

CHAPTER 1.  
**IMMATURITY VS. PAEDOMORPHISM:  
A RHINESUCHID STEREOSPONDYL POSTCRANIUM  
FROM THE UPPER PERMIAN OF SOUTH AFRICA**

*Abstract.* 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 scutes. Interesting features rarely preserved in stereospondyls include the extensive ventral scutes 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 morphogenesis. The assessment of heterochronic processes, especially paedomorphism, in the postcranial skeleton of temnospondyls, and the implications for cladistic analysis, are discussed.

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 and Warren, 2000) (Figure 6). 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; Yates, 1999; Pawley and Warren, 2005). 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* (*Myriodon*) *senekalensis* (Haughton, 1915; van Hoepen, 1915); *Broomistega putterilli* BP/1/3241 (Shishkin and Rubidge, 2000); an unnamed rhinesuchid, field no. M460, consisting of a skull and articulated anterior pectoral girdle; and SAM-PK-K10021. *Uranocentrodon senekalensis* and M460 have large skulls, the skull fragment of SAM-PK-K10021 is of medium size, while the specimens of *Broomistega putterilli* are small and considered by Shishkin and Rubidge (2000) to be paedomorphic when compared to other rhinesuchids. To date, the only rhinesuchid postcranial skeleton described is that of the two metre long *Uranocentrodon senekalensis*, prepared from the dorsal side, however

neither of the descriptions of this material provides sufficient detail for cladistic analysis (Haughton, 1915; van Hoepen, 1915).

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 and 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 putterilli*, found in the Early Triassic (Shishkin and Rubidge, 2000). *Uranocentron senekalensis* has previously been considered to have come from the Early Triassic *Lystrosaurus* Assemblage Zone (Kitching, 1978; Groenewald and Kitching, 1995), but is now firmly placed in the Late Permian *Dicynodon* Assemblage Zone (Latimer et al., 2002).

The only large scale, computer based analysis of ‘higher’ temnospondyl relationships is that of Yates and Warren (2000), who placed the Rhinesuchidae among the most basal stereospondyls. Damiani (2001a) removed the Lydekkerinidae from the Mastodonsauroidea and placed them between the Rhinesuchidae and the Mastodonsauroidea, which was supported by Pawley and 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 and Hutchinson, 1990a; Yates, 1999), and *Lydekkerina huxleyi* (Shishkin et al., 1996; Pawley and Warren, 2005).

The more derived stereospondyls 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

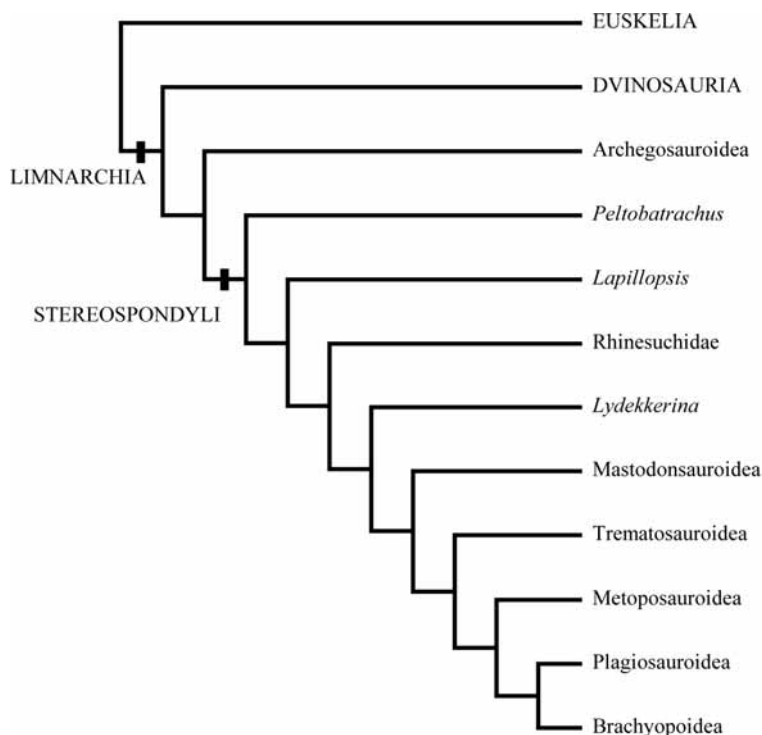


FIGURE 6. Phylogenetic relationships of major taxa within the Temnospondyli, after Yates and Warren (2000); Damiani, (2001).

