A giant skull of the temnospondyl *Xenotosuchus africanus* from the Middle Triassic of South Africa and its ontogenetic implications

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A previously unreported large skull of the mastodonsaurid temnospondyl *Xenotosuchus africanus*, from the *Cynognathus* Assemblage Zone (Early to Middle Triassic) of the Beaufort Group, Karoo Basin of South Africa, is described. The species is plesiomorphic in most aspects of its cranial anatomy, and only one autapomorphy is tentatively identified herein, namely contact between the left and right exoccipitals posterior to the parasphenoid. The new specimen permits recognition of a growth series for *X. africanus* from sub-adult (all previously known specimens) to fully adult (new specimen) stages. Ontogenetic changes associated with this include changes in skull proportions, and changes in the morphology of the lacrimal flexure, frontal, postfrontal, cultriform process and body of the parasphenoid, and the transvomerine tooth row.

Key words: Temnospondyli, *Xenotosuchus africanus*, ontogeny, variation, Triassic, South Africa.

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Introduction

Temnospondyls form an important part of the fauna of the Permo-Triassic aged, non-marine deposits of the Beaufort Group (Karoo Basin) of South Africa (Damiani and Rubidge 2003). Among them, the ubiquitous Mastodonsauridae (= Capitosauridae of earlier workers; see Damiani 2001a), a higher-level taxon within the clade Stereospondyli, are represented by five nominal taxa from the the Early to Middle Triassic *Cynognathus* Assemblage Zone (AZ), the uppermost biozone of the Beaufort Group. Fragmentary mastodonsaurid material has also been described from the underlying Early Triassic *Lystrosaurus* AZ (Damiani et al. 2001). The *Cynognathus* AZ (Fig. 1) has been informally subdivided into three subzones based primarily on the spatial and temporal distribution of mastodonsaurids and the associated fauna (Hancox et al. 1995; Shishkin et al. 1995). The middle subzone, informally termed "subzone B" (Hancox et al. 1995) or the "*Parotosuchus africanus* subzone" (Shishkin et al. 1995), has as its index taxon the mastodonsaurid *Xenotosuchus africanus*.

Broom (1909) briefly described but did not figure a partial skull, SAM-PK-2360, as *Capitosaurus africanus*. That skull was designated the lectotype of *C. africanus* by Haughton (1925), who described and figured a second partial skull, SAM-PK-3008, which he referred to the same species. Watson (1962) transferred *Capitosaurus africanus* to the catchall mastodonsaurid genus *Parotosaurus*, and then Chernin (1978) replaced the pre-occupied name *Parotosaurus* by *Parotosuchus*. In their landmark review of the Stereospondyli, Schoch and Milner (2000) regarded *Parotosuchus africanus* as *incertae sedis* within the "Capitosauroidea", noting its peculiar mixture of apomorphic and plesiomorphic characters. Damiani (2001a) referred *Parotosuchus africanus* to the North American mastodonsaurid genus *Wellesaurus* based largely on phenetic similarity, which had earlier been noted by Maryańska and Shishkin (1996). Most recently, Morales and Shishkin (2002) described a third, near-complete skull of *P. africanus*, UCMP 41286, providing a fuller description of the cranial anatomy including the lower jaw. On the basis of additional diagnostic characters afforded by the new specimen, Morales and Shishkin (2002) referred *P. africanus* to a new genus, *Xenotosuchus*. That taxonomic assignment was accepted by Damiani and Rubidge (2003) in their review of the South African temnospondyl record, and is followed here.

