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Immaturity *vs* paedomorphism: a rhinesuchid stereospondyl postcranium from the Upper Permian of South Africa

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The postcranial skeleton of a medium-sized rhinesuchid from the Late Permian *Dicynodon* Assemblage Zone of South Africa is described. The well-preserved, articulated specimen consists of a partial skull, vertebral column and ribs, pectoral girdle, proximal limb elements, and ventral scales. Interesting features rarely preserved in stereospondyls include the extensive ventral scales and the pectinate anterior border of the interclavicle. SAM-PK-K10021 is of an average size for a rhinesuchid, but possesses a poorly ossified postcranial skeleton in comparison to larger rhinesuchid specimens. The scapulocoracoid lacks an ossified coracoid plate, the humerus lacks a supinator process, and the femur lacks a well-developed internal trochanter and adductor blade. Despite its relatively large size, SAM-PK-K10021 is an immature stage of a large rhinesuchid, thus contributing to our knowledge of the changes to the postcranial skeleton that occur during ontogeny. The assessment of heterochronic processes, especially paedomorphism, in the postcranial skeleton of temnospondyls, and the implications for cladistic analysis, are discussed.

Keywords: Rhinesuchidae, postcranial skeleton, stereospondyl, temnospondyl, ontogeny, heterochrony.

INTRODUCTION

The Rhinesuchidae are a little-studied group of large, semi-aquatic stereospondyls, with a temporal range from the Late Permian to the Early Triassic. They are one of the most basal taxa in the diverse, mainly Mesozoic, group of temnospondyls known as the Stereospondyli (Yates & Warren 2000, Fig. 1). The postcranial skeleton of most of the derived stereospondyls is considered to be paedomorphic (*sensu* McNamara 1986), and adapted to an aquatic existence, as evidenced by the reduced, imperfectly ossified postcranial skeleton commonly seen in these taxa (Watson 1919). In distinct contrast, what is known of the postcranial skeleton of some basal stereospondyls is well-ossified and presumably capable of extended terrestrial locomotion (Panchen 1959; Pawley & Warren 2005; Yates 1999). While the postcranial skeleton of some of the more derived stereospondyls is well described, the description of the most basal stereospondyls is insufficient for comprehensive comparison and determination of the character polarities of many postcranial characteristics.

While many specimens of rhinesuchids have been collected (Kitching 1978), few of these have associated postcranial skeletons. Those that do are: *Uranocentrodon senekalensis* (Haughton 1915; Van Hoepen 1915); *Broomistega putterilli* BP/1/3241 (Shishkin & Rubidge 2000); an unnamed rhinesuchid, field no. M460, consisting of a skull and articulated anterior pectoral girdle; and SAM-PK-K10021. *Uranocentrodon* and M460 have large skulls, the skull fragment of SAM-PK-K10021 is of medium size, while the specimens of *Broomistega* are small and considered by Shishkin & Rubidge (2000) to be paedomorphic compared to other rhinesuchids. To date, the only rhinesuchid postcranial skeleton described is that of the two-metre-long *Uranocentrodon* (Haughton 1915; Van Hoepen 1915), prepared from the dorsal side, however neither of the descriptions of this material provides sufficient detail for cladistic analysis.

All known rhinesuchid specimens are of Gondwanan origin, with the majority found in the Karoo Basin in South Africa, where they are an uncommon component of the fauna (Kitching 1978; Shishkin & Rubidge 2000). Most specimens have been found in Late Permian deposits, but they also represent one of the few higher level taxa to survive the end-Permian mass extinction, with one genus, *Broomistega,* found in the Early Triassic (Shishkin & Rubidge 2000). *Uranocentrodon* has previously been considered to have come from the Early Triassic *Lystrosaurus* Assemblage Zone (Kitching 1978; Groenewald & Kitching 1995), but is now firmly placed in the Late Perm-

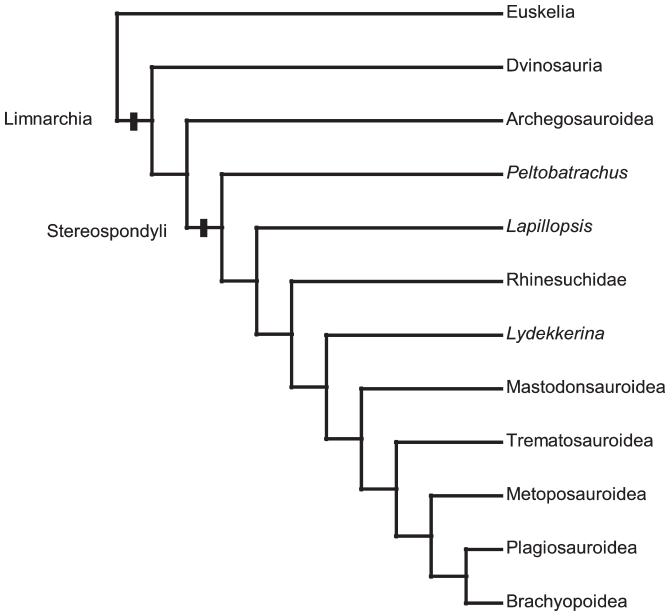


Figure 1. Cladogram depicting relationships of major taxa within the Temnospondyli (after Yates & Warren 2000; Damiani 2001).

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ian *Dicynodon* Assemblage Zone (Latimer *et al.* 2002).

The only large-scale, computer-based analysis of 'higher' temnospondyl relationships is that of Yates & Warren (2000), who placed the Rhinesuchidae among the most basal stereospondyls. Damiani (2001) removed the Lydekkerinidae from the Mastodonsauroidea and placed them between the Rhinesuchidae and the Mastodonsauroidea, which was supported by Pawley & Warren (2005). Some of the basal taxa are terrestrially adapted, with well-ossified limbs and skulls that lack lateral line canals. These include *Peltobatrachus pustulatus* (Panchen 1959), *Lapillopsis nana* (Warren & Hutchinson 1990a; Yates 1999), and *Lydekkerina huxleyi* (Shishkin *et al.* 1996; Pawley & Warren 2005).

The more derived Stereospondyli are all adapted for an aquatic existence, with deep lateral line canals on the skull roof and small, feeble, weakly ossified limbs with reduced processes for muscle attachment. The postcranial skeletons of these stereospondyls is paedomorphic because their prolonged growth phase results in attainment of a large size while retaining an essentially immature morphology (McNamara 1986). These stereospondyls commonly reach 2–3 m in length, with the largest known being *Mastodonsaurus giganteus* at 6 m (Schoch 1999). However, despite the apparently immature nature of the postcranial skeleton of many stereospondyls, there is little data available on ontogenetic stages, apart from those of *Benthosuchus sushkini* (Bystrow & Efremov 1940), *Mastodonsaurus giganteus* (Schoch 1999) and *Gerrothorax pustuloglomeratus* (Hellrung 2003).

Specimen SAM-PK-K10021, a newly discovered specimen of a medium-sized rhinesuchid with postcranial elements preserved, is interesting for several reasons. It is a basal stereospondyl, the ventral surface is exposed unlike other rhinesuchid specimens, and because it is an immature growth stage of a rhinesuchid. It is also one of the latest known rhinesuchids, collected from the Tatarian age deposits just below the Permo-Triassic boundary on Lucerne 70 farm, at Lootsberg Pass near Graaff Reinet, South Africa (Roger Smith, pers. comm.). This locality is noted for the overlap of two stratigraphic marker taxa, the Late Permian *Dicynodon* overlapping in occurrence for a depth of approximately 25 m with the Early Triassic *Lystrosaurus* (Smith & Ward 2001). The Permo-Triassic boundary is not clearly defined in these regions, but has been placed at the uppermost limit of the *Dicynodon* Assemblage Zone (Smith 1995; Smith & Ward 2001; Retallack *et al.* 2003). Collected from a fluvial deposit within the overlap zone, SAM-PK-K10021 is the latest known Permian rhinesuchid.

