

CRANIAL ANATOMY OF THE GIANT MIDDLE TRIASSIC TEMNOSPONDYL *CHERNINIA MEGARHINA* AND A REVIEW OF FEEDING IN MASTODONSAURIDS

by

Ross J. Damiani

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag 3,
Wits 2050, South Africa
e-mail: 106ross@cosmos.wits.ac.za

ABSTRACT

The skull of *Cherninia* ('*Parotosuchus*') *megarhina*, a giant but poorly known mastodontosaurid temnospondyl from the Upper Horizon of the Middle Triassic N'tawere Formation of the Upper Luangwa Valley, Zambia, is redescribed and refigured in detail for the first time. *Cherninia megarhina* is highly derived in most aspects of its cranial morphology and is characterised by the presence of a massively broad and elongated snout, relatively tiny orbits that are set well back on the skull roof, small, near-laterally directed tabular horns, an occipital sensory sulcus, and prominent, forked ridges on the skull roof. The palate is characterised by the presence of a ventral exoccipital-pterygoid contact, a short basicranial suture, a narrow parasphenoid body, a broad pterygoid body, and choanae that are placed far forward of the interpterygoid vacuities. The presence in *Cherninia megarhina* of numerous cranial autapomorphies justifies its separation from *Parotosuchus*. These autapomorphies are shared with *Cherninia* ('*Parotosuchus*') *denwai* from the Middle Triassic Denwa Formation of India. The lateral orientation of the tabular horns and morphology of the otic region suggests that *Cherninia megarhina* is slightly more derived than the Indian species. Mastodontosaurids have traditionally been perceived as passive, benthic suction-feeders. However, recent work on the anatomy and functional morphology of the skeleton of mastodontosaurids suggests that they were designed for active swimming and predation. As such, it is hypothesised that prey capture was achieved using sideways sweeps of the head rather than suction-feeding.

KEYWORDS: Temnospondyl, Triassic, *Cherninia megarhina*, Mastodontosauridae, feeding

INTRODUCTION

The Mastodontosauridae, the senior synonym of the more widely known taxon Capitosauridae (Damiani in press a), is a monophyletic clade of Mesozoic stereospondyls that were widely distributed throughout Triassic Pangaea. Mastodontosaurids were morphologically diverse and were the most abundant and widely distributed of any temnospondyl group, and their ubiquity in non-marine Triassic strata has led to their being amongst the principal vertebrate groups used in biostratigraphy and correlation of Triassic tetrapod faunas (Hancox *et al.* 1995; Ochev & Shishkin 1989; Lucas 1998).

Despite a long history of study dating back to the first half of the 19th century, the taxonomy of the Mastodontosauridae has long been problematic and there remains little consensus as to the taxonomic composition of the group or the relationships within it (Schoch 2000; Damiani in press a). This is due, in part, to the sheer abundance of fossil material attributable to the Mastodontosauridae and to the effects of excessive taxonomic 'splitting', both of which resulted in a large number of names erected on undiagnostic material (Ochev 1966; Welles & Cosgriff 1965; Damiani in press a). The first serious attempt at rationalizing mastodontosaurid taxonomy was the landmark review of Welles & Cosgriff (1965), who surveyed all then known

species and reduced the number of valid genera to four (*Parotosuchus*, *Paracyclotosaurus*, '*Kestrosaurus*', *Cyclotosaurus*) by synonymising most species or referring to them as *nomina vana*. Welles and Cosgriff's paper proved highly influential and most subsequent descriptions of mastodontosaurids were referred to one of these four genera, usually *Parotosuchus*. Although this taxonomy has proved largely stable, recent work on mastodontosaurid systematics (Schoch & Milner 2000; Damiani in press a) has shown that this taxonomy is largely artificial and, perhaps ironically, both authors recognised a greater number of genera within the Mastodontosauridae than the four recognised by Welles & Cosgriff (1965).

The subject of this paper, the mastodontosaurid *Cherninia* ('*Parotosuchus*') *megarhina*, was first described in a brief note by Chernin & Cruickshank (1970) based on a poorly preserved partial skull (BP/1/4223) from the Upper Horizon of the Middle Triassic N'tawere Formation of Zambia (Drysdall & Kitching 1963). Chernin and Cruickshank provided only an outline drawing of the skull roof of the specimen which they referred to '*Parotosuchus*' *pronus* (Howie 1970) from the Middle Triassic Manda Formation of Tanzania, primarily on the basis of the shape of the tabular horns but despite the marked difference in the size and shape of the snout. Chernin (1974) provided a more detailed

description and drawing of the skull roof which included the supposed course of the lateral line sulci and, apparently, an interpremaxillary foramen, although most of the sutures could not be determined. The fragmentary palate was only briefly described but not illustrated. Chernin (1974) tentatively retained the specimen in '*P. pronus*' and argued that the great difference in the size of the snout between BP/1/4223 and the smaller '*P. pronus*' was due to "genetic variability". Chernin also tentatively referred a second skull (BP/1/4221) from the same locality as BP/1/4223 to '*P. pronus*'. Chernin & Cosgriff (1975) provided a revised outline drawing of the skull roof of BP/1/4223 which differed from that of Chernin (1974) in the broader snout proportions and in the size and shape of the nostrils and tabular horns. On this basis, Chernin and Cosgriff referred BP/1/4223 to a new species, '*P. megarhinus*'. The second skull described by Chernin (1974), BP/1/4221, was also tentatively referred by Chernin and Cosgriff to '*P. megarhinus*' but is significantly smaller than BP/1/4223.

In their recent review of the Stereospondyli, Schoch & Milner (2000) recognised, but did not discuss, the distinctive cranial proportions of '*Parotosuchus megarhinus*' and suggested that it may warrant a new genus within the 'Capitosauroida'. In the most recent review of mastodonsaurid taxonomy which included an examination of the holotype (BP/1/4223) and referred specimen (BP/1/4221) of '*P. megarhinus*', Damiani (in press a) listed several cranial autapomorphies of the holotype specimen (see Emended diagnosis below) and erected for it a new genus, *Cherninia*. Principal amongst these autapomorphies are the massively developed snout, the presence of an occipital sensory sulcus and the presence of paired, forked ridges on the skull roof. However, Chernin & Cosgriff's (1975) referred specimen of '*P. megarhinus*', BP/1/4221, was transferred by Damiani (in press a) to '*P. pronus*', for reasons discussed in that paper. On the basis of the listed autapomorphies of *Cherninia*, Damiani (in press a) also referred to *Cherninia* the recently described mastodonsaurid '*Parotosuchus denwai*' (Mukherjee & Sengupta 1998), from the Middle Triassic Denwa Formation of central India. The similarity of that taxon with *C. megarhina* was earlier noted by Bandyopadhyay & Sengupta (1999), but not discussed. As the focus of Damiani's paper was a taxonomic revision of the Mastodonsauridae and not anatomical descriptions, he did not redescribe the holotype skull of *C. megarhina*.

Accordingly, this paper provides a full redescription and a new, revised reconstruction of the skull of *Cherninia megarhina* which differs significantly from previous reconstructions. Airbrasive and mechanical preparation of the skull has revealed hitherto unknown details of the skull roof including the sutural pattern, and permits the first drawing and detailed description of the palate. In view of the ongoing debate (Milner 1990; Maryanska & Shishkin 1996; Schoch 2000; Damiani in press a) concerning the intrarelationships of 'capitosauroid' temnospondyls, detailed osteological descriptions especially of the more poorly known taxa

such as *C. megarhina* are crucial for resolving phylogenetic relationships.

Finally, the feeding strategy of mastodonsaurids has attracted considerable attention from temnospondyl workers. The traditional view held that mastodonsaurids were passive, benthic suction-feeders, while other workers favoured a more active, predatory feeding strategy. In this paper I review aspects of the anatomy and functional morphology of mastodonsaurids in relation to feeding and suggest a likely strategy for prey capture.

SYSTEMATIC PALAEOLOGY

TEMNOSPONDYLI Zittel 1887-1890

STEREOSPONDYLI Zittel 1887-1890 *sensu*

Yates & Warren 2000

MASTODONSAUROIDEA Lydekker 1885 *sensu*

Damiani in press a

MASTODONSAURIDAE Lydekker 1885 *sensu*

Damiani in press a

CHERNINIA Damiani in press a

Type species. Cherninia ('*Parotosuchus*') *megarhina* (Chernin & Cosgriff 1975).

Referred species. Cherninia ('*Parotosuchus*') *denwai* (Mukherjee & Sengupta 1998).