This study is based mainly on a previously unidentified skull of *Xenotosuchus africanus*, CGP/1/135, discovered by the author while inspecting the collections of the Council for Geoscience, Pretoria. The specimen is described and the species rediagnosed on the basis of plesiomorphic and apomorphic characters; one character is identified as a potential autapomorphy. Previously, Schoch and Milner (2000), Damiani (2001a), and Morales and Shishkin (2002) could not identify any clearly autapomorphic characters of *Xenotosuchus africanus*. The diagnostic characters of *X. africanus* formally listed by Morales and Shishkin (2002) are discussed below (see Description). The new skull is considerably larger than previously described *Xenotosuchus africanus* specimens, which provides new information on growth and ontogenetic variation in that taxon.
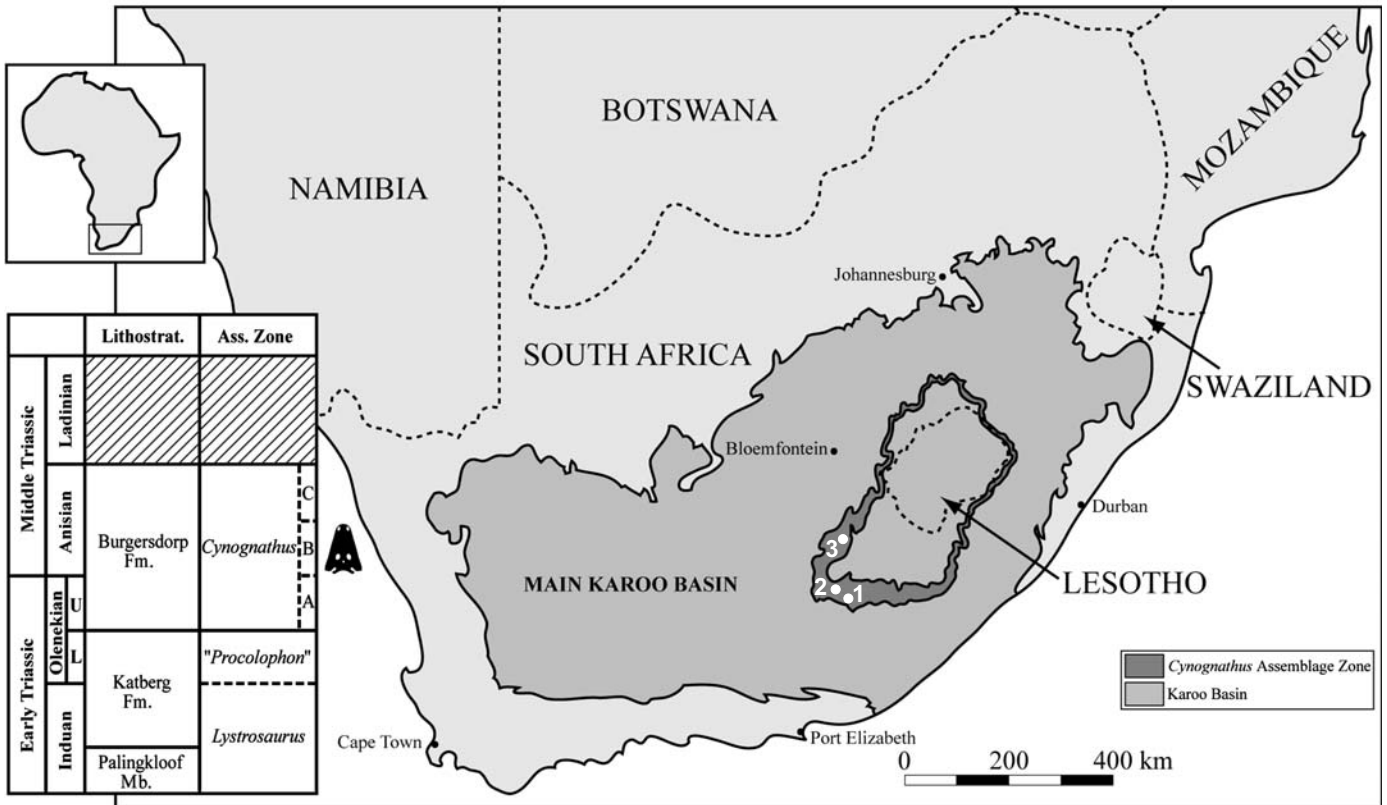
Fig. 1. Locality map and simplified stratigraphic column. The map shows the extent of surface outcrop of the *Cynognathus* Assemblage Zone within the main Karoo Basin, South Africa. Stratigraphic column shows only the Triassic part of the Beaufort Group sequence. Skull icon indicates the horizon of *Xenotosuchus africanus*. Localities: 1, Cuylerville, Queenstown District; 2, Vaalbank, Winaarsbaaken, and Nooitgedacht, Burgersdorp District; 3, Matabele and Koudekraal, Rouxville District.

Institutional abbreviations.—BP, Bernard Price Institute for Palaeontological Research, Johannesburg, RSA; CGP, Council for Geoscience, Pretoria, RSA; SAM, South African Museum, Cape Town, RSA; UCMP, University of California Museum of Paleontology, Berkeley, USA.

Material

The newly referred, partial skull specimen CGP/1/135 (Fig. 2A) comes from the farm Cuylerville (annex of the farm Prospect 152), Queenstown District, Eastern Cape Province. According to the label associated with this specimen, it was found in a small mudstone pocket within a thick channel sandstone unit of the Early to Middle Triassic *Cynognathus* AZ, Beaufort Group, Karoo Supergroup (Fig. 1). The associated fauna at the locality (farm Prospect 152), includes the cynodont therapsid *Diademodon tetragonus* and the dicynodont therapsid *Kannemeyeria simocephalus* (Kitching 1977). Together with *Xenotosuchus africanus*, these taxa are typical faunal elements of "subzone B" of the *Cynognathus* AZ in the southern part of the Karoo Basin (Hancox 1998). Remains of the procolophonid reptile *Procolophon* have also been recovered from farm Prospect 152 (James Kitching, personal communication 2000), indicating that strata of the underlying

Lystrosaurus AZ is also exposed at the locality (Groenewald and Kitching 1995).

The other four referred specimens are: SAM-PK-3008, a partial skull (Fig. 2C) from the farm Winaarsbaaken, Burgersdorp District, Eastern Cape Province (Haughton 1925); UCMP 41286, a partial skull from the farm Matabele, Rouxville District, Free State Province (Morales and Shishkin 2002); SAM-PK-11482, fragments of a skull and right mandible from the farm Koudekraal, Rouxville District, Free State Province; and BP/1/1674/1, the posterior half of a crushed skull from the farm Nooitgedacht, Burgersdorp District, Eastern Cape Province. The lectotype SAM-PK-2360, a posterior half of a skull (Fig. 2B), comes from the farm Vaalbank, Burgersdorp District, Eastern Cape Province (Broom 1909). To the author's knowledge, there are no postcranial remains that can be positively referred to *Xenotosuchus africanus*.

