A RELICT RHINESUCHID (AMPHIBIA: TEMNOSPONDYLI) FROM THE LOWER TRIASSIC OF SOUTH AFRICA

by M. A. SHISHKIN and B. S. RUBIDGE

ABSTRACT. ‘Lydekkerina' putterilli Broom from the Lystrosaurus Assemblage Zone (Middle Beaufort Group, South Africa) is shown to be a paedomorphic rhinesuchid (Broomistega putterilli gen. nov.) rather than a lydekkerinid or juvenile stage of the rhinesuchid Uranocentrodon, as previously presumed. The most conspicuous characters, not related to its paedomorphic condition, include the shape of the parietals and the structure of the parasphenoid body and exoccipitals. The pattern of cranial growth changes in Broomistega has been investigated by comparison of the holotype with two hitherto undescribed immature specimens. For several characters referring to the size and position of the orbits, and re-modelling of the jugal proportions, retarded timing of growth transformations, compared to ontogenetic patterns in Permian rhinesuchids (typified by Muchocephalus) is demonstrated. Some features of the evolution of the basicranial region of the skull, in the transition from rhinesuchids to more advanced capitosauroids, are re-evaluated.

KEY WORDS: temnospondyls, rhinesuchids, relict, paedomorphosis, growth changes.

THE fossil tetrapod succession of the Beaufort Group in South Africa reveals dramatic changes in the amphibian fauna during the Permo-Triassic turnover phase of the evolution of the Gondwanan terrestrial biota. The Rhinesuchidae, the earliest capitosauroid family (for discussion of its taxonomic position, see Shishkin et al. 1996), which ranges through the Late Permian, from the Tapinocephalus to Dicynodon assemblage zones, appears to be almost entirely replaced in the Early Triassic by a number of short-lived groups dominated by the Lydekkerinidae (Rubidge 1995). These are known from the Lystrosaurus Assemblage Zone and are represented by relatively small forms far exceeded in size by their Permian forerunners (Shishkin et al. 1996)

It was long believed (Romer 1947; Watson 1962; Ochev 1966) that Uranocentrodon, a fairly large rhinesuchoid amphibian, reported from a single locality at Senekal, Orange Free State, is one of the few exceptions to this pattern, both with regard to size and affinities, and it was presumed to be a member of the Lystrosaurus Zone assemblage. This form was thereby considered as a last rhinesuchoid relict that persisted into the Triassic. However, its Triassic age has never actually been proved. Our field observations in the Senekal area, made together with J. W. Kitching, revealed that the uppermost part of the Upper Permian mudrock succession of the Dicynodon Assemblage Zone includes a thick sandstone layer which is almost immediately overlain by the Katberg Sandstone of the Lower Triassic, exposed in other outcrops. The sandstone quarry thought to have produced all the known Uranocentrodon specimens clearly falls within the Permian part of the discussed section. In addition, the type of cross-bedding seen in the local Katberg Sandstone characterizes it as high-energy channel deposits, which is not consistent with the state of preservation of the Uranocentrodon specimens represented by fully articulated skeletons.

It should also be noted that the separation of Uranocentrodon from Permian rhinesuchids (Romer 1947, pp. 198, 215), still followed by many authors (Romer 1966; Carroll and Winer 1977; Kitching 1978), is based on the belief that the Rhinesuchidae is more primitive in retaining the occipital exposure of the opisthotic bone, a condition lost in Uranocentrodon. However, according to our observations, this difference does not exist, and in both cases the opisthotic is absent from the occiput. Indeed many earlier
authors considered Uranocentrodon as a junior synonym of Rhinesuchus (Haughton 1925; Olson and Broom 1937).

In spite of our proposed re-dating of Uranocentrodon, there is evidence that other rhinesuchid survivors persisted across the Permo-Triassic boundary. Broom (1930) described ‘Lydekkerina’ putterilli on the basis of an imperfect skull which was recovered together with many specimens of L. huxleyi, the most common amphibian from the Lystrosaurus Assemblage Zone. Hence, the Early Triassic age of this find is well established. However, in distinction from Lydekkerina and other Triassic Temnospondyls, ‘Lydekkerina’ putterilli shows the inclusion of the supratemporal bone in the otic notch as in rhinesuchids.

‘L’. putterilli has never gained general acceptance as a valid lydekkerinid species. Parrington (1948) suggested that it could have been a young individual of Uranocentrodon on the grounds that the latter was also a component of the Lystrosaurus Zone assemblage (see also Colbert and Cosgriff 1974; Kitching 1978). However, as mentioned above, we do not accept that Uranocentrodon is present in this assemblage. Cosgriff (1984, p. 35) briefly inspected the holotype of ‘L’. putterilli and identified it, along with other disputable South African lydekkerinids, as ‘distorted and/or incomplete skulls of Lydekkerina huxleyi’.

In the course of our revision of the Lydekkerinidae (Shishkin et al. 1996) we re-examined the type of ‘L.’ putterilli housed in the Transvaal Museum, Pretoria. In addition, two more ‘Lydekkerina’ specimens from the Lystrosaurus Assemblage Zone, showing the inclusion of the supratemporal in the otic notch, were found in the collections of the Bernard Price Institute (Palaeontology). These specimens, both collected by J. W. Kitching, are relatively small and probably juvenile. One of them, BP/1/3241 from Admiralty Estates in the Oliviershoek area, consists of a disarticulated skeleton and a skull with a midline length of 75 mm, and was identified in 1960 by J. W. Kitching as L. putterilli. This specimen was found in close association with Thrinaxodon and the holotype of the therapsid Lycracyodon darti. The smaller specimen, BP/1/5058, a skull with a midline length of 57 mm, comes from Ndanyana Hill, Hartebeespruit, Bergville. It was found in association with specimens of L. huxleyi, and was presumed to belong to this species until it was recently prepared.

Comparison of the holotype of ‘L.’ putterilli with these two skulls showed them to be consistent in many respects, and justifies consideration of them as successive growth stages of the same species. These three specimens also complement each other in showing details that are not present in any individual specimen. The species they represent is assigned to a new rhinesuchid genus and described below.

Brief methodological notes are necessary to precede the systematic account. The rhinesuchid status of the sample under study is supported by many characters. However, a full listing of diagnostic characters of the new genus is strongly biased by the obviously juvenile age of both referred specimens. As has been recently shown (Shishkin et al. 1996), the pattern of early growth stages of the rhinesuchid skulls is very similar to the condition in adult Lydekkerina, a paedomorphic genus. As a result many diagnostic characters displayed by mature rhinesuchids are barely visible or absent in their juveniles. For this reason, of the traits derived exclusively from the referred specimens, only those that are common for well-established (Permian) rhinesuchids are confidently considered to be normal for the new taxon.