The purpose of this study is to further knowledge of the basal stereospondyl postcranial skeleton as part of work in progress on the temnospondyl postcranial skeleton. In particular, examination of the postcranial skeleton of the Rhinesuchidae is important for providing more information on the morphological variation that occurs amongst the basal members of the Stereospondyli. After preparation, it became apparent that the degree of ossification of the postcranial skeleton of SAM-PK-K10021 was not as extensive as anticipated. Growth stages of post-larval to adult sizes in stereospondyls are uncommon, and, as a medium-sized rhinesuchid, SAM-PK-K10021 provides information on the changes in the postcranial skeleton during these ontogenetic stages.

MATERIALS AND METHODS

Material. SAM-PK-K10021 housed in the South African Museum, Cape Town, consists of a partial skull, vertebral column and ribs, pectoral girdle, proximal limb elements and ventral scales of a rhinesuchid, preserved in a grey mudstone block from the Late Permian (Tatarian), *Dicynodon* Assemblage Zone, Lucerne 70 farm near Graaff-Reinet, South Africa.

Comparative material. M460, a skull and articulated anterior part of the pectoral girdle, *Cistecephalus* Assemblage Zone, Beaufort West. *Uranocentrodon senekalensis* NMQR1438; TM75, 77 79, 85, 103, 208 and 4703, complete skeletons, *Dicynodon* Assemblage Zone, Senekal. *Broomistega putterilli* BP/1/3241, skull and anterior skeleton, *Lystrosaurus* Assemblage Zone, Oliviershoek.

Methods. Staff at the South African Museum initially prepared SAM-PK-K10021, while the senior author, using an Aro airscribe, undertook further preparation. Small cracks were repaired with cyanoacrylate (Paleobond). Terminology in descriptions follows Romer (1922), Bystrow & Efremov (1940) and Coates (1996), unless otherwise noted.

DESCRIPTION

The dorsal surface of SAM-PK-K10021 (Fig. 2) consists of the posterior right side of a skull and mandible, some disarticulated neural arches and intercentra, articulated ribs, scattered ventral scales, a ventrally exposed femur, the dorsal processes of both clavicles, and both humeri. The ventral surface (Fig. 3) consists of an articulated interclavicle, clavicles, humeri, partly articulated ribs, ventral scales, and disarticulated intercentra.

Skull

Only the right posterior portion of the skull is preserved. This consists of parts of the parasphenoid, right pterygoid, right occipital region, squamosal, and quadratojugal. While the posterior portion of the mandible is present, the ventral surface remains buried in matrix. This specimen has been identified as a rhinesuchid because of a particular combination of cranial and mandibular features as follows: the otic flange of the pterygoid is deep, a falciform crest of the squamosal overhangs the otic notch, the postglenoid area on the mandible is absent, the ornament of the skull roof and mandible is coarsely ridged rather than finely reticulate or pustulate, there is a single occipital condyle, 'pockets' are present on the ventral surface of the parasphenoid, and the parasphenoid has a long suture with the pterygoid (not visible in figures) (Damiani 2001).

Assignation of SAM-PK-K10021 to a rhinesuchid genus was not undertaken because it does not have sufficient cranial material for specific taxonomic assessment. The Rhinesuchidae in general are in need of revision (Kitching 1978; Damiani & Rubidge 2003), so it was considered that assignation of SAM-PK-K10021 to a genus was unwise until such revision is undertaken.

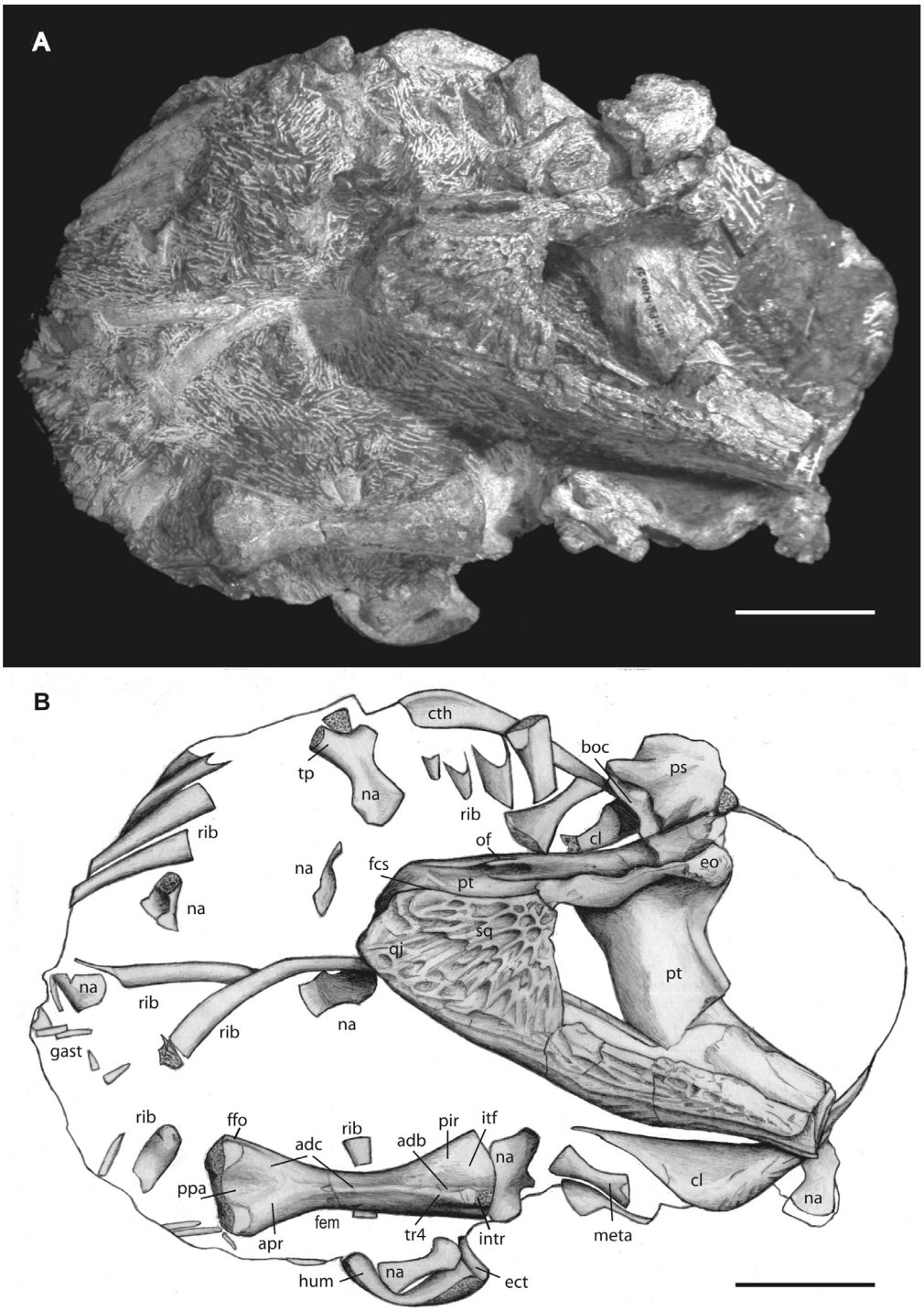


Figure 2. **A, B**. Dorsal view of SAM-PK-K10021. Scale bars = 50 mm.