SAM-PK-2360, SAM-PK-3008, and BP/1/1674/1 are from localities within the *Cynognathus* AZ which have also yielded material of *Kannemeyeria simocephalus* (Kitching 1977), and UCMP 41286 (Morales and Shishkin 2002) from a locality which yielded unspecified dicynodonts, in all likelihood *K. simocephalus*. Hence, these specimens likely pertain to "subzone B" of the *Cynognathus* AZ. Based largely on faunal correlation, "subzone B" of the *Cynognathus* AZ is assigned an early Middle Triassic (Anisian) age (e.g., Hancox et al. 1995; Hancox 1998; Abdala et al. 2005).
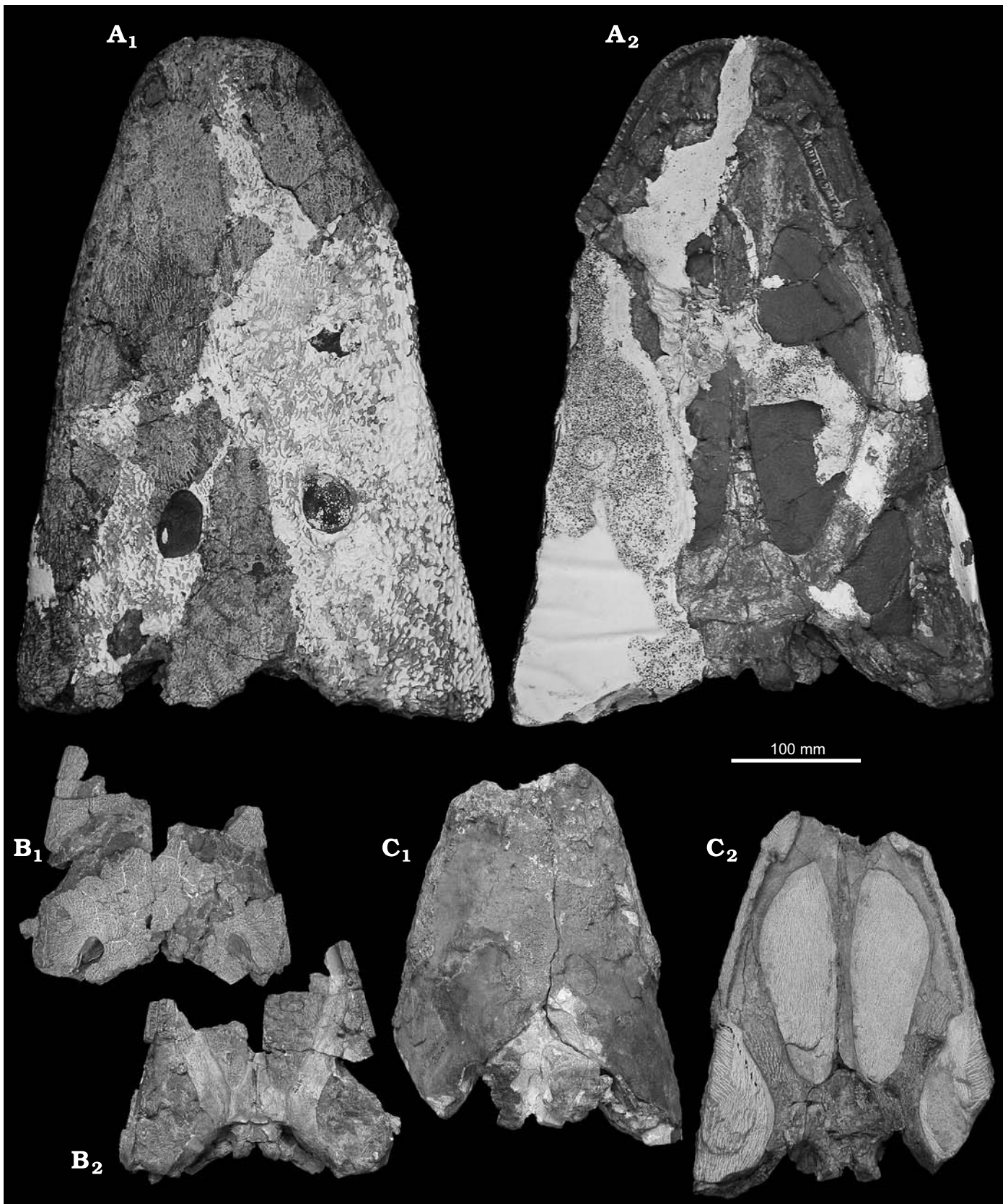
Fig. 2. Mastodonsaurid temnospondyl *Xenotosuchus africanus* (Haughton, 1925) from the Middle Triassic (*Cynognathus* Assemblage Zone, Beaufort Group) of the Karoo Basin, South Africa. Skulls of three specimens used in this study, reproduced to the same scale. **A**. Referred specimen CGP/1/135 in dorsal (A$_1$) and ventral (A$_2$) views. **B**. Lectotype SAM-PK-2360 in dorsal (B$_1$) and ventral (B$_2$) views. **C**. Referred specimen SAM-PK-3008 in dorsal (C$_1$) and ventral (C$_2$) views.

Description

Xenotosuchus africanus specimen CGP/1/135 comprises approximately two-thirds of a large skull, the missing portions being filled with plaster-of-Paris. The bone is lightly weathered but otherwise well preserved, and sutures are for the most part easily traceable. The matrix, a hard, reddish mudstone, could not be removed from around the teeth without significant damage to them. The cranial anatomy of *X. africanus* has been documented by Chernin (1978) and especially Morales and Shishkin (2002), so emphasis in the following description is placed on the most taxonomically important characters, and on comparison with *Wellesaurus peabodyi*.

Skull roof.—Ornament on the skull roof (Figs. 2A$_1$, 3A$_1$) consists of the typical temnospondyl pitted sculpturing. Areas of elongate ridge-groove ornamentation are restricted to a transverse band across the mid-region of the snout, as well as on the jugal. Where visible in section, the bone of the skull roof is remarkably thin, reaching only a few millimetres in thickness. Large specimens of *Wellesaurus peabodyi* (Welles and Cosgriff 1965; RD personal observations) have similarly thin dermal bone, whereas in *Parotosuchus* and other more derived mastodonsaurids the bone tends to be much thicker in large specimens (Damiani 2001b). The sensory canals comprise partially continuous grooves and pits that are conspicuously larger than the grooves and pits of the dermal ornamentation. Their arrangement is typical of mastodonsaurids: the infraorbital sulcus forms a pronounced, Z-shaped flexure on the lacrimal, while the supraorbital sulcus passes medial to that bone. Part of the jugal sulcus is also preserved.