This approach necessitated partial re-examination of the cranial morphology of Permian rhinesuchids, which is still very poorly known. Permian material covered by our inspection includes the holotypes of Rhinesuchus rubidgei Broom (RC 73), Muchocephalus muchas Watson (BP/1/213), ‘Lydekkerina’ kitchingi Broom (BP/1/214), and Laccosaurus watsoni Haughton (SAM 4010) as well as rhinesuchid specimens RMS 606, BP/1/4473, SAM K6983 and GS 645. Unless stated otherwise, all the data on adult rhinesuchid morphology used in the following account are derived from these specimens. In addition, some new observations were made on a series of rhinesuchid juveniles from Beeldhouwersfontein farm, Murraysburg District, Cape Province (BP/1/2931B, 2941, 2942A, 2958, 2965, 3070, 3075 and 3079), most of which have also been reported on elsewhere (Shishkin et al. 1996). To differentiate the main growth stages in rhinesuchids, the term ‘juvenile’ is used for those individuals with a skull length up to 75 mm, and ‘semi-grown’, or ‘immature’, for those with a skull length of 80–100 mm.

Principal skull measurements are shown in Text-fig. 1, and comparative measures are reported in Table 1. Institutional abbreviations: BP/1, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; GS, Council for Geoscience, Pretoria; NMQR, National
TEXT-FIG. 1. Diagram of skull roof measurements. For explanation of abbreviations, see Appendix.

**SYSTEMATIC PALAEOONTOLOGY**

Superfamily **CAPITOSAUROIDEA** Watson, 1919 (nom. transl. Säve-Söderbergh 1935, ex. Capitosauridae Watson)

Family **RHINESUCHIDAE** Watson, 1919 (Rhinesuchidae + Uranocentrodontidae, sensu Romer, 1947)

*Diagnosis.* Skull with elongate preorbital region (A/L 55-60). No interorbital depression or preorbital ‘step’ in skull roof; orbits not elevated. Cheek contours steeply curved (rather than straight) in occipital view, forming nearly a right angle with the palate. Otic notch usually deep, with subparallel lateral margins. Sensory grooves moderately developed; lacrimal flexure of infraorbital groove (when present) step-shaped rather than Z-shaped. Ornamentation of the skull roof consists mostly of pits with thin walls lacking prominent knots at the wall junctions. Supratemporal included in the margin of the otic notch. Septomaxilla with spine-like intranarial process. Posterior border of nasal oblique rather than step-shaped. Frontals excluded from orbital borders, with pointed (not expanded) anterior ends. Lacrimal relatively short (La/C no more than 0.65). Prefrontals sharply narrowed at the orbital border. Postorbital with a marked anterolateral projection. Preorbital projection of jugal usually equal to, or longer than, the postorbital projection. Tabular horns devoid of unsupported terminal projections and leave the dorsal ends of paroccipital bars exposed in dorsal view. Paroccipital bar (formed by tabular and exoccipital) nearly parallel to the upper border of the slit-like posttemporal fenestra. Tabular portion of paroccipital bar blade-shaped (not rod-like), with its lateral end expanded and curved downward in occipital view. Crista obliqua pterygoidei usually deep, and well developed. Tympanic area of squamosal very long, extending over three-quarters of the squamosal occipital flange. Parasphenoid body with deep pockets and strong
muscular crests situated behind (rather than in line with) the posterior ends of the pterygo-parasphenoid sutures. Ventral notch between parasphenoid and exoccipital absent. Choanae relatively short, oval, not slit-like. Vomer forms almost the entire medial border of the choana and extends backwards to the level of the palatine tusks. Anterior palatal vacuities paired, very small, irregular in shape and located in a large common depression. Transverse interchoanal (vomerine) tooth row varies from concave to convex. Lower jaw with long posterior Meckelian foramen, and only rudimentary or absent retroarticular process. Surface of coronoid series slopes down gradually in a dorso-lingual direction rather than faces lingually. Shagreen dentition developed on parasphenoid body, pterygoids, vomers, coronoids, and, rarely, the palatines. Shagreen field on parasphenoid short along the midline and extended backwards along the pterygoid sutures.

Comparison. Rhinesuchids can be differentiated from remaining capitosaurid families by the large depth of the otic notch; the inclusion of the supratemporal in the otic notch; the long and well-defined tympanic area of the occipital flange of the squamosal; the posterior narrowing of the prefrontal; the presence of a spine-like intranarial process of the septomaxilla; the lack of an unsupported end of the tabular horn; the structure and position of the paroccipital process, with its tip exposed dorsally and sloping downward in occipital view; slit-like posttemporal fenestra; deep ventral pockets of the parasphenoid body; the position of the parasphenoid muscular crests behind the basicranial sutures; vomer bordering the entire medial side of the choana and extending behind it; the vestigial, slit-like, paired anterior palatal vacuities; shagreen dentition on the vomers, palatines and entire coronoid series; the shape of the parasphenoid shagreen field; the dorsolinguial (non-vertical) position of the coronoids; variation in shape of the interchoanal tooth row from convex to concave; and the absence or only rudimentary development of the retroarticular process of the lower jaw.

Apart from this, the Rhinesuchidae is distinguished from its closest relative, the Lydekkerinidae by the following: cheek contours steeply curved (rather than straight) in occipital view; interorbital depression and preorbital ‘step’ of skull roof absent; preorbital region of skull not shortened; no marked knots on ornament-ridge junctions; relatively short lacrimal (with La/C less than 0.70, the minimum value for lydekkerinids); postorbital jugal projection shorter than preorbital projection; posterior border of nasal not step-shaped; frontals not expanded anteriorly, anterolateral projection of postorbital well marked; oblique crest of pterygoid not reduced; no ventral notch between parasphenoid and exoccipital; shagreen field on parasphenoid body reduced in extent along the midline. By contrast, both families are similar in the exclusion of the frontal from the orbital margin, the presence of a septomaxilla, and a step-shaped lacrimal flexure of the infraorbital sensory groove. In terms of the extent of the preorbital projection of the jugal relative to the posterior projection (Table 1: J1/J2 index) rhinesuchids are intermediate between lydekkerinids and more advanced Triassic capitosaurid families.

Compared with the Capitosauridae, Stenotosauridae, and Cyclotosauridae (cf. Maryańska and Shishkin 1996), the rhinesuchids show the following distinctions: L-shaped (rather than Z-shaped) lacrimal flexure; exclusion of the frontal from the orbital margin (a character retained only in the earliest capitosaurid Weitlagasaurus); more moderate reduction of the lacrimal, and the wide extent of palatal shagreen, by contrast to its limited occurrence in most primitive capitosaurids, and total absence in stenotosaurids and cyclotosaurids.