while retaining an essentially immature morphology (McNamara, 1986). These stereospondyls commonly reach 2-3 metres in length, with the largest known being *Mastodonsaurus giganteus* at six metres (Schoch, 1999a). However, despite the apparently immature nature of the postcranial skeleton of many stereospondyls, there is little data available on morphogenetic stages, excepting those of *Benthosuchus sushkini* (Bystrow and Efremov, 1940), *Mastodonsaurus giganteus* (Schoch, 1999a) 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 metres with the Early Triassic *Lystrorhynchus* (Smith and 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 and 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 our 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 morphogenetic stages.

## MATERIALS AND METHODS

### *Locality and Repository information*

All specimens examined are listed in Appendix 2, with repository, location and stratigraphic information.

### *Institutional abbreviations*

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

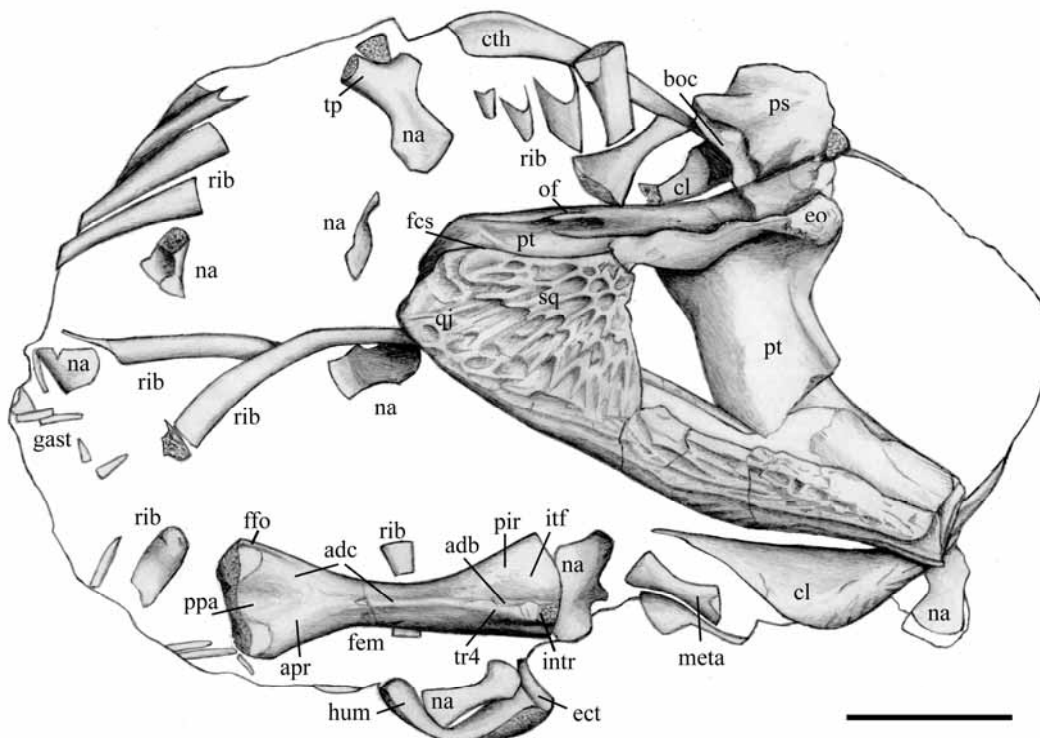
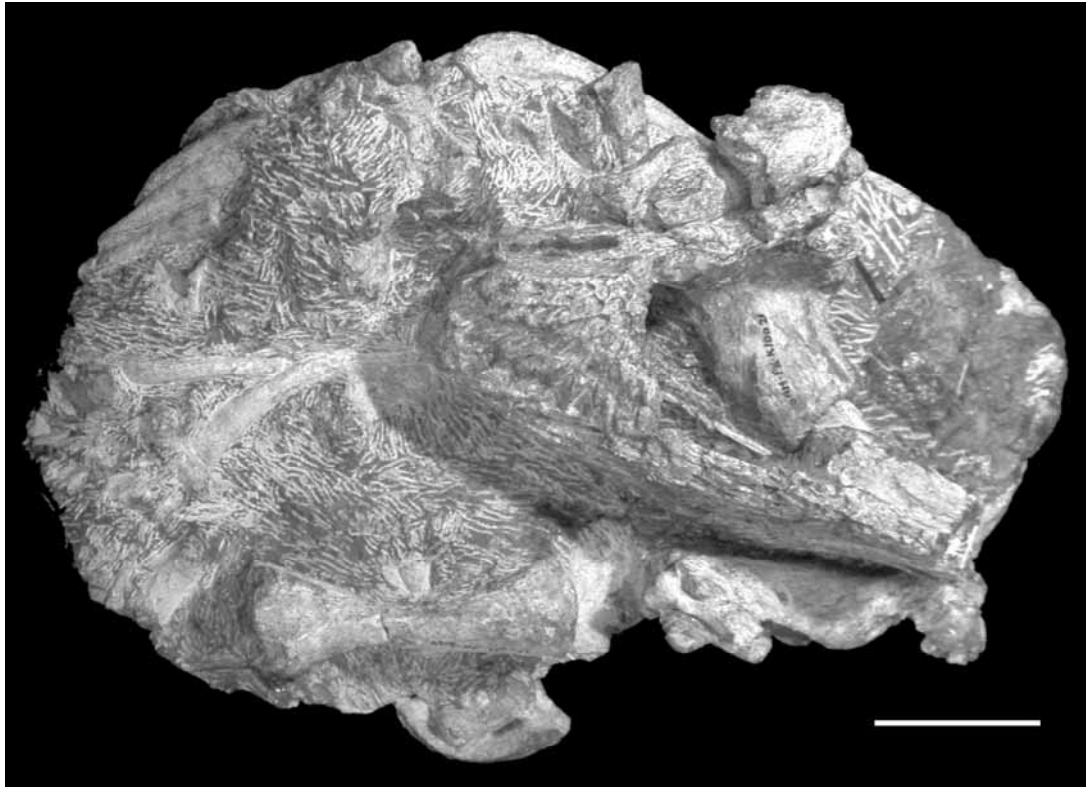