To the extent preserved, the arrangement of dermal bones (Fig. 3A$_2$), as shown on the more complete left side of the skull, departs little from the pattern that has been described by Chernin (1978) and Morales and Shishkin (2002), and the reader is referred to those papers for more detailed descriptions. Here only a few points are discussed. As in UCMP 41286 (Morales and Shishkin 2002), a septomaxilla was probably not present, at least as a distinct element of the skull roof. A septomaxilla is occasionally reported in mastodonsaurids (e.g., Mukherjee and Sengupta 1998) as an exclusively intranarial element. This contrasts with the situation in trematosauroids in which the septomaxilla is commonly present and forms part of skull roof (e.g., Schoch and Milner 2000; Damiani and Yates 2003).

Despite slight damage in the area the frontal bone undoubtedly entered the orbital margin. The frontal bears well developed interorbital expansions, whereas in UCMP 41286 interorbital expansions are lacking altogether. Damage to the lateral margin of the orbit obscures the position of the jugal and postorbital sutures entering the orbital margin.

The postparietal of CGP/1/135 is a conspicuously massive element. Although difficult to quantify, in mastodonsaurids the postparietals tend to be smaller than, or roughly equal in size to, the parietals (Schoch and Milner 2000;

Damiani 2001a). This is the case in the lectotype SAM-PK-2360 (Chernin 1978) and in UCMP 41286 (Morales and Shishkin 2002). In addition, in CGP/1/135 each postparietal is distinctly pointed anteriorly, unlike the relatively straight margin found in SAM-PK-2360 (Chernin 1978), UCMP 41286, and most mastodonsaurids.

The left tabular horn is incomplete but there are two clear indications that the horn was posterolaterally directed. First, the preserved margin of the tabular bordering the otic notch is curved in a lateral orientation. Second, and more tellingly, there is a pronounced—albeit incomplete—crista falciformis of the squamosal, a character associated with the presence of a posterolaterally oriented tabular horn. In more basal mastodonsaurid taxa with pointed tabular horns, the crista falciformis is much less well developed (Damiani 2001a).

Palate.—The palate of CGP/1/135 (Figs. 2A$_2$, 3B) is sufficiently well preserved that the outlines of the various palatal vacuities can be reconstructed with confidence. The anterior palatal vacuity is reniform in outline, as is typical of mastodonsaurids. As per previous descriptions (Haughton 1925; Morales and Shishkin 2002), the choanae are characteristically elliptical in outline, and relatively larger than in *Wellesaurus peabodyi*. The outline of the interpterygoid vacuities differs somewhat from that in UCMP 41286, but the extent to which the shape of the vacuities have been affected by distortion in both specimens is unclear. Subtle differences in the shape of the interpterygoid vacuity in specimens of *W. peabodyi* (Welles and Cosgriff 1965; Damiani 2001a and personal observations) casts further doubt on the utility of this character.

The sutural relationships of bones largely follows what has been described previously (Chernin 1978; Morales and Shishkin 2002), but some additional observations are noted here. The palatine has a slender posterior process extending along the margin of the interpterygoid vacuity. Judging from the posterior extent of this process, the ectopterygoid appears to have been excluded from the interpterygoid vacuity margin. This morphology can be confirmed in SAM-PK-3008. In both the lectotype SAM-PK-2360 and in UCMP 41286, the relationship between these elements is unclear because of poor preservation.