In addition, Rhinesuchidae differs from the Capitosauridae in the following: (1) lack of interorbital depression and preorbital step of the skull roof; (2) curved cheek contour in occipital view; (3) moderate anterolateral projection of the postorbital, showing no trend towards development of a contact with the prefrontal; (4) oval (not slit-like) choanae; and (5) long posterior Meckelian foramen. Characters one and two and to some extent five link the Rhinesuchidae to Stenotosauridae, but characters three and five clearly distinguish these families.

There are also some remarkable similarities between the Rhinesuchidae and the Mid-Late Triassic Cyclotosauridae. Apart from the occasional presence of the septomaxilla in the latter (cf. Schoch 1997), these similarities include the pattern of cheek contouring in occipital view, the shape of the postorbital and the choana, and the elongation of the posterior Meckelian foramen (cf. Maryańska and Shishkin 1996).
Comments. Although they permit a clear-cut demarcation of Rhinesuchidae from the rest of the Capitosauroida, most of the diagnostic characters are plesiomorphic with respect to the condition exhibited by the non-rhinesuchid capitosaurid lineages mentioned above. Characters related to the paroccipital bar, the posttemporal fenestra, and the condition of the anterior palatal vacuities (see Diagnosis) clearly point to a close affinity between rhinesuchids and archegosaurid-related eryopoids.

Rhinesuchid features that are derived relative to other Capitosauridae include: (1) spine-shaped intranarial process of the septomaxilla; (2) posterior narrowing of the prefrontal; (3) the shape of the paroccipital shagreen field; (4) loss of the ventral notch between the parasphenoid and exoccipital; and (5) a long posterior Meckelian foramen. Some typical capitosaurid characters found in the Rhinesuchidae, such as the well-developed crista obliqua pterygoidei, the relatively long preorbital projection of the jugal, shortening of the lacrimal, anteriorly pointed frontals and marked anterolateral projection of the postorbital, are absent or vestigial in lydekkerinids, and so could be mistaken for derived characters. However, as shown by Shishkin et al. (1996), the seemingly primitive state of the characters evident in lydekkerinids represents a secondary condition attained in the course of paedomorphic evolution.

A character deserving special comment is the curved outline of the cheek in occipital view, a pattern shared by the Rhinesuchidae, Stenotosauridae and Cyclotosauridae, and contrasting with the straight cheek contour of the Lydekkerinidae and Capitosauridae (cf. Maryańska and Shishkin 1996; Shishkin et al. 1996). Judging by outgroup comparisons (early temnospondyls, including eryopoids), the rhinesuchid condition is clearly derived from the straight-cheek pattern; but, considering that the Lydekkerinidae and Capitosauridae, which have the straight pattern, are rhinesuchid descendants, the rhinesuchid condition should be regarded as primitive for the Capitosauroida as a whole. Alternatively, it could be suggested that the earliest, still unknown, capitosaurids retained the straight cheek contours and might have given rise to two main lineages, one including rhinesuchids, stenotosaurids and cyclotosaurids, the other comprising lydekkerinids and capitosaurids.

In addition, with reference to such rhinesuchid characters (included in the above diagnosis) as the paired anterior palatal vacuities and exclusion of the frontals from the orbital margins, it should be noted that in our re-examination of the holotype of Muchocephalus muchos (Watson 1962, fig. 5A–B) we were not able to confirm published data on the presence of the alternative condition in this rhinesuchid.

Genus BROOMISTEGA gen. nov.

1930 Lydekkerina, pars; Broom, p. 7.

Derivation of name. In honour of the famous palaeontologist Robert Broom and in reference to stege (Greek), roof.

Diagnosis. Small rhinesuchids with midline skull length of about 110 mm. Orbits large (O1/B 0·25, K/O2 1·25), with orbital width far exceeding interorbital distance (O1/I about 1·50). Parietals very narrow (total width only 0·64 × length), with deeply indented anterior ends. Otic notches relatively short. Oblique crest of pterygoid shallow, extending to only half the depth of the occiput. Muscular crests of parasphenoid located far behind the pterygo-parasphenoid sutural area (distance between crests and sutural area 0·35 × total length of parasphenoid body). Pockets for neck muscles on parasphenoid small and widely separated. Concavity of free lateral margins of parasphenoid body (in front of pockets) very gentle. Subotic process of exoccipital long and shallow.

Juveniles retain the step-shaped posterior border of the nasals, broadened anterior ends of the frontals, lack of posterior narrowing of the prefrontals, preorbital jugal projections that are shorter than the postorbital projections, and short posterior processes of vomers. Shagreen teeth on the vomers are scarce or absent in juveniles, and the configuration of the interchoanal tooth row ranges from arch-shaped and convex anteriorly, to angular and pointing backwards. The lower jaw has a straight ventral border both in front and behind the ventral angular bend.

Comparison. Broomistega differs from Permian rhinesuchids in all quantitative characters listed in the diagnosis, being much more similar in this respect to semi-grown rhinesuchids such as ‘Lydekkerina
kitchingi’ (cf. Table 1). In addition, some of these distinctions (expressed for example by the following indices: Ju2/M, O1/I, O1/B, K/O2, and M/E) reveal retarded timing in allometric changes when compared with a more standard rhinesuchid growth pattern such as that exemplified by Muchocephalus (cf. Discussion). Broomistega is also distinguished from other rhinesuchids by the shape of the parietals, the structure of the subotic process of the exoccipital, the position of the oblique crest of the pterygoid, the muscular crests of the parasphenoid, and the much gentler concavity of the lateral sides of the parasphenoid body (cf. Text-fig. 5A, F). Some of these distinctions (such as the position of the pterygoid oblique crest) are of paedomorphic origin and all are presumed to be derived. Characters listed for Broomistega juveniles also differ from the normal rhinesuchid pattern (except for the ventral contour of the mandible which tends to become angular in some later forms, such as Uranocentrodon).

**Broomistega putterilli** (Broom, 1930)

Text-figures 2–5

1930 *Lydekkerina putterilli* Broom, p. 7, fig. 6.

**Diagnosis.** As for the genus.

**Holotype.** TM 184, postorbital part of skull with a small disarticulated fragment of lower jaw.

**Type horizon and locality.** Upper Lystrosaurus Assemblage Zone, Lower Triassic, Harrismith Commonage, Free State, South Africa.

**Referred specimens.** BP/1/5058, almost complete skull with associated lower jaw and dermal shoulder girdle; Ndanyana Hill, Hartbeespruit, Bergville district; BP/1/3241, partially disarticulated skeleton including nearly complete skull with lower jaw; Admiralty Estates, Oliviershoek Pass. Both specimens are juveniles and come from the Lystrosaurus Assemblage Zone.