FIGURE 7. Dorsal view of SAM-PK-K10021. Abbreviations: adb, adductor blade; adc, adductor crest; apr, anterior popliteal ridge; boc, basioccipital; cl, clavicle; cth, cleithrum; ect, ectepicondyle; eo, exoccipital; fcs, falciform crest of squamosal; fem, femur; ffo, fibula fossa; gas, ventral scutes; hum, humerus; intr, internal trochanter; itf, intertrochanteric fossa; meta, metapodial; na, neural arch; of, otic flange; pir, posterior intertrochanteric ridge; ppa, popliteal area; ps, parasphenoid; pt, pterygoid; qj, quadratojugal; sq, squamosal; tp, transverse process; tr4, fourth trochanter. Scale bar = 50mm.

### *Methods*

Staff at the South African Museum initially prepared SAM-PK-K10021, further preparation was undertaken using an Aro aircscribe. Small cracks were repaired with Cyanoacrylate (Paleobond). Terminology in descriptions follows Romer (1922), Bystrow and Efremov (1940) and Coates (1996), unless otherwise noted.

### DESCRIPTION

The dorsal surface of SAM-PK-K10021 (Figure 7) consists of the posterior right side of a skull and mandible, some disarticulated neural arches and intercentra, articulated ribs, scattered ventral scutes, a ventrally exposed femur, the dorsal processes of both clavicles, and both humeri. The ventral surface (Figure 8) consists of an articulated interclavicle, clavicles, humeri, partly articulated ribs, ventral scutes, 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, 2001a).

Assignment 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 and Rubidge, 2003), so it was considered that assignment of SAM-PK-K10021 to a genus was unwise until such revision is undertaken.

### *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 scutes. On the ventral surface, the pectoral girdle and ventral scutes 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 neorhachitinous (Romer, 1947), in that the intercentrum is the dominant vertebral element. No pleurocentra, sacral vertebrae, or haemal arches were found.