Despite the size of CGP/1/135, the pterygoid is a relatively gracile element. In particular, the palatal ramus is rather slender and, judging from other *Xenotosuchus africanus* specimens (Morales and Shishkin 2002), there was only slight development of the transverse flange. The distal part of the palatal ramus is lightly sculptured; there is no trace of ornament on the proximal part of the pterygoid but this may be a preservational artefact. Medially, the pterygoid has a relatively short contact with the parasphenoid, in contrast to the long contact present in *Wellesaurus peabodyi*, and there is no evidence for an embayment in this area as has been reported in UCMP 41286 (Morales and Shishkin 2002). Among the sample of *X. africanus* specimens, only UCMP 41286 appears to possess this embayment.
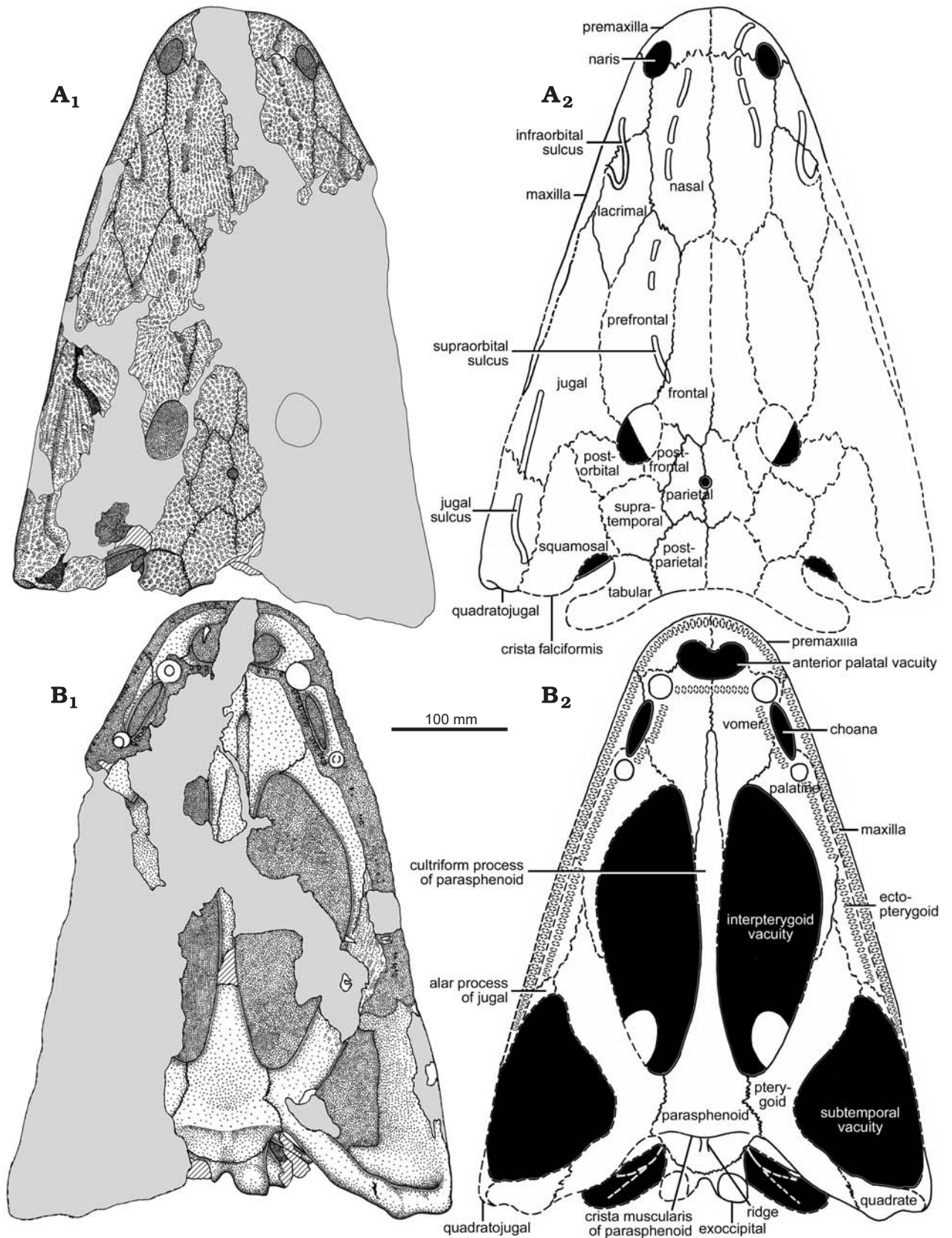
Fig. 3. Mastodonsaurid temnospondyl *Xenotosuchus africanus* (Haughton, 1925) from the Middle Triassic (*Cynognathus* Assemblage Zone, Beaufort Group) of the Karoo Basin, South Africa, referred specimen CGP/1/135. **A**. Interpretive drawing (A$_1$) and reconstruction (A$_2$) in dorsal view. **B**. Interpretive drawing (B$_1$) and reconstruction (B$_2$) in ventral view. Grey shading represents plaster-of-Paris; heavy stiple represents matrix; cross-hatching represents broken bone.

The main body of the parasphenoid is distinctly dished (Fig. 3B$_1$). The transversely oriented crista muscularis forms a raised lip across the entire width of the parasphenoid. In addition, on the posterior rim of the crista muscularis there is, in the midline, a short, inconspicuous ridge, not previously described in mastodonsaurids. This ridge is also present in SAM-PK-3008. However, it is not evident in other specimens examined, and for this reason it cannot be considered an autapomorphy of *Xenotosuchus africanus*. The cultriform process of the parasphenoid, which was not preserved in the lectotype SAM-PK-2360 or in UCMP 41286, is mainly flat throughout, with only slight doming in the mid-region of its length. Anteriorly the cultriform process terminates as a slightly sunken trough at the level of the midpoint of the choanae. The process is clasped on either side by the long processes parasphenoidales of the vomers, as in SAM-PK-3008 (Fig. 2C$_2$). In contrast, in UCMP 41286 the cultriform process does not appear to have reached the level of the choanae, judging from the posterior extent of the intervomerine suture (Morales and Shishkin 2002).

In ventral view, the left and right exoccipitals clearly meet in the midline, thereby excluding the parasphenoid from forming a free margin posteriorly. This condition is also present in the lectotype SAM-PK-2360, SAM-PK-3008, and, possibly, in UCMP 41286 (Morales and Shishkin 2002); it is not known in any other mastodonsaurid and is therefore tentatively identified as an autapomorphy of *X. africanus*. The condyles are positioned a little anterior to the level of the quadrate condyles, but are not as anteriorly positioned as in more basal mastodonsaurids with pointed, posteriorly directed tabular horns (Damiani 2001a). Primitively, there is no contact between the exoccipital and the pterygoid ventrally, whereas in *Wellesaurus peabodyi* and derived mastodonsaurids such a contact is present ventrally.

Although sedimentary matrix partially obscures the marginal dentition, it is apparent that there is a continuous tooth row on the premaxilla and maxilla, and on the vomers, palatines and ectopterygoids (Fig. 3B$_1$). Where visible, the teeth are closely packed, transversely compressed, and the tooth count appears to have been high. The transvomerine tooth row posterior to the anterior palatal vacuity appears to have been oriented strictly horizontally, in contrast to the arcuate path followed by the tooth row in UCMP 41286. There is no evidence for palatal denticles.

Occiput.—The occiput of CGP/1/135 is not figured here because it is does not differ significantly from that of the lectotype (Chernin 1978) or UCMP 41286 (Morales and Shishkin 2002). Indeed, the only difference to be found in occipital aspect is in the presence of a shallow, longitudinal groove between the dorsal and paroccipital processes of the exoccipital in UCMP 41286 (Morales and Shishkin 2002). This groove is absent in both the lectotype and in CGP/1/135, but its significance was not discussed by Morales and Shishkin (2002).

One further feature of the occiput worthy of mention is the absence in CGP/1/135 of a ventral projection of the postparietal (spina supraoccipitalis) above the foramen magnum. This process is also absent in UCMP 41286 (Morales and Shishkin 2002), but as noted by those authors the relevant area was not preserved in the lectotype.