**Preservation.** In the holotype, the postorbital part of the skull roof, known from a schematic drawing by Broom (1930, fig. 6), is well preserved, but lacks the supratemporal and tabular on the right side, and most of the postparietals. The quadratojugal is missing; except for the anterior portion of the right element. The left half of the occiput is reasonably well preserved, except that the lateral portion of the quadrate and the tip of the tabular are missing; however, the shape of the latter is readily recognisable from an impression in the matrix. The occipital surface of the left cheek was partially prepared for this study. The right half of the occiput is clearly distorted and was left unprepared. The skull is slightly compressed dorso-ventrally so that the pterygoids are disjunct from the parasphenoid body, and the left side of the latter has been displaced dorsally. The left exoccipital, the only one preserved, has been slightly displaced from its contact with the parasphenoid. The preserved part of the palate includes most of the pterygo-parasphenoid complex, a portion of the right ectopterygoid, and the adjacent part of the maxilla.

Specimen BP/1/5058 is beautifully preserved, shows no deformation and lacks only the anterior portion of the premaxillae. The palate is prepared for most of its extent, except for the basicranial area which is covered by the dermal shoulder girdle, leaving only the exoccipitals and posterior portion of the parasphenoid exposed. In addition, the palatal dentition is largely obscured by the articulated lower jaw. The occiput is almost completely prepared, with patches of matrix left inside only the otic notches.

In BP/1/3241, the skull is crushed such that the left cheek lies in the same plane as the skull roof, while the right cheek is separated along the squamosal-supratemporal suture and shifted upward and slightly inward. The premaxillae and the anterior parts of the nasals are missing. Most of the palate is covered by the dermal shoulder girdle and lower jaw, except for the area adjacent to the left choana. The snout is slightly curved to the left. This deformation complicates restoration of the skull proportions.

**DESCRIPTION**

**Skull roof** (Text-figs 2–3)

As restored the skull roof of the holotype (Text-fig. 2), is somewhat longer than figured by Broom (1930, fig. 6). Assuming the ratio of the postorbital length of the skull to its total length (M/L) is the same as in the juvenile BP/1/5058,
the minimum total length of the type skull would be about 110 mm. The same assumption with respect to the E/L ratio gives the same figure. In fact, the total length was probably somewhat larger as these ratios normally decrease during capitosauroid ontogeny due to the relatively faster growth of the preorbital region at later stages.

The holotype skull is rather narrow as restored (W/L^0.81). As the postorbital length (M) of the skull is 30 mm and the length of the orbit (O_2) does not exceed 21 mm, the minimum preorbital length (A) can be estimated at 59 mm. This means that the minimum value of the A/L index should be about 0.54.

The preserved portion of the skull roof is almost flat, except for a very slight interorbital depression. The orbital margins are not elevated. The same condition is seen in the smaller juvenile (BP/1/5058), where the skull is undeformed.

The orbits are large and far exceed the interorbital distance in width. The otic notch is moderately deep, with slightly divergent margins posteriorly, thus resembling the condition in *Muchocephalus muchos* rather than that of more typical rhinesuchids.

The dermal ornamentation consists of broad pits surrounded by thin walls, in contrast to the smaller and much thicker walled pits of the contemporary form *Lydekkerina*. Sensory grooves are not present on the preserved parts of the holotype skull. On the facial region of both referred specimens there are faint indications of the supraorbital groove passing along the lacrimal margin, and of the lacrimal flexure of the infraorbital groove. The lacrimal flexure is step-shaped or forms a gentle bend as is evident on the right side of BP/1/5058.

The arrangement of the bones of the skull roof of the holotype can be seen in Text-fig. 2. The most noteworthy points are as follows:

1. The parietals are very narrow and have sharp indentations at the anterior end.
2. The postorbital has a rather broad antero-lateral projection comparable to that of the Permian rhinesuchids.
3. The postorbital jugal projection is very long.
4. As is common for rhinesuchids, the tabular horn lacks a terminal projection above the paroccipital process so that the latter is visible in dorsal view (Text-fig. 2; cf. Broom 1930, fig. 6). This character is also present in both referred specimens (Text-fig. 3).

Comparison of the three specimens with respect to comparative measurements of the skull roof (partially described...
The skull proportions of the smaller referred specimen (BP/1/3241) are the same as those for the restored holotype (W/L 0.81), while the skull of BP/1/3241 seems to be somewhat broader (W/L 0.85). The degree of preorbital elongation increases with size (the referred skulls have A/L values of 0.47 and 0.51 compared to a minimum of 0.54 for the holotype). The same trend is demonstrated by the K/O2 index (with values 1.13 ± 1.25 for the three skulls under study, in order of their size; cf. Table 1), though less markedly, by the O1/B index (0.29 ± 0.24 for the same succession; cf. Table 1), both indicating a reduction in the relative size of the orbits with age. However, the reduction of the size of the orbit with regard to the interorbital distance in specimen BP/1/3241 surpasses that of the holotype (O1/IO values for three specimens in order of skull size are: 1.60–1.55 ± 1.08–1.49; cf. Table 1). Likewise, the posterior jugal projection in BP/1/3241 is relatively shorter than in the other two specimens (J2/M value 0.52 against 0.58–0.60 in BP/1/5058 and 0.57 in the holotype). The relative length of the table (M/E) demonstrated by the entire sample increases very slowly with respect to skull size, from 0.62 to 0.65. By contrast to the holotype, both referred specimens have rather short parietals lacking the anterior indentation, and the otic notches are also shorter. The anterolateral projection of the postorbital is already well developed in both juvenile specimens.

These data show that BP/1/3241 departs from the general trend with regard to the relative width of the skull (W/L), the wide separation of the orbits (O1/IO) and the reduction of the posterior jugal projection (J2/M). In the case of the W/L index, this may be attributed to possible inaccuracies in the estimation of the two pertinent parameters, but it is certainly not the case for the two other indices. The significance of these differences is not clear. In the absence of stronger evidence for taxonomic separation of BP/1/3241 we are inclined to consider it as a developmental variation.