### *Neural arch*

The neural spines (Figure 7) 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

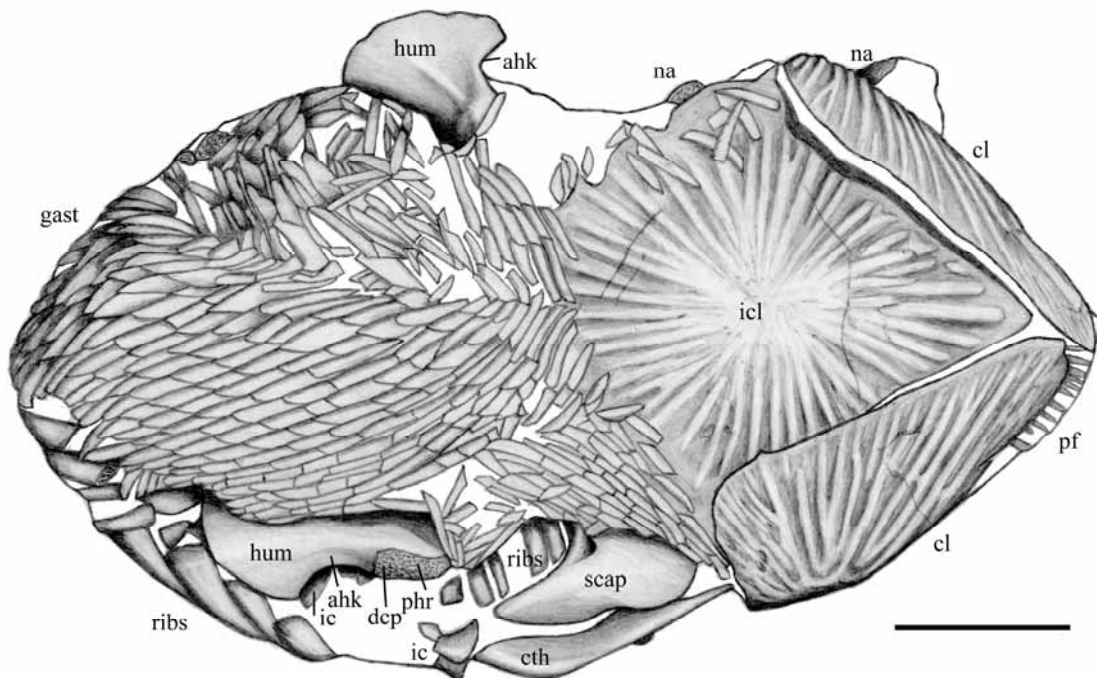
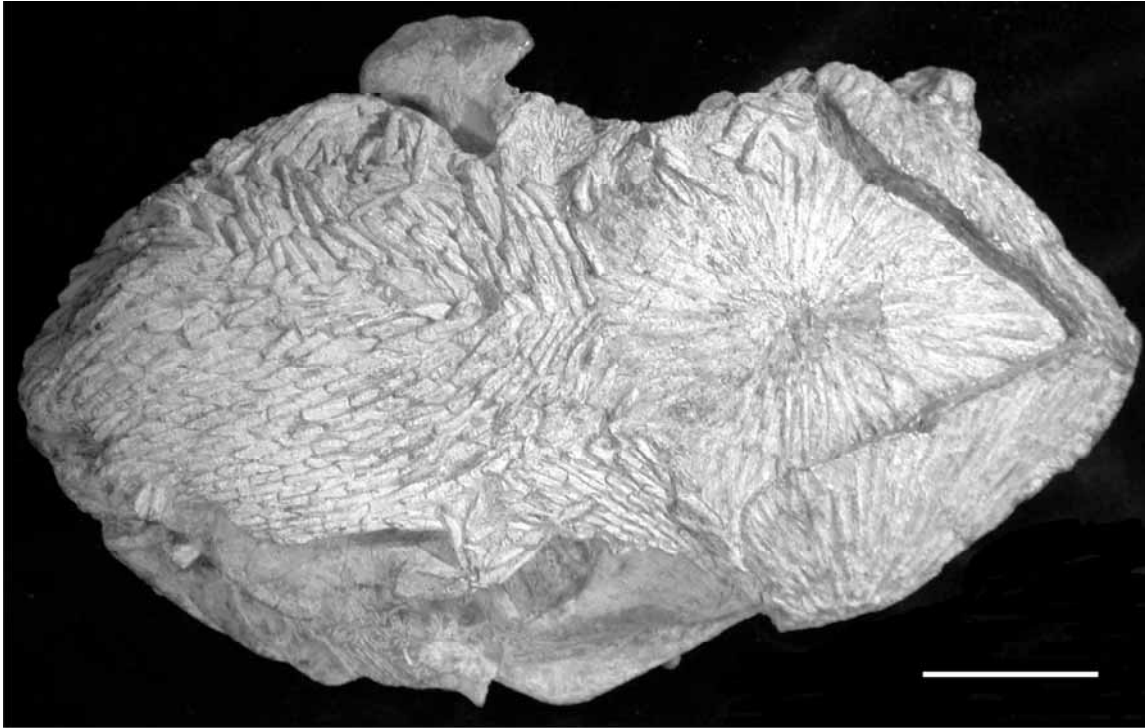