Emended diagnosis. Distinguished from all other mastodonsaurids by the following autapomorphic characters: Snout hyper-elongated; skull table (i.e. postorbital portion of skull roof) exceptionally short; nostrils large, confluent with skull margin anteriorly; skull roof with paired, forked ridges anterior to orbits; loose patch of pustular ornament on jugals and prefrontals; occipital sensory canal present; temporal sensory canal extending to tips of tabular horns; postparietals antero-posteriorly short but exceptionally broad; choanae located far forward of the interpterygoid vacuities.

CHERNINIA MEGARHINA (Chernin and Cosgriff)

Damiani in press a

Parotosaurus pronus (Howie) Chernin &

Cruickshank 1970

Parotosaurus pronus (Howie) Chernin 1974, in part

Parotosaurus megarhinus Chernin & Cosgriff 1975

Parotosuchus megarhinus Chernin 1978

Holotype. BP/1/4223, a partial skull with associated cranial fragments, repositied in the Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa.

Type locality and Horizon. Locality 15, south of the Sangu River 3.5 miles west of Sitwe, in the Upper Luangwa Valley, Zambia (Drysdall & Kitching 1963); Upper Horizon of the N'tawere Formation, Anisian (e.g. Battail 1993; Hancox 2000). This horizon has also yielded the brachyopid temnospondyl *Batrachosuchus*

concordi (Chernin 1977), the dicynodonts *Zambiasaurus* and *Sangusaurus* (Cox 1969), and the cynodont *Luangwa* (Brink 1963).

Diagnosis. As for the genus. The referred species, *Cherninia denwai*, differs from *C. megarhina* in having more posteriorly directed tabular horns, a broader otic notch, a more deeply concave occipital skull margin, well expressed sensory canals, a bony protuberance on the occipital face of the tabular, and, possibly, in possessing a septomaxilla and lacking a circum-narial sulcus.

DESCRIPTION

Preservation

The holotype and only known skull of *Cherninia megarhina* was found fragmented and encased in a soft matrix, the "N'tawere green and purple marls" (Dixey 1937), associated with clumps of extremely hard, black manganese. Until now much of this matrix still covered the skull, and it was decided to undertake additional preparation using an airbrasive unit and pneumatic drill, revealing the skull roof and palate in detail for the first time. The bone is generally poorly preserved with numerous cracks, ranging from broad to hairline in width, present throughout. The skull has clearly suffered from post-mortem distortion which is especially evident on the snout which appears flat but somewhat undulating. Consequently it is difficult to determine such characteristics as the overall depth of the skull and snout, and the presence or absence of a preorbital step. Ornament and sutural patterns on the more posterior parts of the skull roof are well exposed. Anteriorly a thin, resistant layer of matrix clings to the skull roof and could not be removed without serious damage. The ventral surface of the skull roof remains largely covered by manganese-rich matrix which again proved resistant to mechanical removal. Matrix has been cleared from most of the palate except anteriorly, where considerable damage to the bone has occurred.

Skull roof (Figures 1A-3A)

The most prominent aspect of the skull of *Cherninia megarhina* is the extraordinarily massive snout that is expanded both antero-posteriorly and transversely so that the lateral margins are near parallel-sided and the anterior rim is broadly parabolic. The length of the skull, from the tip of the snout to the posterior border of the skull deck, is approximately 800 mm. Posteriorly the cheek region of the skull appears to have been slightly 'flared'. The shape of the skull in the new reconstruction (Figure 3) resembles Chernin's (1974) initial restoration but differs markedly from that of Chernin & Cosgriff (1975) in that the snout as restored by the latter authors is overly broad. A similarly broad but much less elongated snout occurs in *Tatrasuchus kulczyckii* (Maryanska & Shishkin 1996), '*Kupferzellia*' *wildi* (Schoch 1997) and *Cyclotosaurus* (Fraas 1889, 1913; Schoch & Milner 2000), and contrasts with the more

slender, triangular snouts of all other mastodonsaurids. However, the shape and relative proportions of the skull of *C. megarhina* are nearly identical to that of the smaller (570 mm skull length) *Cherninia denwai* (Mukherjee & Sengupta 1998). In *C. denwai* and *C. megarhina*, the snout (i.e. the skull roof anterior to the orbits) accounts for 75 and 80 percent of the total length of the skull, respectively, whereas in most other adult mastodonsaurids the snout accounts for between 65-70 percent of the total skull length. *Cherninia* is thus clearly peramorphic (*sensu* McNamara 1986) with respect to other mastodonsaurids, having undergone increased development of the snout as compared to closely related taxa.

Relative to the size of the skull as a whole the orbits are tiny, set very close together and positioned well back on the skull roof, with their long axes pointing toward the midline. This is identical to the situation in *Cherninia denwai* (Mukherjee & Sengupta 1998). The preserved left orbit is elevated above the surrounding plane of the skull roof so that an interorbital trough is present, as is typical for mastodonsaurids except *Mastodonsaurus* (Schoch 1999). Only a small portion of the right orbit was preserved. The preserved portion of the rim of the parietal foramen indicates that its outline was circular or sub-circular (cf. Chernin 1974), unlike the transversely widened foramen figured by Chernin & Cosgriff (1975). In *C. denwai* the parietal foramen is somewhat irregular in shape but the surrounding area appears to have been damaged. In contrast to Chernin (1974), there is no evidence of an interpremaxillary foramen.

Most of the left and a small margin of the right external naris is preserved. The more complete left nostril indicates that they were exceptionally large in size, oval, and had their long axes parallel to the midline. The anterior portion of the nares appear to have been confluent with the skull margins, as in *Cherninia denwai*. Previous reconstructions of the nostrils (Chernin 1974; Chernin & Cosgriff 1975) are incorrect in being too small and separated from the skull margin in the conventional manner. This condition is clearly an autapomorphy of *Cherninia*, and, as far as can be determined, is unique within the Stereospondyli. In addition, a clearly defined sulcus is present around the margin of the left naris; this sulcus is not apparent on the right naris because of poor preservation. A sulcus in this position was not described in *C. denwai*, and may thus represent an autapomorphy of *Cherninia megarhina*. In *C. denwai* an undifferentiated, ornamented 'lump' of bone within the narial cavity was identified as a septomaxilla (Mukherjee & Sengupta 1998). No trace of such an element is present in *C. megarhina*, although it may easily have been dislodged and hence not preserved. Within the left narial cavity of *C. megarhina* the anterior portion of the choana can clearly be seen, as in *C. denwai* (Mukherjee & Sengupta 1998). This indicates that, as in *C. denwai*, the choanae in *C. megarhina* were positioned extremely far forward on the palate.