Data on the preorbital part of the skull roof could be obtained only from the referred specimens. Both of them have a short lacrimal (La/C = 0.66–0.60) as is common for rhinesuchids. The septomaxilla is best preserved in BP/1/5058 and exhibits the base of the anterior intranarial projection (Text-fig. 3a, ip) which is well developed in, and characteristic of, Permian rhinesuchids (Shishkin et al. 1996).

| Table 1. Skull roof indices in early capitosauroids. Data on juvenile rhinesuchids obtained from skull series BP/1/2931, 2941, 2942A, 2958, 2965, 3070, 3075, 3079, Cistecephalus (Dicynodon?) Assemblage Zone. Semi-grown rhinesuchid condition is typified by the holotype of ‘Lydekkerina kitchingi’ (BP/1/214). Data on adult rhinesuchids are summarized from BP/1/213 (holotype of Muenchus talus) and BP/1/21473 (Kitching 1978, fig. 3) and GS 645, all from the Dicynodon Assemblage Zone; RMS 606, Tapinocephalus Zone (Kitching 1978, fig. 2); and from the figure of Rhiniceps nyasaensis by Watson (1962, fig. 6), Dicynodon(?) Assemblage Zone. Data on Lydekkerina are summarized from the sample listed in Shishkin et al. (1996, Table 1), and presumed to typify the juvenile and semi-grown stages of the standard lydekkerinid ontogeny. Data on adult Eolydekkerina are considered as terminal stage of the same ontogeny. For abbreviations, see Appendix. Index values shown in parentheses calculated from restorations; value in brackets [1.35] refers to the smallest individual of Lydekkerina in the sample examined.

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<th>Broomistega</th>
<th>Typical (Permian) Rhinesuchidae</th>
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<td>Juveniles</td>
<td>Adults</td>
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<td>M/E</td>
<td>0.62</td>
<td>0.63</td>
</tr>
</tbody>
</table>
TEXT-FIG. 3. Skulls of juvenile *Broomistega putterilli*, specimens BP/1/5058 (A–C), and BP/1/3241 (D–E). A, D, line drawings of dorsal view; B, E, photographs of dorsal view; C, photograph of lateral view. Photographs are at the same scale as corresponding line diagram. For explanation of abbreviations, see Appendix.
Many other characters of the preorbital area, seen only in the referred specimens, may possibly be attributable to their immaturity. Both specimens exhibit anterior broadening of the frontals, lack of posterior narrowing of the prefrontals and a step-like posterior border of the nasal. The preorbital projection of the jugal is very short ($J_1/J_2 = 0.43–0.47$; $J_1/C = 0.14–0.23$). The ossification centre of the prefrontal lies in the anterior half of the bone in BP/I/5058, whereas in the larger BP/I/3241 it is more centrally positioned. All these characters are common to rhinesuchid juveniles (Shishkin et al. 1996). In lateral view, BP/I/5058 shows a very faint indication of the preorbital step of the skull roof, a feature present in many non-rhinesuchid capitosauroids (Parrington 1948; Lehman 1961).

**Occiput** (Text-fig. 4)
In all three specimens the table portion of the occiput shows the typical rhinesuchid pattern. Distinctive features include the lack of a central dorsal concavity in the skull roof and the presence of a blade-like dorsolateral projection of the terminal part of the paroccipital bar which lies behind the ornamented surface of the tabular and curves slightly downwards in occipital view. In all specimens the occipital flanges of the postparietal and tabular are flattened and slope backwards. The posttemporal area, observable both in the holotype and BP/I/5058, conforms to the typical rhinesuchid condition in the following characters: the tabular-postparietal occipital flange, which roofs the slit-like posttemporal fenestra, projects slightly posterovertrally behind the fenestra; the paroccipital bar is almost parallel to this flange and has the flattened terminal projection mentioned above. As in all rhinesuchids (cf. Shishkin et al. 1996), the bar is formed by only the tabular and exoccipital, with no opisthotic intervening between them.

In addition to the paroccipital and dorsal processes, the exoccipital bears a thin ascending lamellar process on the medial side, and a fairly long and shallow subotic process on the lateral side. The tenth cranial nerve foramen lies entirely in the paroccipital process.

In both the holotype and BP/I/5058 the cheek portion of the occipital surface shows the tympanic crest of the occipital flange of the squamosal situated very close to the squamosal-quadratojugal suture (Text-fig. 4, ct). From this it is evident that more than three quarters of this flange contributed to the tympanic cavity, leaving only a very small lateral portion to contribute to the depressor area of the occiput. Again, this is the standard rhinesuchid condition, and differs from lydekkerinids wherein the tympanic and depressor areas of the squamosal flange are roughly equal in size.

The depressor area formed by the lateral part of the squamosal occipital flange and the quadratojugal flange is pierced by a small paraquadrate foramen. In the holotype this foramen is situated in the suture between the two bones (which is rather uncommon for temnospondyls), while on the right side of BP/I/5058 it is completely included within the quadratojugal, although still located very close to the squamosal suture.

In occipital view, the ascending lamina of the pterygoid forms the crista obliqua (Text-fig. 4, cob), which occupies a subhorizontal position, at the mid-height of the occiput in the holotype and even lower down in BP/I/5058, a condition which is also present in lydekkerinids. This contrasts with Permian rhinesuchids where the crista obliqua ascends rather steeply towards the otic notch. However, the crista in *Broomistega* is blade-like, as in most capitosauroids, rather than forming a ledge which is typical for lydekkerinids.

The low position of the crista obliqua evident in *Broomistega* is also found in the juveniles of many capitosauroids including the semi-grown rhinesuchids ‘Lydekkerina kitchingi’ (pers. obs.), the holotype of ‘Benthosuchus’ madagascarensis (Lehman 1961), and also in paedomorphic lydekkerinids (Shishkin et al. 1996). The presence in *Broomistega* of this character combined with small body size can be ascribed to the paedomorphic status of the genus.
TEXT-FIG. 5. *Broomistega putterilli*, *Lystrosaurus* Assemblage Zone (A–E); and *Rhinesuchus* sp., *Tapinocephalus* Assemblage Zone (F), palatal structures in ventral view. A, C, holotype TM 184, posterior part of palate; B, BP/1/3241, anterior part of palate; D, BP/1/3241, palate as preserved; E, BP/1/5058, palate; F, GS 86/52, basis cranii. For explanation of abbreviations, see Appendix.
Palate (Text-fig. 5)

Most of the posterior part of the palate is preserved in the holotype (Text-fig. 5A, C). The parasphenoid body is transversely concave and can be subdivided anteroposteriorly into three segments: the sutural area (contacting the pterygoids), the middle zone, and the area of pockets for the attachment of the neck muscles. The middle zone is unusually long and comprises 35 per cent of the total length of the parasphenoid body (compared to 15–20 per cent in Permian rhinesuchids). In palatal view the lateral edge of this zone forms a very gentle concavity, contrasting to the deep embayment in other rhinesuchids (cf. Text-fig. 5A, f). The pockets for muscle attachment are deep, but rather small; their total width is roughly equivalent to the distance between them, unlike the condition in early rhinesuchids, where the pockets are much broader. Most of the ventral surface of the sutural area of the parasphenoid body is covered with shagreen dentition. As is common in the Rhinesuchidae, the middle of the shagreen field is narrow anteroposteriorly and the field extends caudally along the pterygo-parasphenoid sutures, where the denticles become coarser. Anteriorly, the shagreen field continues as a narrow strip over the entire extent of the preserved portion of the cultriform process.