FIGURE 8. Ventral view of SAM-PK-K10021. Abbreviations: ahk, anterior humeral keel; cl, clavicle; cth, cleithrum; dpc, deltopectoral crest; gas, ventral scutes; hum, humerus; ic, intercentrum; icl, interclavicle; na, neural arch; pf, pectinate fringe; phr, proximal humeral ridge; scap, scapula. Scale bar = 50mm.

antero-ventral to posterodorsally inclined diapophyses. A supraneural canal does not penetrate the neural arch.

#### *Intercentrum*

Thin, crescentric intercentra (Figure 8) 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*

Most of the ribs (Figure 7, Figure 8) are only partially exposed. The visible ribs are long and thin, oval in cross section, distally expanded and gently ventrally curved. None of the exposed ribs bears an uncinat process, however the thoracic ribs that are most likely to bear uncinat processes (Moulton, 1974; Schoch, 1999a) are not exposed.

#### *Interclavicle*

The coarsely ornamented main body of the interclavicle (Figure 8) 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. Postero-ventrally, the border of the interclavicle is flat rather than recessed to fit the ventral scutes; the ornament fades out where the ventral scutes overlap. Where the edges of the interclavicle are exposed, they gradually become thinner until they taper out, so that no delimiting edge is discernable. A small portion of the anterior border extends beyond the front of the left clavicle as a thin and delicate pectinate fringe.

#### *Clavicle*

Both articulated clavicles (Figure 8, Figure 9.1) have the medial edges displaced slightly ventrally. Each clavicle has a coarsely ornamented, antero-posteriorly 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 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.