Postcranial skeleton

The partly disarticulated dorsal surface of the specimen consists of the femur lying next to the skull, surrounded by scattered neural arches and ventral scales. On the ventral surface, the pectoral girdle and ventral scales are articulated and well preserved. Pelvic and distal limb elements are absent.

Many of the disarticulated vertebral elements of SAM-PK-K10021 are scattered throughout the block of matrix. The vertebrae are typically neorhachitomous (Romer 1947), in that the intercentrum is the dominant vertebral element. No pleurocentra, sacral vertebrae, or haemal arches were found.

Neural arch (Fig. 2). The neural spines are posteriorly offset and subrectangular in lateral view, with the height of the spines approximately equal in length to the distance between the well-developed pre- and postzygapophyses. Stout transverse processes terminate in anteroventral to posterodorsally inclined diapophyses. A supraneural canal does not penetrate the neural arch.

Intercentrum (Fig. 3). Thin, crescentic intercentra are associated with the ribs. Most intercentra have only the smooth, unornamented periosteal ventral surface exposed. In anterior or posterior view, the intercentra form a half circle, whose walls are uniformly thick.

Ribs (Figs 2, 3). Most of the ribs are only partially exposed. The visible ribs are long and thin, oval in cross-section, distally expanded and gently ventrally curved. None of

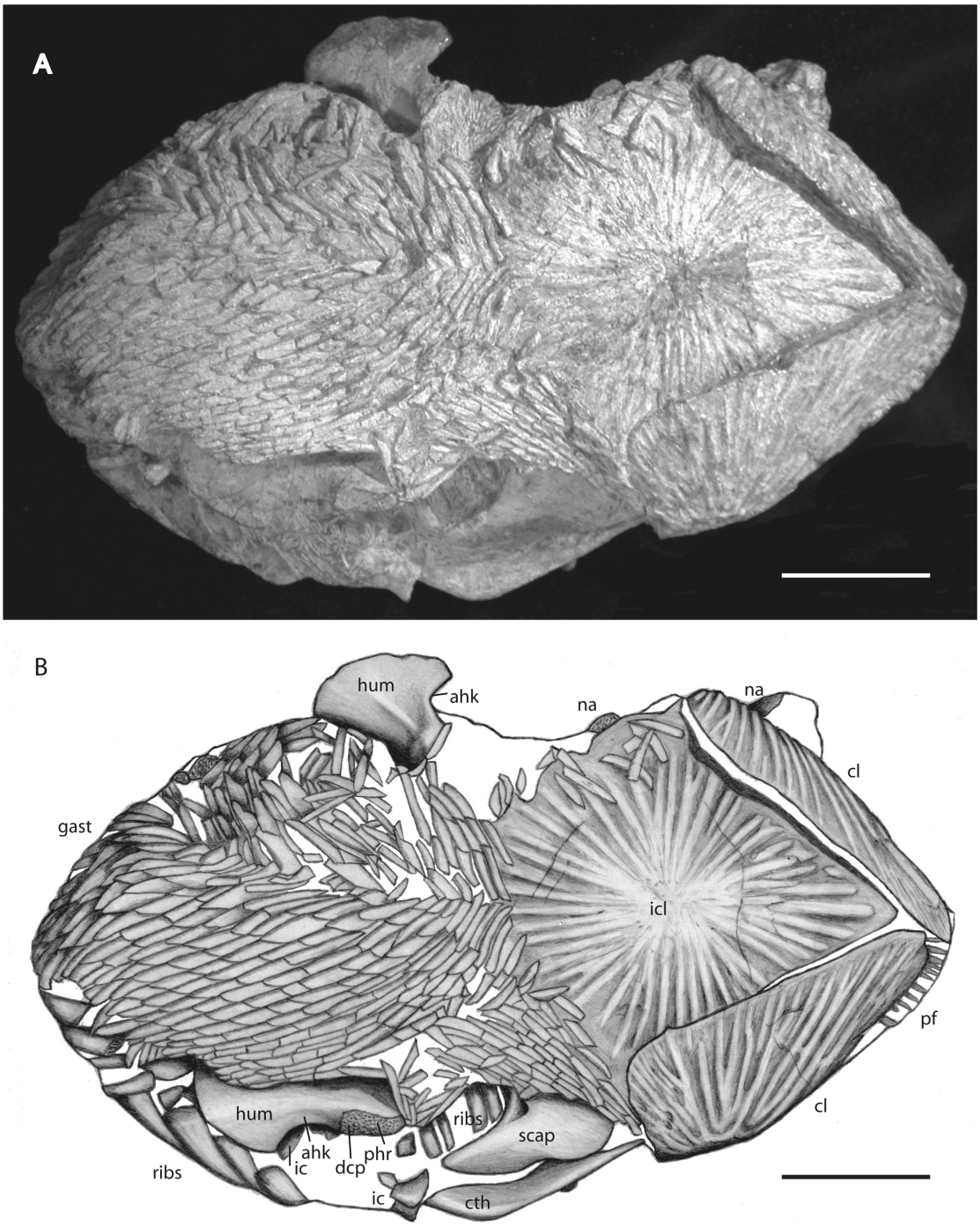


Figure 3. Ventral view of SAM-PK-K10021. Scale bars = 50 mm.

the exposed ribs bears an uncinate process; however, the thoracic ribs that are most likely to bear uncinate processes (Moulton 1974; Schoch 1999) are not exposed.

Interclavicle (Fig. 3). The coarsely ornamented main body of the interclavicle is of the flattened rhomboidal shape typical of stereospondyls, and lacks an elongate parasternal process. In outline, it is symmetrical about the centre of ossification, which is level with the posterior border of the clavicular facets, with the anterior half similar in size to the posterior half. The clavicular facets join anteriorly, so that the articulated clavicles meet and cover the anterior margin of the interclavicle. Posteroventrally, the border of the interclavicle is flat rather than recessed to fit the ventral scales; the ornament fades out where the ventral scales overlap. Where the edges of the interclavicle are exposed, they gradually become thinner until they taper out, so that no delimiting edge is discernible. A small portion of the anterior border extends beyond the front of the left clavicle as a thin and delicate pectinate fringe.

Clavicle (Figs 2, 3, 4A). Both articulated clavicles have the medial edges displaced slightly ventrally. Each clavicle has a coarsely ornamented, anteroposteriorly expanded ventral blade, with reticulate ornament near the origin of the dorsal clavicular process and grooved ornament radiating from here towards the anterior and medial margins. Like the edges of the interclavicle, the ornament terminates a short distance from the border of the medial margins of the clavicles, which continues medially, tapering into a thin almost imperceptible film of bone. The ornament