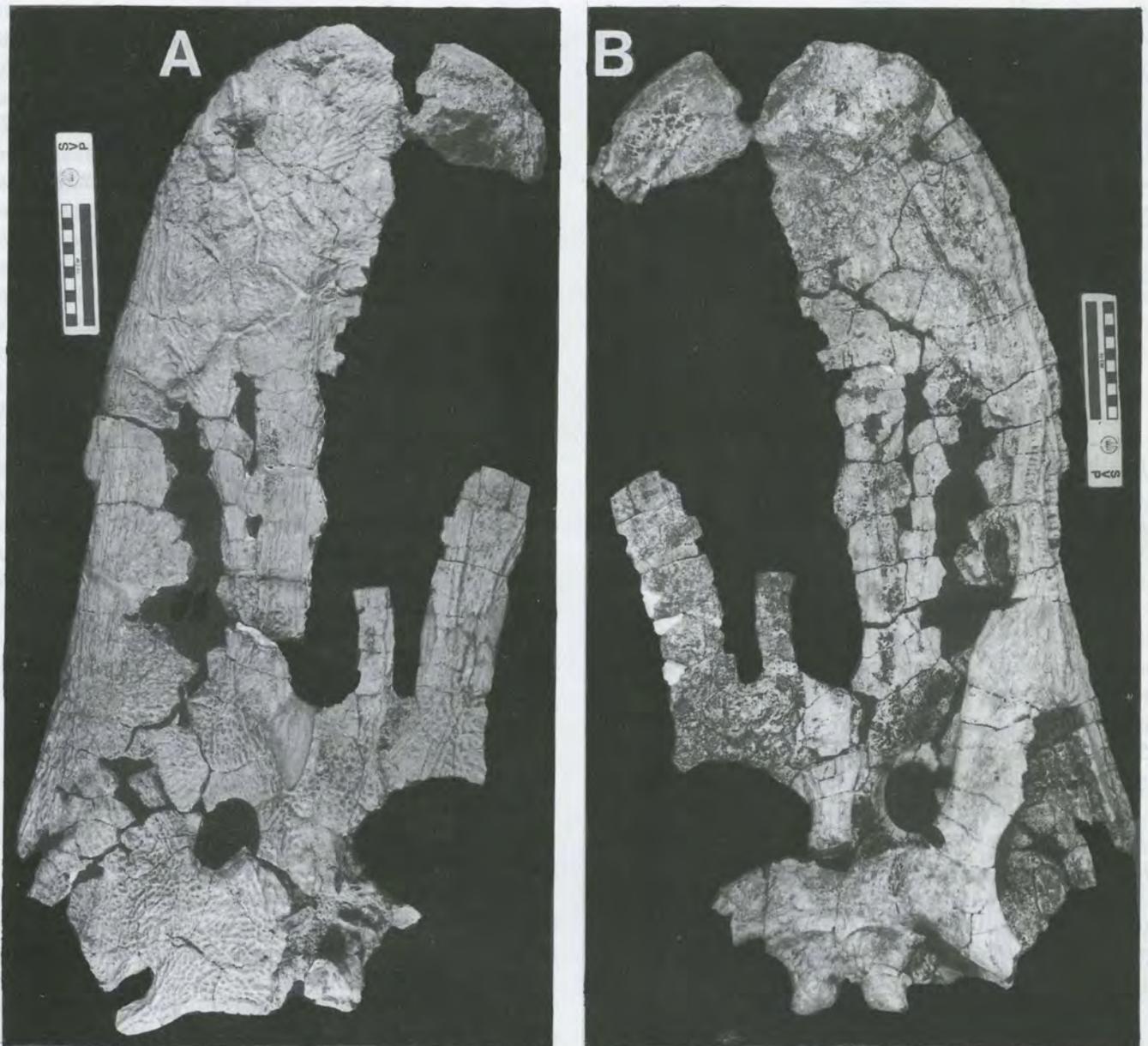


Figure 1. Photographs of the skull of *Cherninia megarhina* (Chernin and Cosgriff), BP/1/4223, from the Upper Horizon of the Middle Triassic N'tawere Formation of the Upper Luangwa Valley, Zambia, in A, dorsal and B, ventral views.

Ornament on the more posterior parts of the skull roof consists mainly of small, shallow, circular to sub-circular pits up to 2 mm in depth. These are separated by low but broad walls which are generally more conspicuous than the pits themselves. Ridge-groove type ornament is present on the jugal, frontal, prefrontal, and to a lesser extent on the squamosal. Further anteriorly the ornament is not well exposed but ridge-groove type ornamentation appears to have been the predominant sculpture pattern up to the tip of the snout. An unusual aspect of the dermal sculpturing of *C. megarhina* is the presence of a loose patch of pustular-type ornamentation on the left (and presumably right) jugal and prefrontal. An identical patch is present in the same position in *Cherninia denwai* (Sengupta pers. com.), and thus represents an autapomorphy of *Cherninia*. Elsewhere pustular ornament is present in most members of the Plagiosauridae (Huene 1922; Nilsson 1937), the lapillopsid *Lapillopsis* (Yates 1999), the

basal stereospondyl *Peltobatrachus* (Panchen 1959), the dissorophoid *Micropholis* (Boy 1985), the rhytidosteid *Pneumatostega* (Cosgriff & Zawiskie 1979), and the laidleriid *Laidleria* (Warren 1998), but the significance of such ornamentation is as yet unknown.

The sensory canal system on the skull roof is very poorly preserved, in contrast to Chernin's (1974: 43) statement that the "course of the canals is distinctly marked by a series of enlarged pits and grooves". The lack of visible canals appears to be due, at least in part, to the poor preservation of the bone in general. Anteriorly the sensory canals, if present, are obscured by the thin layer of mudstone adhering to the bone surface. Posteriorly sections of two sensory canals are partially preserved. The temporal canal cannot be traced anteriorly but posteriorly it skirts the otic rim of the tabular and reaches the tip of the tabular horn, as in *Cherninia denwai*. This contrasts strongly with all

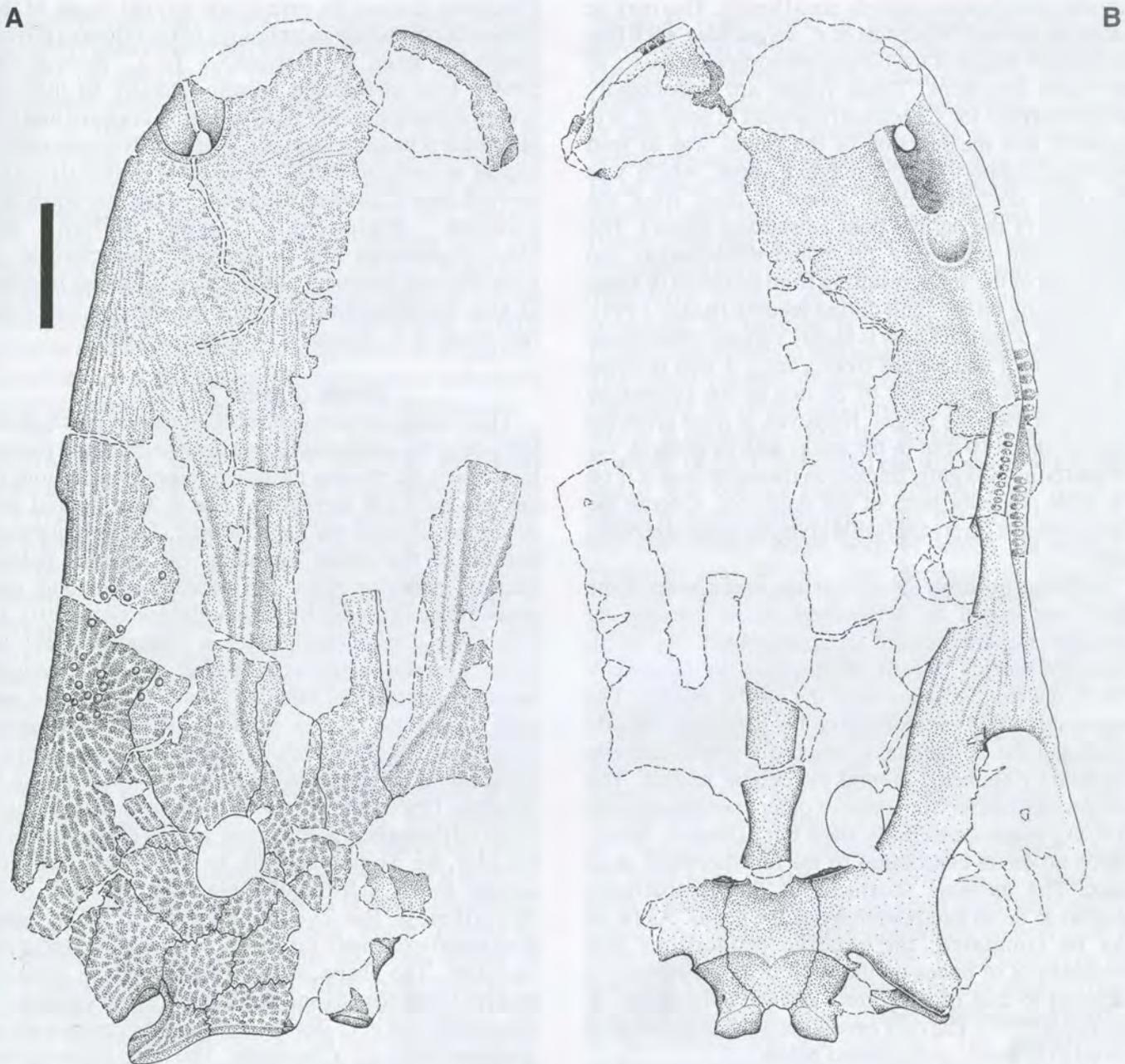


Figure 2. Interpretive drawings of the skull of *Cherninia megarhina* (Chernin and Cosgriff), BP/1/4223, from the Upper Horizon of the Middle Triassic N'tawere Formation of the Upper Luangwa Valley, Zambia, in A, dorsal and B, ventral views. Unshaded areas represent either matrix, plaster or broken bone. Scale bar equals 10 cm.

other mastodonsaurids in which the temporal canal terminates on the supratemporal. An occipital sulcus is also present. This sulcus is smooth and continuous and runs along the posterior margin of the skull deck. In *C. denwai* (Mukherjee & Sengupta 1998) an occipital sulcus was not figured, although examination of Figure 2 in that paper, as well as photographs of the specimen, indicates that this sulcus is present. Within the Mastodonsauroidea (*sensu* Damiani in press a: *Benthosuchus*, Mastodonsauridae, Heylerosauridae) an occipital sulcus is present only in *Benthosuchus* (Bystrow & Efremov 1940; Getmanov 1989) and *Cherninia*.