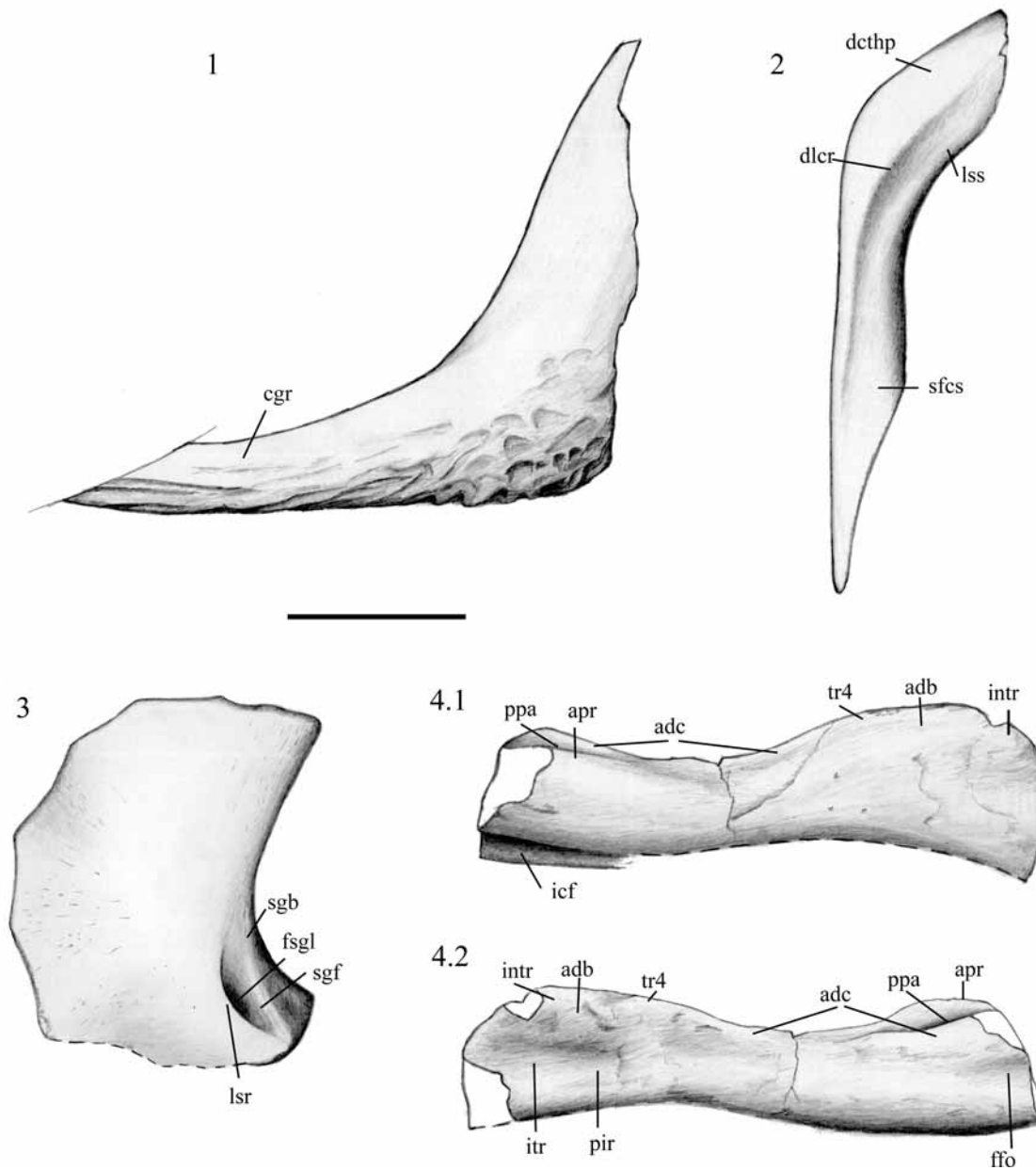


FIGURE 9. Postcranial elements of SAM-PK-K10021. 1, lateral view of left clavicle; 2, lateral view of left cleithrum; 3, lateral view of left scapulocoracoid; 4.1, medial view of right femur; 4.2, lateral view of right femur. Abbreviations: adb, adductor blade; adc, adductor crest; apr, anterior popliteal ridge; cgr, clavicular groove; dcthp, dorsal cleithral process; dlcrl, dorsolateral cleithral ridge; ffo, fibula fossa; fsgl, supraglenoid foramen; icf, intercondylar fossa; itr, intertrochanteric fossa; intr, internal trochanter; lsr, lateral supraglenoid ridge; lss, suprascapular lamina; pir, posterior intertrochanteric ridge; ppa, popliteal area; sfcsl, scapular flange of cleithral shaft; sgb, supraglenoid buttress; sgf, supraglenoid fossa; tr4, fourth trochanter. Scale bar = 25 mm.

### *Cleithrum*

The articulated left cleithrum (Figure 9.2) 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, passing 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*

The poorly ossified, articulated left scapulocoracoid (Figure 9.3) lacks both the dorsal scapular blade and the coracoid portion. The dorsally rounded scapular portion has shallow depressions along the antero-dorsal 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 scutes cover much of the area ventral to the scapular blade.

### *Humerus*

Both articulated humeri (Figure 8) are of the standard waisted temnospondyl form, with the proximal and distal ends set at right angles to each other. Overall, it 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*

A single disarticulated metapodial (Figure 7) 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 manus or pes.