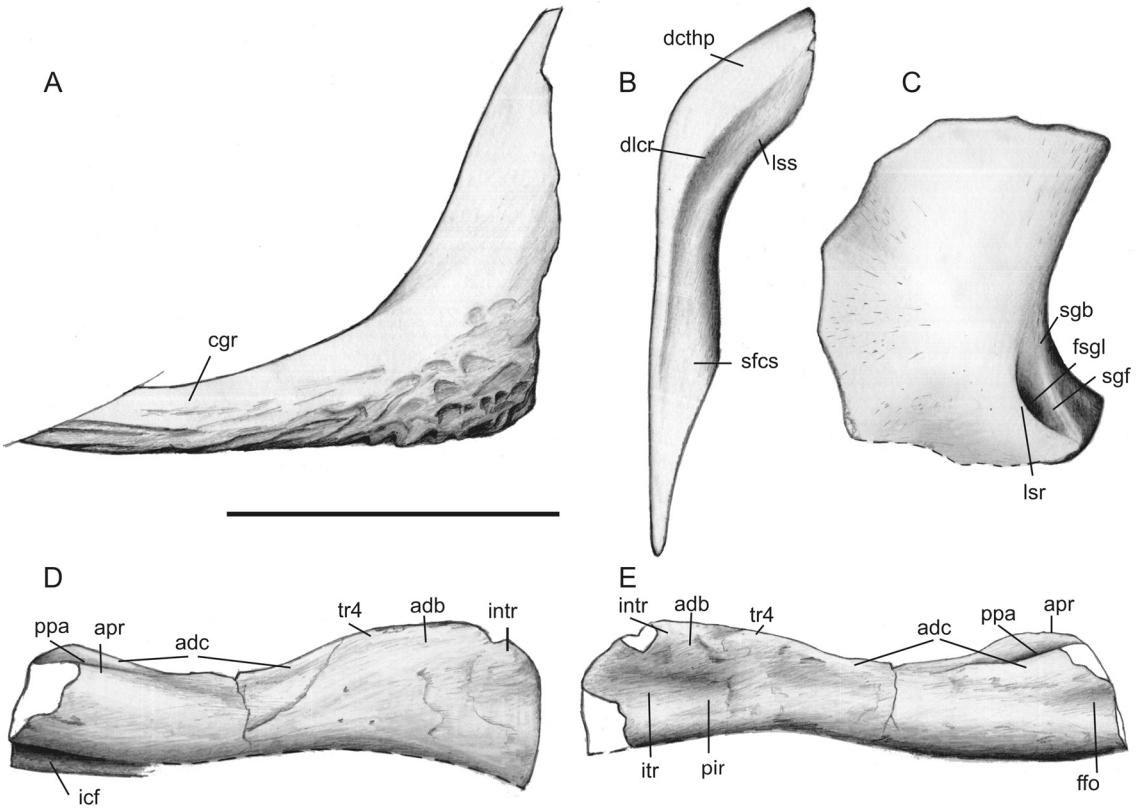


Figure 4. **A**, lateral view of left clavicle; **B**, lateral view of left cleithrum; **C**, lateral view of left scapulocoracoid; **D**, medial view of right femur; **E**, lateral view of right femur. Scale bar = 50 mm.

at the base of the dorsal clavicular process is flush with the dorsal clavicular process rather than raised. A narrow unornamented clavicular groove runs along the anterolateral edge of the blade, terminating at the base of the dorsal clavicular process. The robust dorsal clavicular process arises from the posterolateral corner of the ventral blade. Dorsally it is gently recurved near the tip, anteriorly it lacks a flange, but an extensive, posteriorly convex posterior lamina is present.

Cleithrum (Figs 3, 4B). The articulated left cleithrum is a stoutly constructed, robust element that expands slightly over the dorsal surface of the scapulocoracoid. A gentle posterior curve marks the anterior edge of the dorsal cleithral process, which lacks a cleithral crest; while the ventrolateral surface bears a shallow suprascapular lamina. In lateral view, a shallow ridge, the dorsolateral cleithral ridge (new term) rises from the dorsolateral surface of the dorsal clavicular process, it passes ventrally across the junction of the dorsal cleithral process and cleithral shaft to the anterior edge of the shaft. While the anterior edge of the cleithral shaft is smoothly rounded, the flattened scapular flange of the cleithral shaft (new term) forms the posterolateral border.

Scapulocoracoid (Figs 3, 4C). The poorly ossified, articulated left scapulocoracoid lacks both the dorsal scapular blade and the coracoid portion. The dorsally rounded scapular portion has shallow depressions along the anterodorsal border and ventral surface. A shallow, flattened, lateral supraglenoid ridge (new term) continues the posterior border of the scapular blade. The supraglenoid foramen is anteroventrally directed, so that in lateral view it is aligned with the posterior border of the scapular blade, while in posterior view it is located slightly lateral to the middle of the supraglenoid buttress. While the unfinished ventral edge of the supraglenoid buttress is apparent, the presence or absence of a coracoid plate is difficult to confirm, as the interclavicle and ventral scales cover much of the area ventral to the scapular blade.

Humerus (Fig. 3). Both articulated humeri are of the standard waisted temnospondyl form, with the proximal and distal ends set at right angles to each other. Each humerus displays a low degree of ossification and lacks prominent processes for muscle attachment. On the anterior surface, the proximal humeral ridge (new term) is unossified between the glenoid articulation surface and the deltopectoral crest. The latissimus dorsi process is not apparent, the ectepicondyle reduced, the distal border of the entepicondyle is rounded, and there is no evidence of a capitulum for articulation with the radius. A sharp-edged anterior humeral keel curves smoothly from the distal side of the deltopectoral crest down the anterior margin, with no evidence of a supinator process.

Metapodial (Fig. 2). A single disarticulated metapodial found near the clavicle is of the typical temnospondyl elongated hourglass shape. While the proximal end is steeply angled, it is impossible to determine its position within either the manus or pes.

Femur (Figs 2, 3, 4D,E). The disarticulated slender right femur has a long narrow shaft, with incompletely ossified ends. On the ventral surface, a shallow intertrochanteric fossa is present on the proximal head. The deep adductor blade anterior to the intertrochanteric fossa bears a flattened internal trochanter, barely differentiated from the articulation surface at its proximal end. Distal to the internal trochanter on the adductor blade is the weakly defined bulge of the fourth trochanter. An ill-defined

posterior intertrochanteric ridge bounds the posterior edge of the intertrochanteric fossa; it joins the adductor blade at its junction with the adductor crest. This is distinguished from the adductor blade by a slight change in angle, and rapidly decreases in height as it passes down the midline of the femur. As the adductor crest reaches the proximal side of the shallow popliteal area, it becomes low and ill defined; it bifurcates at this point into the again poorly defined anterior popliteal ridge (new term). Hidden in ventral view, the shallow fibula fossa is located on the distal posterior surface of the femur. The intercondylar fossa on the dorsal side of the femur is hidden underneath it, what can be observed is deep, and smoothly rounded on both dorsal edges.

Ventral scales (Fig. 3). Ventral scales (dermal ossicles) cover the ventral surface of the specimen posterior to the interclavicle. On the left side of the specimen they are articulated, but are partly disarticulated and scattered on the right. All ventral scales are spindle-shaped, with a ridge in the centre of the element, similar to those described in *Uranocentrodon senekalensis* (Findlay 1968). The main body of the ventral scales forms an inverted chevron with the two arms of the V meeting in the midline, beginning at the posterior border of the interclavicle. There are a maximum of ten ventral scales preserved in each row. Additional ventral scales cover the flanks anterior to the humerus. The rows of these ventral scales parallel the posterior border of the interclavicle and clavicles, meeting the main body of the ventral scales at the level of the proximal insertion of the humerus. Unfortunately, the posterior and lateral borders of the ventral scale field are not preserved. The medial ends of the ventral scales expand slightly where they overlap along the midline, although there are no distinct median ventral scales. Dorsal scales are not preserved in this specimen.

DISCUSSION

It is not the intention of this work to compare exhaustively the postcranial skeleton of SAM-PK-K10021 with that of other temnospondyls, as this study contributes to work in progress on the temnospondyl postcranial skeleton. Hence, only basic comparisons will be presented here, and comparative taxa confined to those considered to be sister taxa to the Rhinesuchidae, that is, the Stereospondylomorpha, which includes the Archegosauroidea and Stereospondyli (*sensu* Yates & Warren 2000).

Features of SAM-PK-K10021 that are uncommon in stereospondyls

The pectinate border of the interclavicle is a common feature amongst temnospondyls and basal tetrapods, but its preservation is rare among stereospondyls, because it is thin, fragile, easily broken and readily destroyed in disarticulated specimens. However, it is commonly preserved amongst the sister taxa to the Stereospondyli, the Archegosauroidea, notably *Archegosaurus decheni* (Meyer 1857), *Cheliderpeton latirostre* (Boy 1993), and *Sclerocephalus* spp. (Broili 1926; Boy 1988; Werneburg 1992). The thin edges of the interclavicle and medial edges of the clavicles are also usually broken off in disarticulated specimens and the preservation of SAM-PK-K10021 is useful in demonstrating their true extent.