One of the most extraordinary features of the skull roof of *Cherninia megarhina* is the presence of a pair

of forked, longitudinally oriented ridges, each of which originates on the prefrontals just anterior to the orbits before bifurcating and diverging anteriorly, terminating within the anterior half of the snout. The posterior portion and lateral fork of each ridge is a single, raised, thickened ridge of dermal bone, but the medial fork divides into a pair of ridges separated by a shallow trough. These remarkable structures were first reported but not described in *Cherninia denwai* (Mukherjee & Sengupta 1998), although in that species they appear to originate on the frontals between the orbits, rather than on the prefrontals. Interestingly, in *C. megarhina* the length of the bifurcated portion of each ridge is much greater than the length of the single, posterior portion, whereas in *C. denwai* the bifurcated and un-bifurcated

portions are of approximately equal length. This may be due to the overall larger size of *C. megarhina*, such that the relative length of the bifurcated portion increases as the snout lengthens. These ridges are undoubtedly autapomorphic for *Cherninia* (Damiani in press a). It is apparent that the function of the ridges was to lend structural support for the massive snout, which was otherwise not particularly robust judging from the thickness of the dermal bone (discussed below). The ridges could thus have prevented deformation and fracturing of the snout resulting from torsional or shear forces acting on the skull during feeding (Kathe 1999).

Dermal bone thickness is highly variable throughout the skull roof and ranges from a mere 4 mm in some areas up to a maximum of 20 mm in the immediate vicinity of the bony ridges. However, in most areas the bone is under 10 mm in thickness and, in general, the dermal bone is slightly thicker on the snout than it is on the more posterior parts of the skull roof. Overall the dermal bone is surprisingly thin given the giant size of the skull.

Although not all of the sutures and hence bones of the skull roof could be determined, those present are typically mastodonsaurid in arrangement. As in all mastodonsaurids except *Wetlugasaurus* (Sennikov 1981), the frontal bones enter the orbital margin. The supratemporal is excluded from the margin of the otic notch and the postorbital is markedly antero-laterally expanded ('hooked') around the orbital margin. The postparietals differ from those of other mastodonsaurids in being antero-posteriorly short but extremely broad, which no doubt contributes to the foreshortened skull deck. The extreme shortness of the postparietals appears to be an autapomorphy of the genus. As far as can be compared, the relative proportions and arrangement of bones on the skull of *C. megarhina* is identical to that of *Cherninia denwai* (Mukherjee & Sengupta 1998). The only exception is the orientation of the tabular horns, as discussed below.

The tabular horns of *Cherninia megarhina* are directed almost exclusively laterally, rather than postero-laterally as in most derived Middle Triassic mastodonsaurids (Damiani in press a). Consequently the occipital margin of the skull deck is straight to slightly concave, in contrast to most other mastodonsaurids in which this margin is strongly concave. Distally the tabular horns are unexpanded and of uniform width throughout their length, as in *Wellesaurus peabodyi* (Welles & Cosgriff 1965), *Mastodonsaurus giganteus* (Schoch 1999) and '*Parotosuchus*' *africanus* (Chernin 1978). Thus they lack the antero-distal 'lappet' present in '*Parotosuchus*' *pronus* (Howie 1970), *Eryosuchus* (Ochev 1972) and *Paracyclotosaurus* (Watson 1958; Hancox *et al.* 2000). The orientation of the tabular horns in *C. megarhina* narrows the otic notch distally, so that the channel between the tabular and squamosal broadens anteriorly. Chernin's (1974: Figure 8) diagram of the otic area is inaccurate in this respect because the anterior rim of the otic notch is shown as being angular rather than rounded. In

Cherninia denwai the orientation but not shape of the tabular horns and the morphology of the otic area differs somewhat from *C. megarhina*. In *C. denwai* the tabular horn is directed postero-laterally so that the occipital margin of the skull is deeply concave and the otic notch is broad posteriorly. These differences would appear to indicate that *C. megarhina* is slightly more derived than *C. denwai*, as closure of the otic notch is a common evolutionary trend within the Mastodonsauridae and is generally characteristic of more derived members of the group (Damiani in press a). One further difference is that the anterior rim of the otic notch in *C. denwai* is curiously angular.

Palate (Figures 1B-3B)

The ventral surface of the skull preserves much of the left side of the palate including the marginal and palatal tooth rows, the choana, the basicranium, and portions of the left and right pterygoids, and is here figured and described in detail for the first time. The anteriormost portion of the palate including the anterior palatal vacuity, vomerine tusks, and transvomerine tooth row are completely hidden by the manganese-rich matrix. In *Cherninia denwai* (Mukherjee & Sengupta 1998) the anterior palatal vacuity is paired but set within a single, common depression. The left choana is elongated and oval in outline, not as broad as in *Wetlugasaurus* (Sennikov 1981) or *Watsonisuchus* (Damiani in press a) yet not as narrow as in *Parotosuchus* (Maryanska & Shishkin 1996; Damiani 1999, in press a). The margins of the left interpterygoid vacuity are not clear anteriorly because the vomer appears to have been crushed against and is indistinguishable from the skull roof. Nevertheless the choana appears to have been positioned extremely far forward of the interpterygoid vacuities. The shape of the choana and its position relative to the nostrils and the interpterygoid vacuities is identical to that in *C. denwai*, and probably represents an autapomorphy of *Cherninia*. The left subtemporal vacuity is only partially preserved but it appears to have been transversely narrow, as in *C. denwai*. This narrowing appears to be a result of the marked widening of the body of the pterygoid, as discussed below.

The body of the parasphenoid, forming most of the basicranium, has a very short suture with the pterygoid. This primitive state contrasts with the generally highly derived nature of the skull and its overall size. Other highly derived mastodonsaurids such as *Mastodonsaurus* (Schoch 1999), *Cyclotosaurus* (Fraas 1889, 1913) and *Paracyclotosaurus* (Watson 1958; Hancox *et al.* 2000) all possess elongated basicrania. In addition, the body of the parasphenoid is remarkably narrow and posteriorly forms a free margin between the exoccipitals. A similarly narrow parasphenoid with a short pterygoid suture is present in *Cherninia denwai* (Mukherjee & Sengupta 1998). A well developed *crista muscularis* crosses the body of the parasphenoid level with the posterior border of the body of the pterygoid, merging in the midline as a posteriorly directed point. Remarkably, the *crista*

muscularis continues laterally where it directly overlies the suture between the pterygoid and exoccipital. As far as can be determined this situation is unique to *Cherninia megarhina*. The area directly below each 'half' of the *crista muscularis* forms a trough or 'pocket' that is traditionally thought of as the area for insertion of the *rectus capitus* vertebro-cranial musculature (Watson 1962; Dutuit 1976). In *C. denwai* the *crista muscularis* of the parasphenoid does not appear to merge in the midline but the area is not well preserved. None of the cultriform process of the parasphenoid is preserved. An ossification a little anterior to the body of the parasphenoid is tentatively identified as a sphenethmoid and/or part cultriform process, and is discussed below (see Endocranium).

The exoccipitals bear a long, anteriorly directed subotic process which sutures with the pterygoids ventrally. At the junction of these bones laterally there is a triangular 'swelling' or 'bulge' as is seen in many derived mastodontosaurids including *Mastodontosaurus* (Schoch 1999), *Paracyclotosaurus* (Watson 1958; Hancox *et al.* 2000) and *Cyclotosaurus* (Ingavat & Janvier 1981). On the left-hand side of the skull this 'swelling' is damaged, giving a false impression of a ventral exoccipital-ptyerygoid groove, as in some primitive mastodontosaurids such as '*Parotosuchus' gunganj*' (Warren 1980) and *Parotosuchus haughtoni* (Damiani in press b). The exoccipital-ptyerygoid suture also directly coincides with the lateral portions of the *crista muscularis* of the parasphenoid. In *Cherninia denwai* (Mukherjee & Sengupta 1998) the exoccipitals appear to have been dislodged from their natural position so that the presence or absence of a ventral exoccipital-ptyerygoid contact and of a lateral 'bulge' cannot be determined, although the subotic processes appear to have been similarly elongated. Each exoccipital in *C. megarhina* bears three foramina. The largest, the jugular foramen, lies at the junction between the body of the exoccipital and its paroccipital process (of which only a short stump is preserved), and transmitted cranial nerves IX (glossopharyngeal) and X (vagus). The foramen for cranial nerve XII (hypoglossal) lies on the lateral edge of the condyle a little posterior to the base of the paroccipital process, but is not visible in ventral view. A third foramen, visible in ventral view, lies anterior and ventral to the glossopharyngeal foramen and probably transmitted a nutritive vessel (cf. Bystrow & Efremov 1940). The exoccipital condyles are positioned close to the posterior border of the body of the parasphenoid, so that the condyles are 'unstaked'.