In side view, the lateral part of the parasphenoid body above the middle zone ascends dorsolaterally as a flat triangular wall and is pierced by a rather large foramen for the internal carotid artery. The wall corresponds to the lateral surface of the parapterygoid crest of advanced capitosauroids (cf. Bystrow and Efremov 1940, figs 9A, 10).

The ventral surface of the parapterygoid crest of advanced capitosauroids (cf. Bystrow and Efremov 1940, figs 9A, 10).

The choanae appear to be slightly elongate and bordered by the vomerine (anterior) and palatine (posterior) task pairs (Text-fig. 5b). The anterior half of the cultriform process of the parasphenoid is flat, lacking shagreen and bears longitudinal striations consisting of faint ridges. Its palatal exposure attains maximum breadth just behind the posterior vomerine processes, but is somewhat narrowed between them. The cultriform process terminates at the level of the anterior border of the interpterygoid vacuities in BP/1/3241 and extends a little further forward in BP/1/5058. The vomer has only a rudimentary posterior process, a condition that may be ascribed to the juvenile age of the specimens. Among the structures described above, only a few can be seen in BP/1/5058. The pockets for muscle attachment on the parasphenoid are small, deep and broadly separated, although to a slightly lesser degree than in the holotype. The middle zone of the parasphenoid body seems to be a little shorter, and its lateral embayment more markedly expressed than in the holotype. The right ectopterygoid bears a tusk pair in front of the row of minor teeth. The palatal branch of the pterygoid narrows anteriorly and terminates as a strip of bone along the margin of the interpterygoid vacuity, extending beyond the middle of its length.

Some details of the anterior part of the palate, that are missing in the holotype, can be seen on the referred specimens. In both of them the choana appears to be slightly elongate and is bordered by the vomerine (anterior) and palatine (posterior) task pairs (Text-fig. 5b). The anterior half of the cultriform process of the parasphenoid is flat, lacking shagreen and bears longitudinal striations consisting of faint ridges. Its palatal exposure attains maximum breadth just behind the posterior vomerine processes, but is somewhat narrowed between them. The cultriform process terminates at the level of the anterior border of the interpterygoid vacuities in BP/1/3241 and extends a little further forward in BP/1/5058. The vomer has only a rudimentary posterior process, a condition that may be ascribed to the juvenile age of the specimens. By contrast, the posterolateral process is very long, forms most of the medial border of the choana, and extends far backwards at least to a point medial to the posterior palatine task. This is the typical rhinesuchid condition.

At the level of the vomerine tasks, both referred specimens bear a faint, but rather marked transverse ridge that forms the posterior border of the anterior palatal depression. In BP/1/5058 the contour of this border is gently curved and lies largely between the vomerine task pairs; in BP/1/3241 it protrudes backwards to the level of the choanae, and, as restored from the right side of the palate (the only one exposed), appears to be angular (Text-fig. 5b). The anterior palatal depression is fairly deep, and in BP/1/3241 the posterior wall ascending to the skull roof is especially steep. The bottom of the depression in BP/1/5058 bears two matrix filled anterior palatal foramina separated by a distinct median ridge; the condition in the other referred specimen is unknown as the anterior half of the depression is not prepared.

The arrangement and pattern of tooth rows in the two referred specimens are rather different. In BP/1/5058, the inter- and parachoanal tooth rows extend as a single continuous series of uniformly small teeth, forming an arch that is convex anteriorly and similar to the condition known in many Permian rhinesuchids, including *Rhineceps nyasaensis* (Watson 1962, fig.7), *Laccosaurus watsoni* (SAM 4010) and others. The interchoanal part of the series is interrupted in the midline as is very common in rhinesuchids; there is no indication of tooth bases in the median gap. A number of shagreen denticles seem to ajoin the interchoanal tooth row anteriorly. Behind the row, the surface of the vomers is finely rugose, which may indicate the presence of shagreen dentition in earlier growth stages, though no unquestionable denticles were noted. The parachoanal part of the series continues backwards up to the level of the posterior...
palatine tusk. It is not clear whether it extends over only the vomer, or continues on to the palatine as well. The palatine bears seven to eight postcanine teeth that decrease in size posteriorly.

In contrast to the condition described above, in BP/1/3241 the inter- and parachoanal tooth rows are well differentiated (Text-fig. 5b). The small parachoanal teeth are reduced in number to three or four, and set along the anterior part of the medial choanal border. That part of the interchoanal row exposed on the left vomer consists of three to four somewhat larger, laterally compressed teeth that are separated from the parachoanal tooth row. As restored, the complete interchoanal row forms almost a right angle pointing backwards. Behind it, the central area of the vomer bears a few, small shagreen denticles. The details of the palatine dentition (behind the tusk pair) are not visible.

**Lower jaw**

Both rami of the lower jaw are best preserved in the immature specimen BP/1/5058 (cf. Text-fig. 3c). Although in the present state of preparation of the specimen these cannot be described in detail, some descriptive remarks are warranted. The lower jaw is of typical rhinesuchid configuration, with a fairly long posterior Meckelian foramen, and a coronoid series sloping from a dorsal to lingual plane. The presence of a continuous shagreen field on the entire coronoid series (typical of rhinesuchids) is likely, judging by the presence of shagreen on the intercoronoid; but, on the other hand, the extent of this field seems to be limited to the topmost part of the series. The prearticular extends forward, almost as far as the anterior end of the postplenial, which is a rather primitive condition (cf. *Rhineceps*, Watson 1962, fig. 8a). By contrast, the general pattern of the mandible is advanced beyond the standard rhinesuchid condition in that the rudimentary retroarticular process is developed, and, as in the early Triassic capitosauroids, the ventral contour of the lower jaw is angular rather than rounded.