Discussion

Taxonomic assignment

Given the tentative nature of the sole identified autapomorphy of *Xenotosuchus africanus*, and the much larger size of CGP/1/135 relative to previously described *X. africanus* specimens, its taxonomic assignment requires justification. Within the clade Mastodonsauridae (Damiani 2001a) the relationships of CGP/1/135 should be sought from among those genera in which the tabular horn is posterolaterally directed, a derived character of mastodonsaurids (Schoch and Milner 2000; Damiani 2001a). These include *Cherninia* (Damiani 2001c), *Eryosuchus* (Ochev 1972), *Mastodonsaurus* (Schoch 1999), *Paracyclotosaurus* (Watson 1958), *Tatrasuchus* (Maryańska and Shishkin 1996), *Wellesaurus* (Welles and Cosgriff 1965), and *Xenotosuchus*, as well as a number of Gondwanan species erroneously referred by Damiani (2001a) to *Eryosuchus* (e.g., *Parotosuchus pronus* Howie, 1970). Among these taxa, all but *Tatrasuchus* and *Xenotosuchus* are derived in the presence of a ventral exoccipital-pterygoid contact, a character lacking in CGP/1/135. In addition, all genera except for *Xenotosuchus* are derived in the presence of an elongate basicranial suture, a character also lacking in CGP/1/135. Clearly, CGP/1/135 does not pertain to *Tatrasuchus* because in that taxon the snout is short and broad, the palate anterior to the interpterygoid vacuities is foreshortened, and the choanae are sub-circular in outline (Maryańska and Shishkin 1996; Schoch 1997).

Morales and Shishkin (2002) listed four principle diagnostic characters of *Xenotosuchus africanus*. These are as follows, with comments on their expression in CGP/1/135: (1) lacrimal flexure curved rather than Z-shaped: this was considered by the authors to possibly represent an individual variation, a reasonable conclusion because the flexure assumes the normal, Z-shaped configuration in CGP/1/135; (2) frontals broader anteriorly than posteriorly, and lacking interorbital projections: a character of uncertain significance because the frontals are usually not of uniform width in temnospondyls and minor variation in frontal shape might be expected, while interorbital projections seem to have been present in CGP/1/135; (3) wide nasals: the nasals are wide in the specimen described by Morales and Shishkin (2002), but not especially so in CGP/1/135, so this character may also be subject to normal variation; (4) absence of a ventral projection of the postparietal (spina supraoccipitalis) above the foramen magnum: although CGP/1/135 also lacks this projection, the reliability of such as character is suspect, because the occiput is often crushed in temnospondyls. In conclusion, none of the aforementioned characters are reliable diagnostic indicators for *X. africanus*. However, only *X. africanus* shares

with CGP/1/135 the absence of an exoccipital-pterygoid suture, elliptical choanae, and occipital condyles that are situated anterior to the quadrate condyles. These characters are plesiomorphic but, together with the presence of a midline contact between the exoccipitals (herein identified as an autapomorpy of *X. africanus*) and the fact that all other aspects of the anatomy of CGP/1/135 are consistent with the morphology in that species, referral of CGP/1/135 to *X. africanus* is firmly based. Biostratigraphic evidence also supports this attribution: CGP/1/135 and all known material of *X. africanus* comes from "subzone B" of the *Cynognathus* AZ of South Africa (Damiani 2004).

Skull ontogeny and variation

Ontogenetic stages.—Together with UCMP 41286 and SAM-PK-3008, referral of CGP/1/135 to *Xenotosuchus africanus* results in a partial ontogenetic series for that taxon. These three skulls (Fig. 4) comprise the most complete crania of the six known *X. africanus* specimens, and reasonable comparisons and measurements can be made from them. The smallest specimen in the depicted series, UCMP 41286 (Fig. 4A), has an estimated midline length of some 290 mm (Morales and Shishkin 2002), slightly bigger than the estimated (from reconstruction) length of 285 mm for the lectotype SAM-PK-2360 (Chernin 1978). The preserved portions of SAM-PK-11482 and BP/1/1674/1 indicate that they were of a similar size. SAM-PK-3008 (Fig. 4B) represents a slightly larger individual at an estimated midline length of 300 mm. Dorsally this specimen is very poorly preserved—indeed almost no bone remains and the mould shows little detail—so that the position of the nostrils, orbits, and pineal are hypothetical. The new specimen, CGP/1/135 (Fig. 4C), has an estimated midline length of 500 mm, making it approximately 40 percent larger than all other specimens.

Attribution of CGP/1/135 to *Xenotosuchus africanus* is based on character analysis alone; size or proportional differences have not been taken into consideration. Therefore, the specimen likely represents an extension of the growth series of *X. africanus*; the associated proportional and morphological changes in the skull (outlined below), while consistent with what is known about ontogeny in temnospondyls, thus represent ontogenetic changes. An alternative, though less likely, possibility, is that the great difference in size between CGP/1/135 and all other *X. africanus* specimens might be due to sexual dimorphism, although clear evidence of sexual dimorphism in temnospondyls has yet to be recognized. The ontogenetic status of the specimens in the growth series are considered below.

Morales and Shishkin (2002) considered UCMP 41286 to represent an adult individual presumably on the basis of its size and "adult" proportions. The principle criteria that has been used to identify the adult stage in temnospondyls (e.g., Warren and Hutchinson 1988; Boy and Sues 2000; Steyer 2000, 2003; Schoch 2001) include the following: (1) extent of dermal ossification: this is generally higher in adults compared

to juveniles, although notable exceptions occur especially among paedomorphic species; (2) pattern of dermal ornamentation: adults display a well developed system of pits and grooves with high relief, whereas juvenile ornament has poor differentiation of pits/grooves with little relief; (3) degree of infolding of the marginal dentition: this is much more complex in adults; and (4) overall size and shape of the skull: juvenile skulls are generally parabolic in shape and have large, centrally located orbits, whereas the much larger sub-adult or adult skulls usually show negative allometry of the orbits but positive allometry in such features as the snout. All of the *X. africanus* specimens fulfil the aforementioned criteria, although it has been amply demonstrated that in temnospondyls size alone is not a reliable criterion of age (Bystrow and Efremov 1940; Steyer 2000, 2003). Nevertheless, regarding UCMP 41286 as an adult individual (cf. Morales and Shishkin 2002) would appear to be a reasonable assumption.

