diameter) of orbit
p: parietal
pf: postfrontal
pl: palatine
pmx: premaxilla
po: postorbital
pp: postparietal
ppo: paroccipital process of tabular
pr: retroarticular process
pra: prearticular
prf: prefrontal
ps: parasphenoid
psp: postsplenial
pt: pterygoid
pvn: ventral process of stapedial footplate
q: quadrate
qj: quadratojugal
s: stapes
smx: septomaxilla
sp: splenial
sph: sphenethmoid
sq: squamosal
st: supratemporal
t: tabular
th: hyoid tubercle
v: vomer
vn: ventral notch between basis cranii and occipital arch
W: width of skull across quadrates
X: vagus foramen

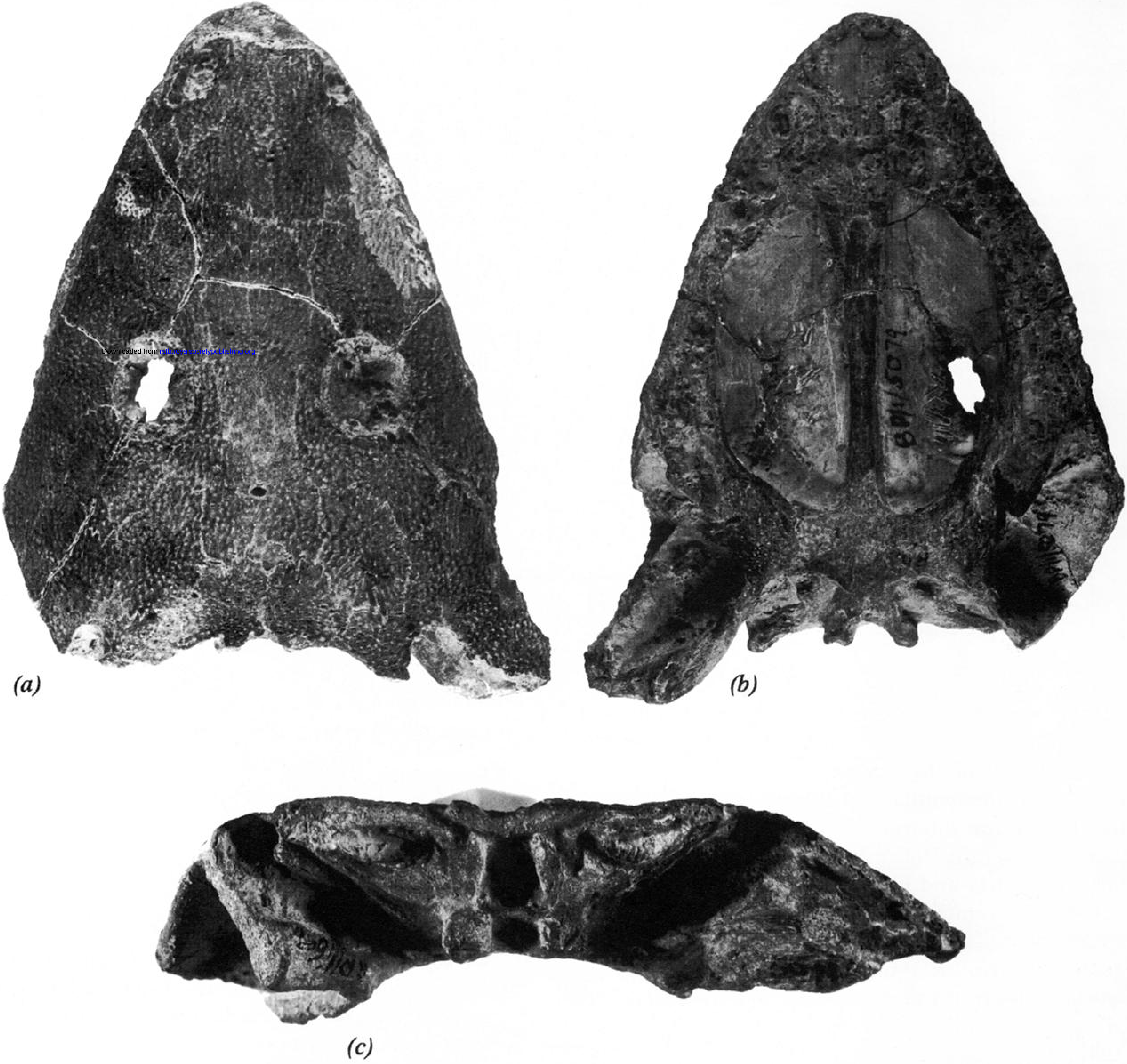

Figure 2. *Eolydekkerina magna* BP/1/5079 holotype, skull: (*a*) dorsal view; (*b*) palatal view; (*c*) occipital view.