The better preserved left pterygoid of *Cherninia megarhina* is the basis for the description of this complex element. The right pterygoid is represented by the articulated basicranial portion and a near-complete but isolated palatal ramus. The basicranial process of the pterygoid (i.e. that portion of the body of the pterygoid which contacts the parasphenoid) is elongated medially, so that the body of the pterygoid is exceptionally broad. This produces a narrowing (noted earlier) of both the body of the parasphenoid and of the subtemporal

vacuities. The latter, in particular, are noticeably narrower than is usual in mastodontosaurids. The body of the pterygoid gives rise to two main branches: the palatal ramus and quadrate ramus. The palatal ramus is unusual in that it lacks ornamentation. This is uncommon in mastodontosaurids but ornament in this area also appears to be absent in *Mastodontosaurus* (Schoch 1999). The palatal ramus bears a very well developed transverse flange of the pterygoid (broken on the left pterygoid but complete on the right) which is oriented ventro-laterally. The distal portion of the palatal ramus probably contacted the palatine in the usual mastodontosaurid fashion, but sutures in this area could not be determined. The distal portion of this ramus is also markedly roughened by ridges and furrows, the significance of which is uncertain. Only the proximal portion of the quadrate ramus is preserved but its curvature suggests that it was convex ventrally. Dorsally the quadrate ramus gives rise to two processes, the ascending ramus and the oblique ridge, both of which are partially preserved (see below). The pterygoid of *Cherninia denwai* (Mukherjee & Sengupta 1998) closely resembles that of *C. megarhina* in possessing a broad body that constricts both the parasphenoid and the subtemporal vacuities, the convex quadrate ramus, and the lack of ornament on the palatal ramus.

The dentition consists of a marginal tooth row on the premaxilla and maxilla, and an inner tooth row on the vomer, palatine and ectopterygoid. Except where obscured by matrix, the inner tooth row is complete, as in *Cherninia denwai* (Mukherjee & Sengupta 1998). No teeth were preserved on either dental arcade but tooth sockets indicate that the teeth were very closely spaced and strongly antero-posteriorly compressed, in the usual mastodontosaurid fashion. Tooth sockets on the marginal row appear to increase in size slightly from posterior to anterior, although the posterior-most portion of the maxilla was not preserved. The palatal tooth sockets appear to have been of uniform size throughout and of approximately half the size as the maxillary tooth sockets. A large pit for the palatine tusk is present immediately posterior to the choana. The ectopterygoid does not bear a tusk.

Occiput

The poorly preserved occiput was adequately figured by Chernin (1974), to which the reader is referred, and, as no further aspects of the occiput were exposed during preparation of the skull, a drawing is unnecessary. The occiput is preserved mainly on the left side in two sections: an upper section which includes the tabular, postparietal, squamosal and part exoccipital, and a lower section which includes part exoccipital, parasphenoid and pterygoid. These sections do not join perfectly as large areas of bone are missing, particularly on the more lateral parts of the occiput. Nevertheless, a detailed description and comparison of the occiput is presented in light of the well preserved occiput of *Cherninia denwai* (Mukherjee & Sengupta 1998). However, the occiput of that species has clearly undergone considerable

compaction. It is worth noting that figure six in Mukherjee & Sengupta (1998) shows the occiput of *C. denwai* and not '*P. crookshanki*', the figures having been inadvertently transposed (Sengupta pers. com.).

The occiput of *Cherninia megarhina* appears to have been moderately vaulted judging from the down-turning of the medial portions of the quadrate rami of the pterygoids. Thus the quadrate condyles would have been positioned ventral to the occipital condyles. The same degree of down-turning is present in *Cherninia denwai* (Mukherjee & Sengupta 1998) and most mastodontosaurids except *Cyclotosaurus* (Ingavat & Janvier 1981; Schoch & Milner 2000) and *Mastodontosaurus* (Schoch 1999). The quadrate rami give rise to two processes, the ascending ramus (*lamina ascendens* of Bystrow & Efremov 1940) and the oblique ridge, only small sections of the proximal portions of which are preserved on both sides of the skull. The arrangement of these bony processes appear to have been typically mastodontosaurid. The ascending ramus is a tall, thin lamina of bone which arises from the occipital margin of the quadrate ramus. The proximal portions clearly curve medially and appear to terminate near the edge of the basicranial process of the pterygoid, thereby forming the anterior wall of the middle ear cavity in the usual mastodontosaurid fashion. The presence or absence of a *crista praeotica* (Shishkin 1960; 'dorsal column' of Warren 1980; '*crista praeotica lamina ascendens*' of Getmanov 1989) on the medial margin of the ascending ramus cannot be determined because of incomplete preservation. This structure, a vertical thickening of the medial margin of the ascending ramus, is apparently present in all stereospondyls in which the area is known except brachyopids (Damiani & Warren 1996). The oblique ridge arises from the occipital margin of the quadrate ramus medial to the ascending ramus, and is just visible in occipital view. Its dorsal margin is incomplete.

The occipital portion of the squamosal is only partially preserved and consists of a descending flange (largely incomplete) and the *crista falciformis*. Unlike in most mastodontosaurids, especially those of comparably large size, the *crista falciformis* is very poorly developed, only projecting some five millimetres from the descending flange of the squamosal. A similarly poorly developed *crista falciformis* was reported for *Cherninia denwai*.

The posttemporal fenestrae, supraoccipital foramen and foramen magnum have clearly been affected by compaction so that their size and shape cannot be accurately described. The body of the exoccipitals are massive in being dorso-ventrally short but exceptionally broad, as in *Cherninia denwai*. In contrast, the body of the exoccipitals in most other mastodontosaurids is considerably less robust. The long paroccipital process bears a sharp crested bony ridge, or *crista muscularis*, which runs the length of the paroccipital process ventrally. This ridge continues onto the ventral surface of the tabular horn as the prominent *crista tabularis*

externa (Bystrow & Efremov 1940), terminating near the tip of the horn. The presence or absence of a *crista terminalis* cannot be determined because manganese-rich matrix covers much of the ventral surface of the tabular proximally. There is no trace of any bony protuberance on the occipital face of the tabular dorsally, unlike in *C. denwai*.

Endocranium

The endocranium is generally poorly preserved, particularly the dorsal surface of the parasphenoid and middle ear areas which are obscured by recalcitrant matrix. Of the former, a near-laterally directed ridge of bone on the right-hand side, likely the *crista parapterygoidea* (Bystrow & Efremov 1940), is visible jutting out from the underlying matrix. No other structures are visible in this area.

Anterior to the body of the parasphenoid a large but poorly preserved ossification, which may or may not represent two separate bones, is present (Figure 2B). Little structural details are apparent except as follows. The larger, posterior section markedly broadens anteriorly and, except where broken or obscured by matrix, the lateral margins curve smoothly downward and inward and are apparently contiguous with a deep but narrow ossification. The bony texture of this ossification is spongy. The ventral surface of the element is generally smooth and there are no visible foramina or canals. This element is tentatively identified as a sphenethmoid as it is clearly too broad, deep and irregular in shape to represent the cultriform process of the parasphenoid, but nevertheless does not resemble the typical stereospondyl sphenethmoid structure as described by Bystrow & Efremov (1940). The smaller, anterior element is uniformly wide, has a smooth ventral surface, but appears to be only a few millimetres thick. It may represent part of the cultriform process of the parasphenoid but if so is extraordinarily wide to a degree unparalleled among mastodontosaurids.

The dorsal surface of the left pterygoid bears a wide *sulcus marginalis* (Bystrow & Efremov 1940) on its lateral edge bordering the subtemporal vacuity, and a prominent *torus marginalis* (Bystrow & Efremov 1940) on its medial edge bordering the interpterygoid vacuity. These structures apparently bordered the embryonic palatoquadrate cartilage (Bystrow & Efremov 1940; Romer 1947). Anterior and slightly medial to the inner margin of the right ascending ramus of the pterygoid is an ossification which is tentatively identified as an epipterygoid. The element is poorly preserved and apparently incomplete, but appears to have possessed a large base abutting against the basicranial process of the pterygoid and a robust ascending process. Its identification as an epipterygoid is consistent with the position of the element and its robust nature, judging from well known mastodontosaurid material (e.g. Howie 1970; Schoch 1999; Damiani in press b).