There is, however, evidence to suggest that UCMP 41286, and by implication all *Xenotosuchus africanus* specimens of a similar size, may be sub-adult rather than adult individuals. First, Morales and Shishkin (2002: 4) stated that the "absence of interorbital expansions of the frontals occurs only as a juvenile character", but attributed its occurrence in UCMP 41286 to paedomorphosis. The presence of well developed interorbital expansions in the larger CGP/1/135 instead suggests that the condition in UCMP 41286 may well be related to its sub-adult nature. Second, the presence of narrow, anteriorly tapered postfrontals in UCMP 41286 was regarded by Morales and Shishkin (2002) to be similar to the condition in juvenile mastodonsaurids. However, the broader, anteriorly blunt-ended postfrontals in CGP/1/135 again suggests that the condition in UCMP 41286 is a reflection of immaturity. The state of these characters in the lectotype SAM-PK-2360 and in BP/1/1674/1 appears to be identical to that in UCMP 41286 (cf. Morales and Shishkin 2002). The same trends are evident in the growth series of *Watsonisuchus aliciae* (Warren and Hutchinson 1988; Warren and Schroeder 1995) and *Watsonisuchus madagascariensis* (Steyer 2003). Third, UCMP 41286 has a curved rather than Z-shaped lacrimal flexure (Morales and Shishkin 2002), a condition that is found in juvenile (and possibly sub-adult) mastodonsaurids (Damiani and Warren 1997; Steyer 2003). Finally, changes in skull proportions between UCMP 41286 and CGP/1/135 suggest that UCMP 41286 was not yet fully adult; these changes are described below. In summary, UCMP 41286 and, probably, the slightly larger SAM-PK-3008, are here considered to represent sub-adult individuals, whereas CGP/1/135 probably represents a mature adult.

Ontogenetic variation.—Proportional changes are evident in the growth series of *Xenotosuchus africanus*. In the sub-adult UCMP 41286, the snout accounts for 55% of total skull length (measured from the tip of the snout to the back of the postparietals), while skull width across the quadratojugals is 79% of skull length. In contrast, in the adult CGP/1/135 the snout accounts for 68% of skull length, and skull width across
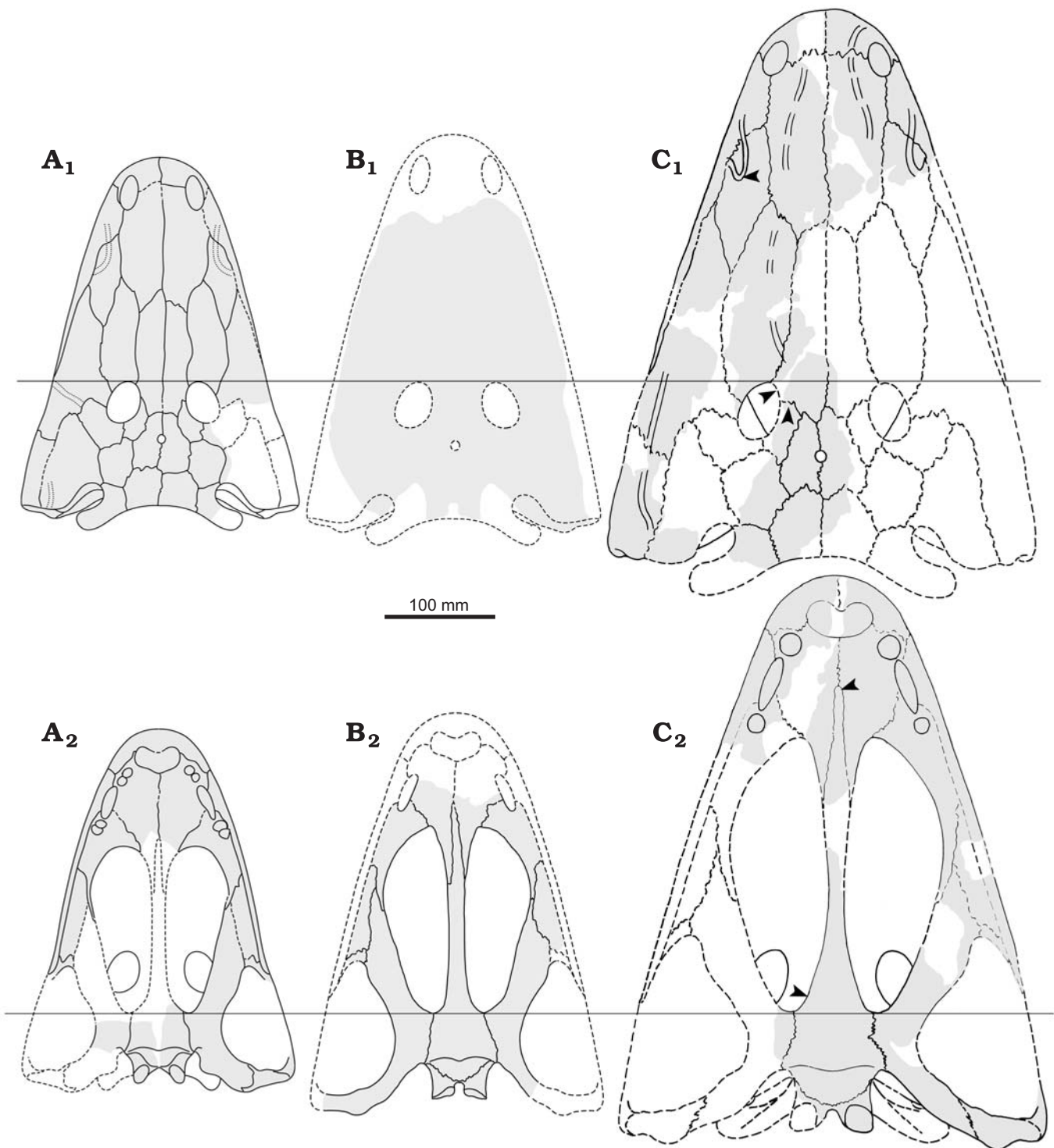
Fig. 4. Partial ontogenetic sequence representing sub-adult to adult stages in the temnospondyl *Xenotosuchus africanus* (Haughton, 1925) from the Middle Triassic (*Cynognathus* Assemblage Zone, Beaufort Group) of the Karoo Basin, South Africa. **A**. UCMP 41286 in dorsal (A_1) and ventral (A_2) views. **B**. SAM-PK-3008 in dorsal (B_1) and ventral (B_2) views. **C**. CGP/1/135 in dorsal (C_1) and ventral (C_2) views; arrows indicate ontogenetically variable characters of the cranium of *X. africanus*, as discussed in the text. Grey shading represents the preserved portions of each skull.