**DISCUSSION**

*On the cranial pattern in Broomistega as compared with other early capitosauroids*

Data on the cranial proportions of *Broomistega* can be evaluated in terms of the early capitosauroid structural patterns demonstrated by Permian rhinesuchids, Early Triassic lydekkerinids and their juveniles. For lydekkerinids, the juvenile and adult conditions are typified by the paedomorphic *Lydekkerina*, the more fully developed *Eolydekkerina*, and to some extent *Luzocephalus* (Shishkin 1980; Shishkin et al. 1996). For rhinesuchids, morphological data for early growth stages are based on a number of rhinesuchid juveniles with a skull length of 50–65 mm, from the *Dicynodon* Assemblage Zone at the farm Beeldhouersfontein, in Murraysburg District (Text-fig. 6a). These skulls possibly belong to *Mucosocephalus muchos*, known from a somewhat higher horizon of the adjacent area (Kitching 1978; Shishkin et al. 1996). Of particular interest is a semi-grown individual of *M. muchos*, previously described as the holotype of ‘*Lydekkerina kitchingi*’ (Broom 1950), that is relatively close in size to the holotype of *Broomistega* (Text-fig. 6b). Results of comparisons of *Broomistega* with the forms listed above are presented in Table 1. This shows that the maximum relative width of the skull that may be restored for *Broomistega* (W/L = 0.81), corresponds to the maximum value known in adult rhinesuchids (W/L ranges from 0.80 to 0.70 in larger forms). This is much less than in juvenile rhinesuchids (0.98–0.92) and lydekkerinids, including both adult (up to 0.90) and paedomorphic forms (well above 0.90) (cf. Table 1).

Likewise, the minimum value of the relative preorbital length calculated for *Broomistega* (A/L = 0.54) corresponds to the lower limit of the range for rhinesuchids (0.55–0.60), but greatly exceeds the maximum value for *Lydekkerina* (less than 0.50) and juveniles of Permian rhinesuchids (0.46). However, in some lydekkerinids, such as *Eolydekkerina*, that exhibit relatively little truncation of ontogeny, this index can be as high as that for *Broomistega*.

An additional rhinesuchid character of *Broomistega* is the shortness of the lacrimal (La/C = 0.65–0.60), present even in young individuals with a skull length of 57–75 mm. This value also falls within the lower part of the range for adult rhinesuchids (0.65–0.56), but is markedly different from those in the other morphotypes being compared, all of which retain the primitive condition of a longer lacrimal. This is seen in both fully developed and paedomorphic lydekkerinids (La/C value 0.70–0.68 and 0.91–0.75 respectively) and in juvenile rhinesuchids (0.86–0.65).

With regard to other quantitative characters, *Broomistega* is much more similar to the generalized juvenile condition of early capitosauroids than to adults of its Permian forerunners. The extent of the posterior projection of the jugal in *Broomistega* (J2/M = 0.57) is similar to that of both lydekkerinids (0.70–0.57 in *Lydekkerina*, 0.55 in *Eolydekkerina*) and juvenile rhinesuchids (0.57–0.50). In adult
rhinesuchids a J₂/M value of 0.54–0.56 occurs in two specimens (BP/1/4473 and R645), but it is more commonly closer to 0.35. The relative length of the preorbital projection of the jugal in adults of Broomistega is unknown, but in the immature individuals it also corresponds to the normal juvenile condition of early capitosauroids, in that Ju₁/Ju₂ = 0.43–0.47 and Ju₁/C = 0.14–0.23 (Table 1).

A further point of similarity with the juvenile pattern, evident in Broomistega, are the large orbits separated by a narrow interorbital bridge. The O₁/I value in this genus (1.49) is close to the range exhibited by the juvenile Permian rhinesuchids (1.44–1.0), whereas in adult rhinesuchids, ‘normal’ (not markedly paedomorphic) lydekkerinids and Lydekkerina this value is considerably smaller (0.83–0.54, 0.72–0.50 and 1.18–0.77 respectively). Only the smallest Lydekkerina specimen, with a skull length of 49 mm, was found to approach the condition of Broomistega (O₁/I = 1.35).

The same picture is evident for other indices characterizing the size of orbits (cf. Table 1). The O₁/B value in Broomistega (0.25) falls within the range shown by Lydekkerina (0.26–0.18) and immature rhinesuchids (0.26–0.22), while in fully developed early capitosauroids it does not exceed 0.20 (0.20–0.13 in rhinesuchids and 0.19–0.17 in Eolydekkerina and Luzocephalus). Likewise, the ratio of the orbit-otic notch distance to the orbit length (K/O₂ = 1.25) seen in Broomistega is markedly different from that in rhinesuchids (1.34–1.51) and lydekkerinids (1.34–1.78 in Lydekkerina, 2.2–2.6 in Eolydekkerina and Luzocephalus), but falls within the range exhibited by juvenile rhinesuchids (1.20–1.42).

A further, although not so marked resemblance with early growth stages of primitive capitosauroids is seen in the proportions of the ‘table’, i.e. the postorbital part of the dermal roof of the braincase (M/E). The M/E value for adults of Broomistega is 0.65, compared to 0.66–0.72 in juvenile rhinesuchids and 0.60–0.70 in Lydekkerina. Fully developed lydekkerinids exhibit the same proportions (M/E close to 0.65), while in adult rhinesuchids the table is somewhat longer (M/E above 70) (cf. Table 1).

This demonstrates that at least in some characters (related to the size and relative position of the orbits, the extent of the posterior jugal projection and the proportions of the skull table) Broomistega deviates...
from the typical adult rhinesuchid pattern, but corresponds to that of juvenile rhinesuchids. For some characters, such as the O\textsubscript{1}/I index, the degree of deviation exhibited by *Broomistega* is even greater than that for juvenile rhinesuchids.

Important comparisons can also be made between *Broomistega* and a semi-grown individual of *Muchocephalus muchos* (the holotype of ‘Lydekkerina kitchingi’; cf. Broom, 1950) that is intermediate in size (midline length of skull = 84 mm) between juveniles from Beeldhouersfontein (50–65 mm) and a presumed adult of this species (236 mm). As this immature specimen of *Muchocephalus muchos* is much smaller than the holotype of *Broomistega* it might be expected to exhibit more juvenile features than the latter genus. However, as seen from Table 1, the state of these characters (Ju\textsubscript{2}/M, O\textsubscript{1}/I, O\textsubscript{1}/B, K/O\textsubscript{2}, M/E) is more advanced in the holotype of ‘Lydekkerina kitchingi’ than in *Broomistega*. In this respect the specimen occupies an intermediate position between *Broomistega* and adult Permian rhinesuchids.

This appears to provide evidence that when compared with the more generalized pattern of rhinesuchid development, thought to be exemplified by *Muchocephalus*, the ontogeny of *Broomistega* was retarded in respect to a number of characters. However, this retardation is combined with a more normal developmental timing for some other rhinesuchid characters, such as elongation of the skull and its preorbital region (W/L, A/L) and the shortening of the lacrimal (La/C). This combination enables us to define *Broomistega* as a paedomorphic genus, a conclusion that is in accordance with the small size of the form, which is uncommon in Permian rhinesuchids. It may be further concluded that within Rhinesuchidae, *Broomistega* demonstrates the same trend toward paedomorphic miniaturization as does the coeval form *Lydekkerina* in the Lydekkerinidae.