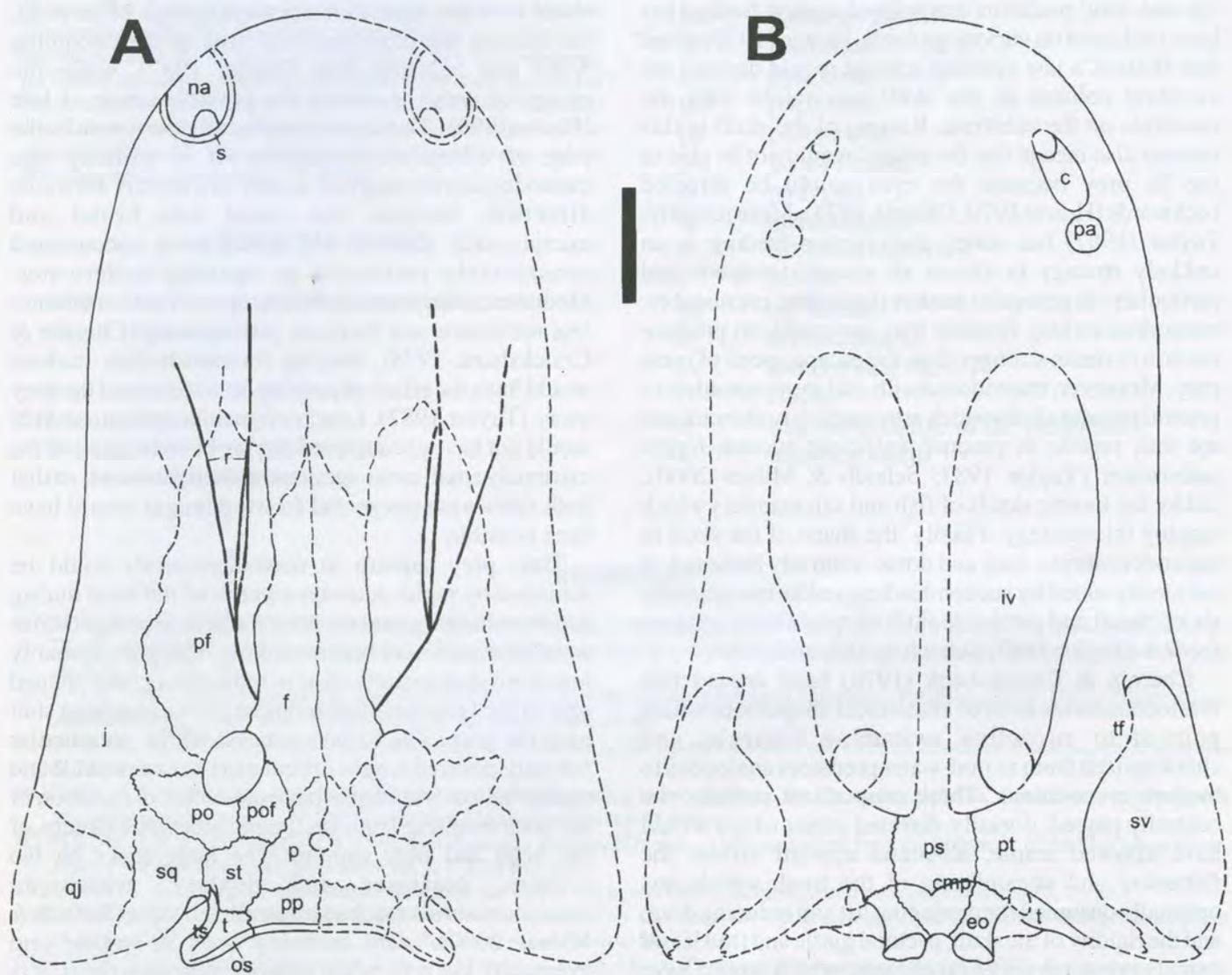


Figure 3. Reconstructions of the skull of *Cherninia megarhina* (Chernin and Cosgriff), BP/1/4223, from the Upper Horizon of the Middle Triassic N'tawere Formation of the Upper Luangwa Valley, Zambia, in A, dorsal and B, ventral views. Scale bar equals 10 cm.

FEEDING IN MASTODONSAURIDS

The lifestyle of mastodonsaurid temnospondyls has long presented a puzzle to temnospondyl workers particularly in relation to their method of feeding. Adult mastodonsaurids were large, carnivorous, dorso-ventrally flattened and superficially crocodile-like in appearance. As with most stereospondyls (Warren & Snell 1991; Schoch & Milner 2000), mastodonsaurids probably spent most of their time in water, with limited potential for terrestrial excursions. Evidence for this comes from a number of sources: the skull and trunk was dorso-ventrally flattened and streamlined; the postcranial skeleton, in particular the limbs, were generally weak and poorly ossified in most genera, while the carpals, tarsals and digits were usually unossified; lateral line sensory sulci were well developed; long bone histology points to aquatic adaptations; limb-trunk ratios may not have accommodated effective movement on land; an increased number of presacral vertebrae relative to terrestrial taxa; the disproportionately large skull which would have hindered effective terrestrial locomotion; and depositional environments which

include fluviatile, lacustrine, nearshore marine and marine facies (Watson 1958; Howie 1970; Chernin & Cruickshank 1978; DeFauw 1989; Schoch 1999; Damiani 2000; Schoch & Milner 2000).

Watson (1958, 1962) considered mastodonsaurids to have been essentially bottom-dwelling (i.e. benthic) animals. Opening of the mouth was thought to occur by the action of a *depressor mandibulae* muscle which originated on the highest point of the occiput and inserted onto the post-glenoid area of the mandible, contraction of which would raise the skull if the jaw rested on the substrate. Watson thus envisaged a lie-and-wait strategy in which approaching prey would be engulfed by suction-feeding in a manner similar to various extant fish and salamanders. The hypothesis that mastodonsaurids were passive, benthic animals has been adopted by other workers (Ochev 1966; Sennikov 1996; Shishkin 2000), the implication being that suction-feeding or at least a 'snap-and-grab' feeding strategy was employed. DeFauw (1989), while favouring more active swimming, also employed a suction-feeding strategy in mastodonsaurids.

The hypothesis that mastodonsaurids were benthic, 'sit-and-wait' predators that utilized suction-feeding has been criticized on various grounds. Howie (1970) noted that Watson's jaw opening scheme would depress the vertebral column as the skull was raised with the mandible on the substrate. Raising of the skull in this manner also means that the animal would not be able to see its prey because the eyes would be directed backwards (Howie 1970; Chernin 1974). More recently, Taylor (1987) has stated that suction-feeding is an unlikely strategy in almost all aquatic tetrapods and particularly in generalist feeders (including, presumably, mastodonsaurids), because they are unable to produce suction currents stronger than the escape speed of most prey. Moreover, mastodonsaurids and stereospondyls in general possess skulls which are completely akinetic and are thus unable to produce sufficient suction forces underwater (Taylor 1987; Schoch & Milner 2000), unlike the kinetic skulls of fish and salamanders which employ this strategy. Finally, the shape of the skull in mastodonsaurids, long and dorso-ventrally flattened, is not ideally suited for suction-feeding, unlike the optimally short, broad and parabolic skull of specialized suction-feeders (Taylor 1987; Schoch & Milner 2000).

Chernin & Cruickshank (1978) have argued that mastodonsaurids showed anatomical adaptations which pointed to an active swimming lifestyle, and characterised them as mid-water predators analogous to modern crocodylians. These adaptations include: the centrally placed, dorsally-directed orbits which would have allowed ample, all-round upward vision; the flattening and streamlining of the trunk which was optimally designed for producing lift and reducing drag; and the rigidity of the skull, pectoral girdle and (to a lesser extent) presacral vertebral column, which would have acted as a strut to transmit the propulsive force produced by the tail which was generally weakly ossified and perhaps highly flexible (Howie 1970; Chernin 1974; Chernin & Cruickshank 1978). Mechanisms for opening the mouth that do not require the mandible to rest on the substrate were proposed by Howie (1970) and Chernin (1974), both requiring the action of a *depressor mandibulae* that lowers the jaw (and a *cleidomastoideus* to raise the skull in the case of Howie) if it was not grounded. It is also interesting to note that virtually all amphibious tetrapods with dorsally-directed orbits, such as hippopotami, crocodylians, and various anurans and salamanders, usually lurk close to the water surface with only the eyes protruding. The hypothesis that mastodonsaurids were active rather than passive predators has been supported by Cosgriff & Hammer (1983), DeFauw (1989) and Schoch & Milner (2000).