Preservation of ventral scales is uncommon among stereospondyls, having been described so far only in the rhinesuchid *Uranocentrodon senekalensis* (Haughton 1915; Van Hoepen 1915; Findlay 1968), *Laidleria gracilis* (Kitching 1957; Warren 1998) and *Gerrothorax* spp. (Nilsson 1946; Hellrung 2003). The arrangement in SAM-PK-K10021, whereby the anterolaterally directed rows of ventral scales meet the posterolaterally directed rows at the level of the humerus, is similar to that of other temnospondyls and basal tetrapods. The ventral scales are similar in shape and arrangement to those described by Findlay (1968) in *Uranocentrodon senekalensis*. One of the specimens of *Uranocentrodon* (TM75) has the pectoral girdle prepared from the dorsal surface, showing a comparable arrangement of ventral scales around the pectoral girdle. Findlay did not comment on the arrangement of the ventral scales but described in detail how the inverted chevron shape on the thorax would reduce friction from belly drag during locomotion.

Among the Stereospondylomorpha, similar ventral scales are common in the Archegosauroidea, particularly *Archegosaurus decheni* (Meyer 1857), *Cheliderpeton vranyi* (Werneburg & Steyer 2002), *Sclerocephalus* spp. (Broili 1926; Boy 1988; Lohmann & Sachs 2001), and *Platyoposaurus stuckenbergi* (Konzhukova 1955). The apparent absence of dorsal scales or osteoderms in SAM-PK-K10021 may be an artefact of preservation, as the dorsal surface of the specimen is not particularly well preserved.

Plesiomorphic characteristics of the postcranial skeleton of SAM-PK-K10021

In comparison with other stereospondyls, even as an immature specimen, SAM-PK-K10021 displays some of the plesiomorphic postcranial skeleton characters found in *Uranocentrodon senekalensis* and *Lydekkerina huxleyi* (Pawley & Warren 2005) and not seen in more derived stereospondyl taxa. Unlike the intercentra of many stereospondyls (Warren & Snell 1991), the intercentra are not thick in cross-section, although this may also be due to the immature condition of SAM-PK-K10021. The enclosed supraglenoid foramen is present on the scapula even though the coracoid is not present, indicating that the ventrally open supraglenoid foramen found in more derived taxa within the Stereospondyli is a derived characteristic rather than an indication of immaturity, or a retention of a juvenile character into adulthood. The lack of an anterior flange on the dorsal process of the clavicle is also a plesiomorphic trait among stereospondyls.

Morphological comparison of SAM-PK-K10021 within the Rhinesuchidae

In contrast to the interpretation of its skeleton as immature, the poorly ossified postcranial skeleton of SAM-PK-K10021 invites the proposal that SAM-PK-K10021 represents a more derived type of rhinesuchid, closer to the typical paedomorphic stereospondyls as understood by Watson (1919). It could be argued that there are two types of rhinesuchid postcranial skeleton, dividing the Rhinesuchidae into two phylogenetic groups, one retaining the primitive fully ossified condition and one develop-

ing the poorly ossified postcranial skeleton. The idea that the Rhinesuchidae may be composed of two taxonomic groups was put forward by Romer (1947), who considered that the Rhinesuchidae were more primitive than the Uranocentrodonidae because they retained the exposure of the opisthotic in the paraoccipital bar. More recently, Shishkin & Rubidge (2000) concluded that this morphological interpretation was incorrect, and division of the Rhinesuchidae was not justifiable on the basis of cranial characteristics. However, if two separate taxonomic groups were present, one would be represented by postcranial material of the well-ossified and large M460 (*Cistecephalus* Assemblage Zone, (Johann Neveling, pers. comm.) and *Uranocentrodon* (*Dicynodon* Assemblage Zone, Latimer *et al.*(2002), both found lower stratigraphically than the other group, which is represented by the small to medium, poorly ossified and stratigraphically higher SAM-PK-K10021 (uppermost *Dicynodon* Assemblage Zone, Roger Smith, pers. comm.) and *Broomistega* which is from the Early Triassic *Lystrosaurus* Assemblage Zone (Shishkin & Rubidge 2000), just above the level of SAM-PK-K10021. This could imply that the Rhinesuchidae were evolving reduced postcranial skeletons over time, following the trend shown by later stereospondyls. However, the correlation between size and degree of ossification in the specimens does not support this hypothesis.

Comparison of the postcranial skeleton of SAM-PK-K10021 with that of other rhinesuchids is necessarily limited because most specimens do not have associated postcranial material. Of those that do, the large specimens of *Uranocentrodon senekalensis* (NMQR1438, and TM75) and M460 are the best preserved and prepared. Although many rhinesuchid skulls of medium size are known, SAM-PK-K10021 is the only specimen of medium size with an associated postcranial skeleton. A single small rhinesuchid, the Triassic *Broomistega putterilli* BP/1/3241 (Shishkin & Rubidge 2000), has associated postcranial material although these remain undescribed.

Surprisingly, SAM-PK-K10021 has a poorly ossified postcranial skeleton, more like that of some of the later stereospondyls and *Broomistega,* making an interesting contrast to the robust and well-ossified postcranial skeleton of *Uranocentrodon* and M460. This suggests that it is an immature growth stage. However the assessment of the state of maturity of SAM-PK-K10021 can only be achieved by comparison with a growth series. While postcranial skeletons of the early larval stages of some temnospondyls have been identified (e.g. Schoch 1992; Schoch 2003), the ontogenetic changes that occur in the postcranial skeleton between the larval and the mature condition in rhinesuchids, and indeed in most stereospondyls, are almost unknown.

The evidence that SAM-PK-K10021 is an immature growth stage of a larger rhinesuchid is by necessity based on comparisons with the ontogenetic changes in the postcranial skeleton observed in closely related but more derived taxa. A partial growth series of small to large and presumably adult specimens is known for the mastodonsaurids *Benthosuchus sushkini* (Bystrow & Efremov 1940) and *Mastodonsaurus giganteus* (Schoch 1999). A large number of specimens of *Lydekkerina huxleyi* are known (Kitching 1978), but the postcranial skeleton is known only in the largest specimens. In *Mastodonsaurus,* a correlation exists between size and degree of ossification; only the largest specimens become comparatively well ossified (Schoch 1999). While an increase in ossification correlates with size in *Benthosuchus,* none of the specimens shows the same degree of ossification as the largest *Mastodonsaurus.* In *Lydekkerina* (Pawley & Warren 2005) the postcranial skeleton is comparable in its degree of ossification to that of *Uranocentrodon,* although it is much smaller. There is no doubt that the specimens of *Lydekkerina* studied are mature, as nearly 200 specimens of varying sizes have been collected (Kitching 1978) and the skulls of specimens described were of a large size. The similarity of the postcranial skeleton of *Lydekkerina* to that of *Uranocentrodon* indicates that they both differ from SAM-PK-K10021 in exactly the same features. A study of the postcranial skeleton of smaller-sized specimens of *Lydekkerina* would be useful in determining the immature condition of the postcranial skeleton in that taxon for comparative purposes, but unfortunately none of the smaller skulls collected has associated postcranial material.