Further evidence of the paedomorphic status of *Broomistega* is indicated by the low position of the oblique crest of the pterygoid, a condition paralleled in semi-grown individuals of *Muchocephalus*, as well as in lydekkerinids and juveniles of advanced capitosauroids (cf. Shishkin et al. 1996).

A more ambiguous piece of evidence is the position of the muscular crests of the parasphenoid which are located well behind the pterygo-parasphenoid sutures. The possibility of a paedomorphic origin for this character deserves some consideration. It is sometimes argued (Ochev 1966; cf. pp. 106, 115) that the evolution of the muscular crests from the condition seen in rhinesuchids (Text-fig. 5\texttextsubscript{f}) to that evident in more advanced capitosauroids, proceeded by backward extension of the pterygo-parasphenoid sutures until they reached the level of the crests. This view is not corroborated by our observations, which show that the sutures are no shorter in rhinesuchids than in Early Triassic capitosauroids. We support the alternative hypothesis (Watson 1951, p. 60, fig. 22) that the advanced condition was attained by a forward shifting of the muscular crests, rather than elongation of the sutures. It is especially noteworthy that intermediate forms of this character are evident in some rhinesuchids that show a different position of the crests on either side of the same individual. For example, in the skull fragment SAM K6983 the crest on the right side of the palate lies at the level of the posterior end of the pterygo-parasphenoid suture (as in non-rhinesuchid capitosauroids), while on the left side it is still situated well behind this level. From this evidence it can be assumed that some degree of forward shift of the muscular crests might have occurred in rhinesuchids, with this trend being recapitulated in their ontogeny.

Providing the latter assumption is correct, the position of the crests far posterior to the basicranial sutures, evident in *Broomistega*, may correspond to the early stage of the normal rhinesuchid growth pattern and thus might be even more accentuated in juvenile individuals. However, as seen from the description above, this is not immediately confirmed by comparison of the adult specimen of *Broomistega* with the juvenile stage represented by BP/1/5058. This seems to imply that in *Broomistega* the unusually large degree of separation between the basicranial suture and the muscular crest is not necessarily caused by paedomorphic evolution. However, this suggestion does not affect the hypothesis supported above that the anterior position of the muscular crests in advanced capitosauroids did not result from posterior extension of the basicranial sutures in their rhinesuchid ancestors.

In conclusion, some remarks may be made with regard to the assumption that the holotype of *Broomistega* is actually represented by an immature individual. As the material available for this study is limited, it cannot be ruled out that fully grown individuals of *Broomistega* were somewhat larger than the holotype. However, it is evident that this specimen does not represent a transitional growth stage of typical large rhinesuchids, such as *Rhinesuchus* and *Uranocentrodon*. Apart from the specific (retarded)
timing of development of some of the characters discussed earlier, this is also supported by a number of morphological distinctions, of both paedomorphic and non-paedomorphic origin. The former are primarily expressed in the low position of the parasphenoid oblique crest. The latter include the elongation and shallowness of the exoccipital subotic processes, the large separation between the basioccipital sutures and the parasphenoid muscular crests and, most notably, the shape of the parietals whose narrowness and deep anterior indentation (Text-fig. 2) are unparalleled in any other known rhinesuchids, adult or juvenile. The total width:length ratio of the parietals in rhinesuchid adults, including *Uranocentrodon* (NMQR 1483, TM 185), is much larger (0.95–0.78) than in *Broomistega* (0.64). In juvenile and semi-grown rhinesuchids, the parietal proportions are more nearly isometric (close to 1:1), in spite of their short interorbital distance, which might be expected to correlate with the narrowness of the parietals; and the frontal-parietal suture of these stages tends to be transversely straight (Text-fig. 6A–B; Shishkin et al. 1996). The same pattern is present in juveniles of *Broomistega* (Text-fig. 3A–B).

**Palaeoenvironmental implications**

As seen from the above morphological analysis, *Broomistega* should be regarded as a small paedomorphic genus rather than the growth stage of some of the larger rhinesuchids described previously. Another line of evidence in support of this idea is the absence, in the *Lystrosaurus* Assemblage Zone, of any other rhinesuchid finds that correspond to the adult stage of the presumed growth series represented by the *Broomistega* individuals described here.

Removal from the list of the *Lystrosaurus* Zone fossils of both *Uranocentrodon* and the advanced capitosauroid *Kestrosaurus*, which is now known to be of younger age (Hancox et al. 1995; Shishkin et al. 1995), means that the amphibian assemblage from this zone consists only of small or medium-sized forms. As all the most common amphibian components of the assemblage, such as *Lydekkerina*, *Micropholis*, and *Broomistega*, were paedomorphic and largely aquatic, this suggests that there may have been some environmental limitations that affected the local amphibian habitats. Possible factors include the small size and shallowness of water bodies populated by amphibians, as well as seasonal aridity, which, except for the smallest, frog-sized forms such as *Micropholis*, would have rendered amphibian life outside pools impossible. This interpretation of the local environment is consistent with data on the global aridification of Pangea during the earliest Triassic (Shishkin and Ochev 1993; Shishkin 1997), and is exactly the reverse of that suggested by Parrington (1948) to account for miniaturization of the components of the *Lystrosaurus* tetrapod assemblage.

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Abbreviations
A, preorbital length; apd, anterior palatal depression; B, width of skull across the centres of orbits; C, orbitonarial distance; ch, choana; cm, muscular crest of parasphenoid body (= crista muscularis parasphenoidei); cob, oblique crest of pterygoid (= crista obliqua pterygoidei); ct, tympanic crest of squamosal (= crista tympanica squamosi); E, distance between the anteriormost points of otic notches; Ect, ectoperygoid; Ex, exoccipital; F, frontal; I, interorbital distance; ip, intranarial process of septomaxilla; J, jugal; Ju1, preorbital extent of jugal measured along the skull border; Ju2, postorbital extent of jugal measured along the skull border; K, distance between orbit and otic notch; L, total midline length; La, lacrimal (in Text-fig. 1, length of lacrimal); M, postorbital midline length, Mx, maxilla; O1, width of orbit; O2, length of orbit; N, nasal; P, parietal; Pf, postfrontal; Pl, palatine; Pmx, premaxilla; Po, postorbital; Pp, postparietal; ppr, unornamented tip of paroccipital process; Prf, prefrontal; Ps, parasphenoid; Pt, pterygoid; Q, quadrate; Qj, quadratojugal; S, stapes; Smx, septomaxilla; Sq, squamosal; St, supratemporal; T, tabular; th, hyoid tubercle (= tuberculum hyoideum quadrati); V, vomer; W, total width (across the quadrates); X, vagus foramen.