### *Femur*

The disarticulated slender right femur (Figure 7, Figure 8, Figure 9.4) 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 on the anterior side of 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 scutes*

Ventral scutes (dermal ossicles) (Figure 8) 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 scutes 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 scutes form 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 scutes preserved in each row. Additional ventral scutes cover the flanks anterior to the humerus. The rows of these ventral scutes parallel the posterior border of the interclavicle and clavicles, meeting the main body of the ventral scutes at the level of the proximal insertion of the humerus. Unfortunately, the posterior and lateral borders of the ventral scute field are not preserved. The medial ends of the ventral scutes expand slightly where they overlap along the midline, although there are no distinct median ventral scutes. 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 Archegosauroidae and Stereospondyli (sensu Yates and 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 Archegosauroidae, 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 scutes 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, 1998a) and *Gerrothorax* spp. (Nilsson, 1946a; Hellrung, 2003). The arrangement in SAM-PK-K10021, whereby the anterolaterally directed rows of ventral scutes meet the posterolaterally directed rows at the level of the humerus, is again similar to that of other temnospondyls and basal tetrapods. The ventral scutes are similar in shape and arrangement to those described by Findlay (1968) in *Uranocentrodon senekalensis*. One of the specimens of *Uranocentrodon senekalensis* (TM75) has the pectoral girdle prepared from the dorsal surface, showing a comparable arrangement of ventral scutes around the pectoral girdle. Findlay did not comment on the arrangement of the ventral scutes 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 scutes are common in the Archegosauroida, particularly *Archegosaurus decheni* (Meyer, 1857), *Cheliderpeton vranji* (Werneburg and Steyer, 2002), *Sclerocephalus* spp. (Broili, 1926; Boy, 1988; Lohmann and Sachs, 2001), and *Platyoposaurus stuckenbergi* (Konzhukova, 1955b). The apparent absence of dorsal scales or dermal 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 and Warren, 2005) and not seen in more derived stereospondyl taxa. Unlike the intercentra of many stereospondyls (Warren and 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 developing 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 *Uranocentrodontidae* because they retained the exposure of the opisthotic in the paraoccipital bar. More recently, Shishkin and 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 senekalensis* [*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 putterilli* which is from the Early Triassic *Lystrosaurus* Assemblage Zone (Shishkin and Rubidge, 2000), just above the level of SAM -PK-K10021. This could imply that the Rhinesuchidae were evolving reduced postcranial skeletons over time, and 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 and Rubidge, 2000), has associated postcranial material although this remains undescribed.

Surprisingly, SAM-PK-K10021 has a poorly ossified postcranial skeleton, more like that of some of the later stereospondyls and *Broomistega putterilli*, making an interesting contrast to the robust and well ossified postcranial skeleton of *Uranocentrodon senekalensis* and M460. This implies 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, 2003), the morphogenetic 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 morphogenetic 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 and Efremov, 1940) and *Mastodonsaurus giganteus* (Schoch, 1999a). 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 giganteus*, a correlation exists between size and degree of ossification; only the largest specimens become comparatively well ossified (Schoch, 1999a). While an increase in ossification correlates with size in *Benthosuchus sushkini*, none of the specimens shows the same degree of ossification as the largest *Mastodonsaurus giganteus*. In *Lydekkerina huxleyi* (Pawley and Warren, 2005) the postcranial skeleton is comparable in its degree of ossification to that of *Uranocentrodon senekalensis*, although it is much smaller. There is no doubt that the specimens of *Lydekkerina huxleyi* 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 huxleyi* to that of *Uranocentrodon senekalensis* 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 huxleyi* 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 (Figure 9.3) is again comparable with that of the medium-sized specimens of *Mastodonsaurus giganteus* (Schoch, 1999a). The coracoid plate of *Mastodonsaurus giganteus* is separate from the scapular blade until late in morphogenesis, when it fuses to form a scapulocoracoid similar to that of *Uranocentrodon senekalensis* and *Lydekkerina huxleyi*. In other mastodonsaurids such as *Benthosuchus sushkini* 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 morphogenesis in the archegosaur *Sclerocephalus haeuseri* (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 and Snell, 1991), SAM-PK-K10021 retains the plesiomorphic, ventrally enclosed supraglenoid foramen seen in *Uranocentrodon senekalensis* and *Lydekkerina huxleyi*.