Comparison of the individual postcranial elements of SAM-PK-K10021 with those of the stereospondyls listed above highlights various similarities and differences. The scapulocoracoid of SAM-PK-K10021 (Figs 3, 4C) is again comparable with that of the medium-sized specimens of *Mastodonsaurus* (Schoch 1999). The coracoid plate of *Mastodonsaurus* is separate from the scapular blade until late in ontogeny, when it fuses to form a scapulocoracoid similar to that of *Uranocentrodon* and *Lydekkerina.* In other mastodonsaurids such as *Benthosuchus* and *Eryosuchus* (*Parotosaurus*) *pronus* (Howie 1970), the coracoid is unknown and presumably remains unossified even in the largest specimens. The scapula also becomes much better ossified with ontogeny in the archegosaur *Sclerocephalus hauseri* (Meckert 1993), with the coracoid ossified only in the largest specimens. While a ventrally open supraglenoid foramen is found in most of the more derived stereospondyls (Warren & Snell 1991), SAM-PK-K10021 retains the plesiomorphic, ventrally enclosed supraglenoid foramen seen in *Uranocentrodon* and *Lydekkerina.*

The humerus of SAM-PK-K10021 (Fig. 3) is comparable in morphology with that of medium-sized specimens of *Mastodonsaurus* and *Benthosuchus,* where the proximal humeral ridge is unossified, the supinator process absent and the entepicondyle distally rounded rather than square. In the larger specimens of *Uranocentrodon, Mastodonsaurus,* and *Benthosuchus,* and in *Lydekkerina,* the proximal humeral ridge becomes ossified between the proximal articulation surface and the deltopectoral crest, a well-developed supinator process is present and the distal edge of the entepicondyle becomes squared off.

The morphology of the femur in SAM-PK-K10021 (Figs 2, 4D,E), with its slender outline, reduced adductor crest, and ill-defined fourth and internal trochanters, is consistent with that of immature specimens of *Mastodonsaurus* and *Benthosuchus.* In immature specimens of *Benthosuchus* the internal trochanter lacks a distinct process so that it is not distinct from the proximal articula-

tion surface, similar to that of SAM-PK-K10021. In mature mastodonsaurids, and in *Uranocentrodon* and *Lydekkerina,* the adductor crest is deep and the trochanters well defined, with the internal trochanter terminating distal to the proximal articulation surface. The internal trochanter in SAM-PK-K10021 is broken, but there is no evidence for the large ventromedial expansion seen in *Uranocentrodon* and *Lydekkerina.*

In summary, the postcranial skeleton of SAM-PK-K10021 displays ontogenetic characteristics consistent with that of the medium-sized specimens of *Mastodonsaurus* and *Benthosuchus,* whereas the postcranial skeletons of *Uranocentrodon* and M460 are most similar to the largest specimens of *Mastodonsaurus.* The undescribed postcranial skeleton of *Broomistega* BP/1/3241 is most consistent with the smallest specimens of *Mastodonsaurus* and *Benthosuchus.* SAM-PK-K10021 most likely represents the immature condition for the rhinesuchid postcranial skeleton, with *Uranocentrodon* representing the mature morphology and *Broomistega* BP/1/3241 the most immature.

Certain features of the postcranial skeleton are only seen in the largest and most mature specimens and these are all absent in SAM-PK-K10021. The largest specimens possess a fully ossified scapulocoracoid, a humerus with an ossified proximal humeral ridge and supinator process, a femur with a robust internal trochanter distinct from the proximal head, and a deep adductor crest. The presence of these features of the postcranial skeleton in any stereospondyl indicates that the specimen is likely to be of a late ontogenetic stage. It is possible that specimens lacking these features may be immature even if they are of a substantial size.

These results also indicate that the specimen of *Broomistega putterilli* BP/1/3241 discussed in this study may be immature. *Broomistega* BP/1/3241 is one of three specimens considered by Shishkin & Rubidge (2000) to be paedomorphic adults. *Broomistega* BP/1/3241, with a midline skull length of 75 mm is substantially smaller than the largest *Broomistega* specimen, TM 184, with an estimated midline skull length of 110 mm. It is reasonable to assume that specimen BP/1/3241 represents an immature individual rather than a paedomorphic adult.

Assessment of the paedomorphic condition of the postcranial skeleton in temnospondyls

Temnospondyls, including stereospondyls, display indeterminate growth in that, after an initial rapid growth phase, they continue to increase in size during their lifespan (Steyer *et al.* 2004). The postcranial skeleton of many large stereospondyls is paedomorphic through the process of neoteny; the postcranial skeleton remains immature for an extended period, finally reaching the most ossified condition in the largest specimens. Thus, the postcranial skeleton of these taxa progresses through ontogenetic stages throughout the life of the animal, supported by the evidence presented above.

Studies of heterochronic processes within temnospondyls (McNamara 1988; Schoch 1995) have focused exclusively on cranial characteristics, with the exception of McKinney & McNamara (1991), who discussed some postcranial heterochronies of taxa they erroneously placed within the Temnospondyli.

Traditionally, heterochronic processes are determined within a group of organisms relative to the ancestral condition. Current conflicting phylogenies of temnospondyl taxa (Yates & Warren 2000; Ruta *et al.* 2003a; Ruta *et al.* 2003b) make determination of the ancestor–descent relationships within temnospondyl taxa uncertain, and therefore it is difficult to determine the most plesiomorphic temnospondyls. Outgroup comparison is possible but fraught with the same phylogenetic instability. Analysis of heterochronic processes among temnospondyls is limited because few taxa have growth series. This means it is currently impossible to determine the ontogenetic age of most temnospondyl taxa for comparison with that of more plesiomorphic or derived taxa. It is simpler and more feasible to look for the most advanced ontogenetic stages for comparison with apparently less well-developed taxa.

Well-ossified taxa are the most likely to display the greatest fulfilment of ontogenetic potential. Members of the Euskelia such as *Eryops megacephalus* (Cope 1888; Case 1911; Romer 1922; Miner 1925; Moulton 1974) and *Acheloma cumminsi* (*Trematops milleri*) (Williston 1909; Olson 1941; Schaeffer 1941) are temnospondyls that possess postcranial skeletons with the highest degree of ossification. Their limb bones have convex ends with relatively small amounts of cartilage between the joints, as well as fully ossified carpals and tarsals. These taxa can provide a benchmark for the fully ossified condition of the postcranial skeleton within temnospondyls. It is possible to interpret this high degree of ossification as peramorphic (extension of the growth phase to include more stages than that of the ancestor, resulting in a derived morphology (*sensu* McNamara 1986). Ongoing research indicates that other unrelated taxa such as diadectomorphs share many derived similarities of their postcranial skeletons with temnospondyls, and achieve similar high degrees of ossification. Either the Euskelia and diadectomorphs have independently evolved similar peramorphic changes to the postcranial skeleton or, more parsimoniously, they both display the fully or near fully ossified condition, which implies that they share a common ancestor above the level of stem tetrapods, including the Anthracosauria (*sensu* Panchen 1970), as suggested by Pawley & Warren (2001). This interpretation contradicts current understanding of basal tetrapod relationships (Ruta *et al.* 2003a).

If members of the Euskelia (e.g. *Eryops megacephalus* and *Acheloma cumminsi*) represent the fully ossified and most ontogenetically developed condition then, by comparison, most temnospondyls are paedomorphic. Study of a growth series of a taxon that develops a highly ossified postcranial skeleton, such as *Eryops megacephalus* would resolve this issue. A partial growth series of the humerus was briefly described by Bakker (1982). The smallest humerus in this series lacks the ossified proximal humeral ridge, enlarged supinator process, convex radial condyle, and squared off entepicondyle seen in the larger specimens. The smallest humerus displays features consistent with those of later ontogenetic stages of other temnospondyls which remain poorly ossified throughout their growth

series. This small amount of evidence supports the hypothesis that the majority of temnospondyls are paedomorphic. Further evidence is needed to clarify the issue.