the quadratojugals is also 79% of skull length. Thus, the snout has increased proportionally in size, whereas skull width remains proportionally the same. A proportional increase in snout length is the most commonly reported growth trend in

stereospondyls (e.g., Bystrow and Efremov 1940; Welles and Cosgriff 1965; Warren and Hutchinson 1988; Shishkin et al. 1996; Steyer 2002, 2003; Schoch 2000). In the palate, the prefenestral division (i.e., anterior to the interpterygoid vacu-

ities) accounts for 32%, 29%, and 23% of total palate length (measured from the tip of the snout to the back of the occipital condyles) in UCMP 41286, SAM-PK-3008, and CGP/1/135, respectively. Hence, there is a proportional decrease in the length of the prefenestral division of the palate. This is accompanied by only a slight increase in proportion of the interpterygoid vacuities, from 47% of total palate length in UCMP 41286 and SAM-PK-3008 to 49% in CGP/1/135. Note that in SAM-PK-3008 the anteriormost part of the skull was not preserved, so the stated values are estimates only.

In addition to the changes in skull proportions, a number of morphological changes occur in the *Xenotosuchus africanus* ontogenetic series (Fig. 4). Three of these were identified earlier in connection with determination of the ontogenetic status of CGP/1/135, namely the development of a lacrimal flexure, interorbital expansion of the frontals, and anterior tapering of the postfrontals. A further character of the skull roof is the change in morphology of the postparietal: in the sub-adult specimens SAM-PK-2360 and UCMP 41286, the postparietal is a relatively small element with a straight anterior margin, whereas in the adult CGP/1/135 it is relatively massive with a pointed anterior margin. Sulej (2002) distinguished two subspecies of metoposaurid based on differences in postparietal morphology only. However, in the absence of a larger sample size for *X. africanus* it seems inadvisable to draw similar comparisons.

In the palate, the cultriform process of the parasphenoid shows a trend toward anterior expansion, terminating well behind the choanae in UCMP 41286 (Morales and Shishkin 2002) and moving successively farther forward in SAM-PK-3008 and CGP/1/135. In addition, the cultriform process is massively expanded posteriorly in the adult CGP/1/135 but not in the lectotype SAM-PK-2360 or in SAM-PK-3008. The cultriform process was not preserved in UCMP 41286. Finally, the transvomerine tooth row is arcuate in UCMP 41286 but is strictly transversely aligned in CGP/1/135. However, whether this change is growth related is uncertain because marked variation in both the shape and expression of the transvomerine tooth row occurs in some adult temnospondyls (e.g., *Benthosuchus sushkini*, *Thoosuchus yakovlevi*; Bystrow and Efremov 1940; Getmanov 1986, 1989).

Conclusions

In most aspects of its cranial anatomy *Xenotosuchus africanus* is a primitive mastodonsaurid, little derived over the suite of Lower Triassic taxa with posteriorly directed tabular horns such as *Watsonisuchus* and *Parotosuchus* (cf. Morales and Shishkin 2002). The taxon has not yet been included in a phylogenetic analysis but a comprehensive study is in preparation by the author together with Rainer Schoch.

On the basis of changes in skull proportions and morphological differences, CGP/1/135 is here considered to represent a mature adult *Xenotosuchus africanus*, while UCMP 41286 and SAM-PK-3008 are considered to represent sub-adult indi-

viduals. An alternative possibility is that all specimens represent adult individuals and that the documented changes in proportions are occurring within an adult population. However, in the absence of juvenile stages and/or independent criteria for age assessment, the evidence remains equivocal.

Changes in skull proportions and morphology with ontogeny are being increasingly documented in stereospondyls. As has previously been stressed (Warren and Hutchinson 1988; Schoch 2001; Steyer 2000; Pawley and Warren 2004), this has taxonomic implications because ontogenetic variation may preclude the identification of apomorphic character states. In the *Xenotosuchus africanus* growth series this is manifest in such characters as, for example, the anterior extent of the cultriform process and the orientation of the transvomerine tooth row. In addition, recognition of CGP/1/135 as an adult cautions against the use of size as a criterion for determination of growth status even in relatively large temnospondyl specimens that might otherwise be considered adults.

Acknowledgements

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