The humerus of SAM-PK-K10021 (Figure 8) is comparable in morphology with that of medium-sized specimens of *Mastodonsaurus giganteus* and *Benthosuchus sushkini*, 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 senekalensis*, *Mastodonsaurus giganteus*, and *Benthosuchus sushkini*, and in *Lydekkerina huxleyi*, 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 (Figure 7, Figure 9.4), with its slender outline, reduced adductor crest, and ill-defined fourth and internal trochanters, is consistent with the immature specimens of *Mastodonsaurus giganteus* and *Benthosuchus sushkini*. In immature specimens of *Benthosuchus sushkini* the internal trochanter lacks a distinct process so that it is not distinct from the proximal articulation surface, similar to that of SAM-PK-K10021. In mature mastodonsaurids, and in *Uranocentrodon senekalensis* and *Lydekkerina huxleyi*, 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 senekalensis* and *Lydekkerina huxleyi*.

In summary, the postcranial skeleton of SAM-PK-K10021 displays morphogenetic characteristics consistent with that of the medium-sized specimens of *Mastodonsaurus giganteus* and *Benthosuchus sushkini*, whereas the postcranial skeletons of *Uranocentrodon senekalensis* and M460 are most similar to the largest specimens of *Mastodonsaurus giganteus*. The undescribed postcranial skeleton of *Broomistega putterilli* BP/1/3241 is most consistent with the smallest specimens of *Mastodonsaurus giganteus* and *Benthosuchus sushkini*. SAM-PK-K10021 most likely represents the immature condition for the rhinesuchid postcranial skeleton, with *Uranocentrodon senekalensis* representing the mature morphology and *Broomistega putterilli* 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 morphogenetic 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 putterilli* BP/1/3241 is one of three specimens considered by Shishkin and Rubidge (2000) to be paedomorphic adults. *Broomistega putterilli* BP/1/3241, with a midline skull length of 75mm is substantially smaller than the largest specimen, TM 184, with an estimated midline skull length of 110mm. It is reasonable to assume that specimen BP/1/3241 represents an immature individual rather than a paedomorphic adult.

#### *Paedomorphism 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 morphogenetic 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 and 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 and Warren, 2000; Ruta et al., 2003) 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 impossible to determine the morphogenetic 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 morphogenetic stages for comparison with apparently less well-developed taxa.

Well-ossified taxa are the most likely to display the greatest development of morphogenetic potential. Members of the Euskelia such as *Eryops megacephalus* (Cope, 1888; Case, 1911a; Romer, 1922; Miner, 1925; Moulton, 1974) and *Acheloma cumminsi* (*Trematops milleri*) (Williston, 1909a; 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 a complete fully ossified carpus and tarsus. 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 proposed by

Pawley and Warren (2002). This interpretation contradicts current understanding of basal tetrapod relationships (Ruta et al., 2003).

If members of the Euskelia (e.g. *Eryops megacephalus* and *Acheloma cumminsi*) represent the fully ossified and most morphogenetically mature condition then, by comparison, many 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 morphogenetic stages of other temnospondyls that 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. Peramorphic processes do, however, occur in the postcranial skeletons of temnospondyls, as features such as the anterior flange of the clavicle seen in mastodontosaurids such as *Eryosuchus (Parotosaurus) pronus* (Howie, 1970) are not present in the morphogenetic stages of more plesiomorphic temnospondyls, and are obviously derived.

#### *Paedomorphosis and implications for cladistics*

Some cranial characters previously used for classification purposes have been shown to change with morphogenesis in *Watsonisuchus aliciae* (Warren and Hutchinson, 1990b; Warren and Schroeder, 1995). Steyer (2000) demonstrated that using morphogenetically 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 and Warren, 2000; Ruta et al., 2003), it is important that these 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 morphogenesis 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 and Warren, 2000; Ruta et al., 2003) 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 morphogenetic potential rather than convergent evolution. Careful analysis of growth series is necessary to determine other characters affected by morphogenesis. 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 morphogenetic stage of a taxon that retains a paedomorphic postcranial morphology throughout its life. As a rhinesuchid, SAM-PK-K10021 contributes to our knowledge of morphogenetic 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 morphogenesis is cautioned.

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