Paedomorphosis and implications for cladistics

Some cranial characters previously used for classification purposes have been shown to change with ontogeny in *Watsonisuchus aliciae* (Warren & Hutchinson 1990b; Warren & Schroeder 1995). Steyer (2000) demonstrated that using ontogenetically variable characters for phylogenetic analysis can have marked effects on the resulting cladogram topologies, and cautioned their use in taxonomy. As characters of the postcranial skeleton are starting to be used in analysis of temnospondyl relationships (Yates & Warren 2000; Ruta *et al.* 2003a; Ruta *et al.* 2003b), it is important that the characters chosen are not simply separating immature specimens from more mature specimens.

The paedomorphic status of many temnospondyls means that some character states that develop with ontogeny may not be present in specimens of a taxon due to the immature morphology of even the largest and presumably most mature specimens available. This presents problems for cladistic analysis. An example of a character used in phylogenetic analysis of temnospondyls (e.g. Yates & Warren 2000; Ruta *et al.* 2003a) is the absence (plesiomorphic state) or presence (derived state) of a supinator process of the humerus. These analyses considered that the sporadic distribution of the derived state was due to homoplasy. The evidence presented in this study instead indicates that it may be more parsimonious to suggest that the emergence of the derived state, shown above to be present only in the largest specimens of some taxa, is a fulfilment of ontogenetic potential rather than convergent evolution. Careful analysis of growth series is necessary to determine other characters affected by ontogeny. A further implication is that some postcranial character states may be universally present within the Temnospondyli, but unexpressed in the majority of taxa due to their immature morphology.

CONCLUSIONS

The postcranial skeleton of SAM-PK-K10021 represents an immature ontogenetic stage of a taxon that retains a paedomorphic postcranial morphology throughout its life. As a rhinesuchid, SAM-PK-K10021 contributes to our knowledge of ontogenetic changes of the postcranial skeleton among temnospondyls. Determination of the paedomorphic status of the postcranial skeleton among temnospondyls is most feasible through comparison with well-ossified taxa. The use for cladistic purposes of characters affected by ontogeny is cautioned.

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ABBREVATIONS

Institutional

BP:	Bernard Price Institute, Johannesburg, South Africa;
M:	Field abbreviation of the Council of Geosciences, Pretoria, South Africa;
NMQR:	National Museum at Bloemfontein, Bloemfontein South Africa;
SAM:	South African Museum, Cape Town, South Africa;
TM:	Transvaal Museum, Pretoria, South Africa.

Anatomical

adb	adductor blade
adc	adductor crest
ahk	anterior humeral keel
apr	anterior popliteal ridge
boc	basioccipital
cgr	clavicular groove
cl	clavicle
cth	cleithrum
dcthp	dorsal cleithral process
dlcr	dorsolateral cleithral ridge
dcp	deltopectoral crest
ect	ectepicondyle
eo	exoccipital
fcs	falciform crest of squamosal
fem	femur
ffo	fibula fossa
fsgl	supraglenoid foramen
gast	gastralia
hum	humerus
ic	intercentrum
icf	intercondylar fossa
icl	interclavicle
itf	intertrochanteric fossa
intr	internal trochanter
lsr	lateral supraglenoid ridge
lss	suprascapular lamina
meta	metapodial
na	neural arch
of	otic flange
pf	pectinate fringe
pir	posterior intertrochanteric ridge
phal	phalange
phr	proximal humeral ridge
ppa	popliteal area
ps	parasphenoid
pt	pterygoid
qj	quadratojugal
scap	scapula
sfcs	scapular flange of cleithral shaft
sgb	supraglenoid buttress
sgf	supraglenoid fossa
sq	squamosal
tp	transverse process
tr4	fourth trochanter
vs	ventral scales

REFERENCES

BAKKER, R.T. 1982. Juvenile–adult habitat shift in Permian fossil reptiles and amphibians. *Science* **217**, 53–55.

BOY, J.A. 1988. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem Europäischen Rotliegend (höchstes Karbon – Perm). 1. *Sclerocephalus. Paläontologische Zeitschrift* **62**, 107–132.

BOY, J.A. 1993. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem Europäischen Rotliegend (höchstes Karbon – Perm). 4. *Cheliderpeton. Paläontologische Zeitschrift* **67**, 123–143.

BROILI, F. 1926. Über Sclerocephalus hauseri Goldfuss. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung* **1926**, 199–122.

BYSTROW, A.P. & EFREMOV, J.A. 1940. *Benthosuchus sushkini* Efremov: a labyrinthodont from the Eotriassic of the Sharzhenga River. *Trudy Paleontologicheskogo Instituta* **10**, 1–152 (in Russian).

CASE, E.C. 1911. Revision of the Amphibia and Pisces of the Permian of North America. *Carnegie Institution of Washington Publication* **146**, 1–179.

COATES, M.I. 1996. The Devonian tetrapod *Acanthostega gunnari* Jarvik: postcranial anatomy, basal tetrapod interrelationships and patterns of skeletal evolution. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **87**, 363–421.

COPE, E.D. 1888. On the shoulder girdle and extremities of *Eryops. Transactions of the American Philosophical Society* **16**, 362–367.

DAMIANI, R.J. 2001. A systematic revision and phylogenetic analysis of Triassic mastodonsauroids (Temnospondyli: Stereospondyli). *Zoological Journal of the Linnean Society* **133**, 379–482.

DAMIANI, R.J. & RUBIDGE, B.S. 2003. A review of the South African temnospondyl amphibian record. *Palaeontologia africana* **39**, 21–36.

FINDLAY, G.H. 1968. On the structure of the skin in *Uranocentrodon* (*Rhinesuchus*) *senekalensis,* Van Hoepen. *Palaeontologia africana* **11**, 15–21.

GROENEWALD, G.H. & KITCHING, J.W. 1995. Biostratigraphy of the *Lystrosaurus* Assemblage Zone. **In**: Rubidge, B.S. (ed.), *Biostratigraphy of the Beaufort Group (Karoo Supergroup),* 29–39. South African Committee for Stratigraphy, Biostratigraphic Series No. 1. Pretoria, Council for Geoscience.

HAUGHTON, S.H. 1915. Investigations in South African fossil Reptilia and Amphibia (Parts 5–9). *Annals of the South African Museum* **12**, 65–77.

HELLRUNG, H. 2003. *Gerrothorax pustuloglomeratus,* ein Temnospondyle (Amphibia) mit knöchner Branchialkammer aus dem Unteren Keuper von Kupferzell (Süddeutschland). *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)* **330**, 1–130.

HOWIE, A.A. 1970. A new capitosaurid labyrinthodont from East Africa. *Palaeontology* **13**, 210–253.

KITCHING, J.W. 1957. A new small stereospondylous labyrinthodont from the Triassic beds of South Africa. *Paleontologia africana* **5**, 67–82.

KITCHING, J.W. 1978. The stratigraphic distribution and occurrence of South African fossil amphibia in the Beaufort beds. *Palaeontologia africana* **21**, 101–12.

KONZHUKOVA, E.D. 1955. *Platyops stuckenbergi* Trautsch: an archegosaurid from the lower zone of the Upper Permian in the Ural region. *Trudy Paleontologicheskogo Instituta* **49**, 89–127 (in Russian).

LATIMER, E.M., HANCOX, P.J., RUBIDGE, B.S., SHISHKIN, M.A. & KITCHING, J.W. 2002. The temnospondyl amphibian *Uranocentrodon,* another victim of the end-Permian extinction event. *South African Journal of Science* **98**, 191–193.