If mastodonsaurids were not passive, benthic suction-feeders but active, surface or sub-surface predators, how did they feed? As with crocodylians, mastodonsaurids possess a simple, orthally-hinged, open-and-shut 'pincers' jaw (Taylor 1987) that would snap shut onto prey. The mastodonsaurid skull is long, moderately narrow (in most taxa), and highly dorso-

ventrally flattened, especially anterior to the orbits. This shape is well designed for sideways sweeps of the head, minimizing the cross-sectional area to the oncoming water and reducing drag (Taylor 1987), while the elongated snout increased the possible range of bite (Kathe 1999). The latter is especially pertinent in the case of *Cherninia megarhina*. It is unlikely that mastodonsaurids snapped at prey in a strictly forwards direction, because the snout was broad and exceptionally shallow and would have encountered considerable resistance to opening underwater. Moreover, if the jaw was slightly open so as to encounter less resistance and facilitate jaw opening (Chernin & Cruickshank 1978), lunging forward in this manner would have the effect of pushing both water and the prey away (Taylor 1987). Lonchorhynchine trematosaurids would not have encountered this problem because of the extremely small cross-sectional area of the snout, so that both sideways sweeps and forward lunges would have been possible.

Thus prey capture in mastodonsaurids could be achieved by rapid sideways sweeps of the head during active swimming, and the prey could be kept sight of for as long as necessary before striking. The jaws probably remained shut initially so as to reduce drag, and opened only at the latest possible moment before snapping shut onto the prey. The hamate process of the prearticular not only ensured a tight articulation between skull and mandible, but would also have prevented dislocation of the jaws resulting from such rapid sideways sweeps of the head and prey capture. The large tusks on the vomers, palatines and dentary, which in mastodonsaurids reached unparalleled sizes (Schoch & Milner 2000), were probably used to impale and eventually kill prey when snapped shut onto them. It is also likely that the tusks were used to hold and drown prey, perhaps underwater if taken at the surface as in crocodylians. This is suggested by the deep and massive adductor musculature and the posterior deepening of the mandible, both of which are adaptations for holding (Busbey 1995; Schoch & Milner 2000). Mastodonsaurids were probably generalist aquatic top-predators (Sennikov 1996), with a putative diet of fish, amphibians and small reptiles. However, the deep mandibles, massive tusks and jaw musculature would have allowed for larger prey to be taken (Schoch & Milner 2000). It is doubtful that the marginal dentition, which consists of an exceptionally large number of uniform, tightly packed, transversely compressed, slightly recurved teeth, played an important role in prey capture, but may have aided in holding prey in the mouth (Schoch & Milner 2000).

ACKNOWLEDGEMENTS

The holotype of *Cherninia megarhina* was collected in 1961 by Prof. J. W. Kitching of the Bernard Price Institute for Palaeontological Research (BPI), Johannesburg. I am grateful to Dr D. P. Sengupta (Indian Statistical Institute, Calcutta) for providing valuable information on the skull of *Cherninia denwai* and for confirming my suspicions about the transposed figure captions in Mukherjee & Sengupta (1998). I also thank Prof. B. S. Rubidge (BPI, Johannesburg)

for comments on an earlier version of the manuscript, and Drs A. A. Warren (La Trobe University, Melbourne) and P. J. Hancox (University of the Witwatersrand, Johannesburg) for information and discussions. Mr Richard Lewis (formerly BPI, Johannesburg) performed the initial airbrasive preparation of the skull. Reviews of the manuscript by Drs Andrew Milner (Birkbeck College, London) and Rainer Schoch (Humboldt Universität, Berlin) improved the quality of this work. The author is supported by a University of the Witwatersrand postdoctoral fellowship.

ABBREVIATIONS

c	choana
cmp	<i>crista muscularis</i> of the parasphenoid
eo	exoccipital
f	frontal
iv	interpterygoid vacuity
j	jugal
na	naris
os	occipital sulcus

p	parietal
pa	palatine tusk pit
pf	prefrontal
po	postorbital
pof	postfrontal
pp	postparietal
ps	parasphenoid
pt	pterygoid
qj	quadratojugal
r	ridges on skull roof
s	sulcus
sq	squamosal
st	supratemporal
sv	subtemporal vacuity
t	tabular
tf	transverse flange of the pterygoid
ts	temporal sulcus

REFERENCES

- BANDYOPADHAY, S. & SENGUPTA, D.P. 1999. Middle Triassic vertebrate faunas of India. *Journal of African Earth Sciences* **29**, 233-241.
- BATTAIL, B. 1993. On the biostratigraphy of Triassic therapsid-bearing formations. *New Mexico Museum of Natural History & Science Bulletin* **3**, 31-35.
- BOY, J.A. 1985. Über *Micropholis*, den letzten Überlebenden der Dissorophoidea (Amphibia, Temnospondyli; Unter-Trias). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1985**, 29-45.
- BRINK, A.S. 1963. Two cynodonts from the Ntawere Formation in the Luangwa Valley of Northern Rhodesia. *Palaeontologia africana* **8**, 77-96.
- BUSBY, A.R. 1995. The structural consequences of skull flattening in crocodylians. **In:** Thomason, J.J., Ed, *Functional morphology in vertebrate paleontology*, 173-192. Cambridge, Cambridge University Press.
- BYSTROW, A.P. & EFREMOV, J.A. 1940. *Benthosuchus sushkini* Efremov - a labyrinthodont from the Eotriassic of the Sharzenga River. *Trudy Paleontologicheskogo Instituta* **10**, 1-152 (in Russian).
- CHERNIN, S. 1974. Capitosaurid amphibians from the Upper Luangwa Valley, Zambia. *Palaeontologia africana* **17**, 29-55.
- CHERNIN, S. 1977. A new brachyopid, *Batrachosuchus concordi* sp. nov. from the Upper Luangwa Valley, Zambia with a redescription of *Batrachosuchus browni* Broom, 1903. *Palaeontologia africana* **20**, 87-109.
- CHERNIN, S. 1978. Three capitosaurids from the Triassic of South Africa: *Parotosuchus africanus* (Broom 1909); *Kestrosaurus dreyeri* Haughton 1925, and *Parotosuchus dirus* sp. nov. *Palaeontologia africana* **21**, 79-100.
- CHERNIN, S. & COSGRIFF, J.W. 1975. Further consideration of the capitosaurids from the Upper Luangwa Valley, Zambia. *Palaeontologia africana* **18**, 143-148.
- CHERNIN, S. & CRUICKSHANK, A.R.I. 1970. A capitosaurid amphibian from the Upper Luangwa Valley, Zambia. **In:** Haughton S.H., Ed, *I.U.G.S. 2nd International Symposium on Gondwana Stratigraphy and Palaeontology*, 1970, 649-652. Pretoria, C.S.I.R.
- CHERNIN, S. & CRUICKSHANK, A.R.I. 1978. The myth of the bottom-dwelling capitosaur amphibians. *South African Journal of Science* **74**, 111-112.
- COSGRIFF, J.W. & HAMMER, W.R. 1983. The labyrinthodont amphibians of the earliest Triassic from Antarctica, Tasmania and South Africa. **In:** Oliver, R.L., James, P.R. & Jago, J.B., Eds, *Antarctic Earth Science*, 590-592. Canberra, Australian Academy of Science.
- COSGRIFF, J.W. & ZAWISKIE, J.M. 1979. A new species of the Rhytidosteoidea from the *Lystrosaurus* Zone and a review of the Rhytidosteoidea. *Palaeontologia africana* **22**, 1-27.
- COX, C.B. 1969. Two new dicynodonts from the Triassic Ntawere Formation, Zambia. *Bulletin of the British Museum (Natural History), Geology* **17**, 257-294.
- DAMIANI, R.J. 1999. *Parotosuchus* (Amphibia, Temnospondyli) in Gondwana: biostratigraphic and palaeobiogeographic implications. *South African Journal of Science* **95**, 458-460.
- DAMIANI, R.J. 2000. Bone histology of some Australian Triassic temnospondyl amphibians: preliminary data. *Modern Geology* **24**, 109-124.
- DAMIANI, R.J. in press a. A systematic revision and phylogenetic analysis of Triassic mastodonsauroids (Temnospondyli: Stereospondyli). *Zoological Journal of the Linnean Society*.
- DAMIANI, R.J. in press b. *Parotosuchus* (Amphibia, Temnospondyli) from the *Cynognathus* Assemblage Zone of South Africa: cranial morphology and relationships. *Alcheringa*.
- DAMIANI, R.J. & WARREN, A.A. 1996. A new look at members of the Superfamily Brachyopoidea (Amphibia, Temnospondyli) from the Early Triassic of Queensland and a preliminary analysis of brachyopoid relationships. *Alcheringa* **20**, 277-300.
- DEFAUW, S.L. 1989. Temnospondyl amphibians: a new perspective on the last phases in the evolution of the Labyrinthodontia. *Michigan Academician* **21**, 7-32.
- DIXEY, F. 1937. The geology of part of the upper Luangwa Valley, north-eastern Rhodesia. *Quarterly Journal of the Geological Society of London* **93**, 77-93.
- DRYSDALL, A.R. & KITCHING, J.W. 1963. A re-examination of the Karroo succession and fossil localities of part of the upper Luangwa Valley. *Memoirs of the Geological Survey Department of Northern Rhodesia, Lusaka* **1**, 1-62.
- DUTUIT, J.-M. 1976. Introduction à l'étude paléontologique du Trias Continental Marocain. Descriptions des premiers Stégocéphales recueillis dans le Couloir d'Argana (Atlas Occidental). *Memoires du Muséum National d'Histoire Naturelle, Paris* **36**, 1-253.