LOHMANN, U. & SACHS, S. 2001. Observations on the postcranial morphology, ontogeny and palaeobiology of *Sclerocephalus haeuseri* (Amphibia: Actinodontidae) from the Lower Permian of Southwest Germany. *Memoirs of the Queensland Museum* **46**, 771–781.

McKINNEY, M.L. & McNAMARA, K.J. 1991. *Heterochrony: The Evolution of Ontogeny*. New York, Plenum Press.

McNAMARA, K.J. 1986. A guide to the nomenclature of heterochrony. *Journal of Paleontology* **60**, 4–13.

McNAMARA, K.J. 1988. The abundance of heterochrony in the fossil record. **In:** McKinney, M.L. (ed.), *Heterochrony in Evolution: A Multidisciplinary Approach,* 287–325. New York, Plenum Press.

MECKERT, D. 1993. Der schultergürtel des *Sclerocephalus haeuseri* Goldfuss, 1847 im vergleich mit *Eryops* Cope, 1877 (Eryopoida, Amphibia, Perm). *Palaeontographica Abteilung A – Palaozoologie –Stratigraphie* **229**, 113–140.

MEYER, H. 1857. Reptilien aus der Steinkohlen-Formation in Deutschland. *Palaeontographica* **6**, 59–218.

MINER, R.W. 1925. The pectoral limb of *Eryops* and other primitive tetrapods. *Bulletin of the American Museum of Natural History* **51**, 145–312.

MOULTON, J.M. 1974. A description of the vertebral column of *Eryops* based on the notes and drawings of A. S. Romer. *Breviora* **428**, 1–10.

NILSSON, T. 1946. A new find of *Gerrothorax rhaeticus* Nilsson, a plagiosaurid from the Rhaetic of Scania. *Lunds Universitets Arsskrift N. F.* **42**, 1–42.

OLSON, E.C. 1941. The family Trematopsidae. *Journal of Geology* **49**, 149–176.

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.

PANCHEN, A.L. 1970. Anthracosauria. **In**: Kuhn, O. (ed.), *Encyclopedia of Paleoherpetology* **5A**. Stuttgart and Portland, Gustav Fischer Verlag.

PAWLEY, K. & WARREN, A.A. 2001. The postcranial skeleton of temnospondyl amphibians. *Journal of Vertebrate Paleontology,* Supplement to No. 22, 95A.

PAWLEY, K. & WARREN, A.A. 2005. A terrestrial stereospondyl from the Lower Triassic of South Africa: the postcranial skeleton of *Lydekkerina huxleyi* (Amphibia: Temnospondyli). *Palaeontology* **48**, 1–18.

RETALLACK, G.J., SMITH, R.M.H. & WARD, P.D. 2003. Vertebrate extinctions across Permian–Triassic boundary in Karoo Basin, South Africa. *Geological Society of America Bulletin* **115**, 1133–1152.

ROMER, A.S. 1922. The locomotor apparatus of certain primitive and mammal-like reptiles. *Bulletin of the American Museum of Natural History* **46**, 517–606.

ROMER, A.S. 1947. Review of the Labyrinthodontia. *Bulletin of the Museum of Comparative Zoology, Harvard College* **99**, 1–352.

RUTA, M., COATES, M.I. & QUICKE, D.L.J. 2003a. Early tetrapod relationships revisited. *Biological Review* **78**, 251–345.

RUTA, M., JEFFERY, J.E. & COATES, M.I. 2003b. A supertree of early tetrapods. *Proceedings of the Royal Society of London B* **270**, 2507–2516.

SCHAEFFER, B. 1941. The morphological and functional evolution of the tarsus in amphibians and reptiles. *Bulletin of the American Museum of Natural History* **78**, 395–472.

SCHOCH, R.R. 1992. Comparative ontogeny of Early Permian branchiosaurid amphibians from Southwestern Germany. *Palaeontographica Abteilung A – Palaozoologi e– Stratigraphie* **222**, 43–83.

SCHOCH, R.R. 1995. Heterochrony and the development of the amphibian head. **In:** McNamara, K.J. (ed.), *Evolutionary Change and Heterochrony,* 107–124. Chichester, John Wiley.

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* (*Geologie und Paläontologie*) **278**, 1–175.

SCHOCH, R.R. 2003. Early larval ontogeny of the Permo-Carboniferous temnospondyl *Sclerocephalus. Palaeontology* **46**, 1055–1072.

SHISHKIN, M.A., RUBIDGE, B.S. & KITCHING, J.W. 1996. A new lydekkerinid (Amphibia, Temnospondyli) from the Lower Triassic of South Africa – implications for evolution of the early capitosauroid cranial pattern. *Philosophical Transactions of the Royal Society of London B* **351**, 1635–1659.

SHISHKIN, M.A. & RUBIDGE, B.S. 2000. A relict rhinesuchid (Amphibia: Temnospondyli) from the Lower Triassic of South Africa. *Palaeontology* **43**, 653–670.

SMITH, R.M.H. 1995. Changing fluvial environments across the Permian–Triassic boundary in the Karoo Basin, South Africa and possible causes of tetrapod extinctions. *Palaeogeography, Palaeoclimatology, Palaeoecology* **117**, 81–104.

SMITH, R.M.H. & WARD, P.D. 2001. Pattern of vertebrate extinctions across an event bed at the Permian–Triassic boundary in the Karoo Basin of South Africa. *Geology* **29**, 1147–1150.

STEYER, J-S. 2000. Ontogeny and phylogeny in temnospondyls: a new method of analysis. *Zoological Journal of the Linnean Society* **130**, 449–467.

STEYER, J-S., LAURIN, M., CASTENET, J. & DE RICQLÈS, A. 2004. First histological and skeletochronological data on temnospondyl growth: palaeoecological and palaeoclimatological implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* **206**, 193–201.

VAN HOEPEN, E.C.N. 1915. Stegocephalia of Senekal, O.F. S. *Annals of the Transvaal Museum* **5**, 129–149.

WARREN, A.A. & HUTCHINSON, M.N. 1990a. *Lapillopsis,* a new genus of temnospondyl amphibians from the Early Triassic of Queensland. *Alcheringa* **14**, 149–158.

WARREN, A.A. & HUTCHINSON, M.N. 1990b. The young ones – small temnospondyls from the Arcadia Formation. *Memoirs of the Queensland Museum* **28**, 103–106.

WARREN, A.A. & SNELL, N. 1991. The postcranial skeleton of Mesozoic temnospondyl amphibians: a review. *Alcheringa* **15**, 43–64.

WARREN, A.A. & SCHROEDER, N. 1995. Changes in the capitosaur skull with growth: an extension of the growth series of *Parotosuchus aliciae* (Amphibia, Temnospondyli) with comments on the otic area of capitosaurs. *Alcheringa* **19**, 41–46.

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.

WATSON, D.M.S. 1919. The structure, evolution and origin of the Amphibia. The 'Orders' Rachitomi and Stereospondyli. *Philosophical Transactions of the Royal Society of London B* **209**, 1–73.

WERNEBURG, R. 1992. *Sclerocephalus jogischneideri* n. sp. (Eryopoidea, Amphibia) aus dem Unterrotliegenden (Unterperm) des Thuringer Waldes. *Fieberger Forshungsheft, Palaontologie* **445**, 29–48.

WERNEBURG, R. & STEYER, J-S. 2002. Revision of *Cheliderpeton vranyi* Fritsch, 1877 (Amphibia, Temnospondyli) from the Lower Permian of Bohemia (Czech Republic). *Paläontologische Zeitschrift* **76**, 149–162.

WILLISTON, S.W. 1909. New or little known Permian vertebrates: *Trematops,* new genus. *Journal of Geology* **17**, 636–658.

YATES, A.M. 1999. The Lapillopsidae: 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.