- FRAAS, E. 1889. Die Labyrinthodonten der Schwäbischen Trias. *Palaeontographica* **36**, 1-158.
- FRAAS, E. 1913. Neue Labyrinthodonten aus der Schwäbischen Trias. *Palaeontographica* **60**, 275-294.
- GETMANOV, S.N. 1989. Triassic amphibians of the East European platform (family Benthosuchidae Efremov). *Trudy Paleontologicheskogo Instituta* **236**, 1-102 (in Russian).
- HANCOX, P.J. 2000. The continental Triassic of South Africa. *Zentralblatt für Geologie und Paläontologie Teil I* **1998**, 1285-1324.
- HANCOX, P.J., DAMIANI, R.J., & RUBIDGE, B.S. 2000. First occurrence of *Paracyclotosaurus* (Temnospondyli, Capitosauridae) in the Karoo Basin of South Africa and its biostratigraphic significance. *South African Journal of Science* **96**, 135-137.
- HANCOX, P.J., SHISHKIN, M.A., RUBIDGE, B.S., & KITCHING, J.W. 1995. A threefold subdivision of the *Cynognathus* Assemblage Zone (Beaufort Group, South Africa) and its palaeogeographical implications. *South African Journal of Science* **91**, 143-144.
- HOWIE, A.A. 1970. A new capitosaurid labyrinthodont from East Africa. *Palaeontology* **13**, 210-253.
- HUENE, F.von. 1922. Beiträge zur Kenntnis der Organisation einiger Stegocephalen der schwäbischen Trias. *Acta Zoologica* **3**, 395-460.
- INGAVAT, R. & JANVIER, P. 1981. *Cyclotosaurus* cf. *posthumus* Fraas (Capitosauridae, Stereospondyli) from the Huai Hin Lat Formation (Upper Triassic), northeastern Thailand, with a note on capitosaurid biogeography. *Géobios* **14**, 711-725.
- KATHE, W. 1999. Comparative morphology and functional interpretation of the sutures in the dermal skull roof of temnospondyl amphibians. *Zoological Journal of the Linnean Society* **126**, 1-39.
- LUCAS, S.G. 1998. Global Triassic tetrapod biostratigraphy and biochronology. *Palaeogeography, Palaeoclimatology, Palaeoecology* **143**, 347-384.
- LYDEKKER, R. 1885. The Reptilia and Amphibia of the Maleri and Denwa Groups. *Palaeontologia Indica (Ser. IV. Indian pre-Tertiary Vertebrata)* **1**(5), 30-38.
- MARYANSKA, T. & SHISHKIN, M.A. 1996. New cyclotosaurid (Amphibia: Temnospondyli) from the Middle Triassic of Poland and some problems of interrelationships of capitosauroids. *Prace Muzeum Ziemi* **43**, 53-83.
- McNAMARA, K.J. 1986. A guide to the nomenclature of heterochrony. *Journal of Paleontology* **60**, 4-13.
- MILNER, A.R. 1990. The radiations of temnospondyl amphibians. *Systematics Association Special Volume* **42**, 321-349.
- MUKHERJEE, R.N. & SENGUPTA, D.P. 1998. New capitosaurid amphibians from the Triassic Denwa Formation of the Satpura Gondwana Basin, Central India. *Alcheringa* **22**, 317-327.
- NILSSON, T. 1937. Ein Plagiosauride aus dem Rhät Schonens. Beiträge zur Kenntnis der Organisation der Stegocephalengruppe Brachyopoidei. *Lunds Universitets Arsskrift N. F.* **34**, 1-75.
- OCHEV, V.G. 1966. *Systematics and phylogeny of capitosauroid labyrinthodonts*. Saratov, Saratov State University Press (in Russian).
- OCHEV, V.G. 1972. *Capitosauroid labyrinthodonts from the southeastern European part of the U.S.S.R.* Saratov, Saratov State University Press (in Russian).
- OCHEV, V.G. & SHISHKIN, M.A. 1989. On the principles of global correlation of the continental Triassic on the tetrapods. *Acta Palaeontologica Polonica* **34**, 149-173.
- PANCHEN, A.L. 1959. A new armoured amphibian from the Upper Permian of East Africa. *Philosophical Transactions of the Royal Society of London B* **242**, 207-281.
- ROMER, A.S. 1947. Review of the Labyrinthodontia. *Bulletin of the Museum of Comparative Zoology, Harvard College* **99**, 1-352.
- SCHOCH, R.R. 1997. A new capitosaur amphibian from the Upper Lettenkeuper (Triassic: Ladinian) of Kupferzell (Southern Germany). *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen* **203**, 239-272.
- SCHOCH, R.R. 1999. Comparative osteology of *Mastodonsaurus giganteus* (Jaeger, 1828) from the Middle Triassic (Lettenkeuper: Longobardian) of Germany (Baden-Württemberg, Bayern, Thüringen). *Stuttgarter Beiträge zur Naturkunde Serie B* **278**, 1-175.
- SCHOCH, R.R. 2000. The origin and intrarelationships of Triassic capitosaurid amphibians. *Palaeontology* **43**, 705-727.
- SCHOCH, R.R. & MILNER, A.R. 2000. *Stereospondyli*. Handbuch der Paläoherpetologie, Teil 3B. München, Verlag Dr. Friedrich Pfeil.
- SENNIKOV, A.G. 1981. A new wetlugasaur from the Samara River Basin. *Paleontological journal* **1981**, 111-116.
- SENNIKOV, A.G. 1996. Evolution of the Permian and Triassic tetrapod communities of Eastern Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* **120**, 331-351.
- SHISHKIN, M.A. 1960. Concerning a new family of Triassic labyrinthodonts, the Yarengiidae. *Palaontologicheskii Zhurnal* **1960**, 97-106 (in Russian).
- SHISHKIN, M.A. 2000. Evolution of the cervical vertebrae in temnospondyl amphibians and differentiation of the early tetrapods. *Paleontological Journal* **34**, 534-546.
- TAYLOR, M.A. 1987. How tetrapods feed in water: a functional analysis by paradigm. *Zoological Journal of the Linnean Society* **91**, 171-195.
- WARREN, A.A. 1980. *Parotosuchus* from the Early Triassic of Queensland and Western Australia. *Alcheringa* **4**, 25-36.
- WARREN, A.A. 1998. *Laidleria* uncovered: a redescription of *Laidleria gracilis* Kitching (1957), a temnospondyl from the *Cynognathus* Zone of South Africa. *Zoological Journal of the Linnean Society* **122**, 167-185.
- WARREN, A.A. & SNELL, N. 1991. The postcranial skeleton of Mesozoic temnospondyl amphibians: a review. *Alcheringa* **15**, 43-64.
- WATSON, D.M.S. 1958. A new labyrinthodont (*Paracyclotosaurus*) from the Upper Trias of New South Wales. *Bulletin of the British Museum of Natural History* **3**, 233-263.
- WATSON, D.M.S. 1962. The evolution of the labyrinthodonts. *Philosophical Transactions of the Royal Society of London B* **245**, 219-265.
- WELLES, S.P. & COSGRIFF, J.W. 1965. A revision of the labyrinthodont family Capitosauridae and a description of *Parotosaurus peabodyi* n. sp. from the Moenkopi Formation of Northern Arizona. *University of California Publications in Geological Sciences* **54**, 1-148.
- YATES, A.M. 1999. The Lappilopsidae, a new family of small temnospondyls from the Early Triassic of Australia. *Journal of Vertebrate Paleontology* **19**, 302-320.
- YATES, A.M. & WARREN, A.A. 2000. The phylogeny of the 'higher' temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. *Zoological Journal of the Linnean Society* **128**, 77-121.
- ZITTEL, K.A. von. 1887-1890. *Handbuch der Paläontologie. Abteilung I. Paläozoologie Band III. Vertebrata (Pisces, Amphibia, Reptilia, Aves)*. Munich and Leipzig, Oldenbourg.