The Postcranial Skeleton of the Early Triassic Parareptile Sauropareion anoplus, with a Discussion of Possible Life History

Authors: MacDougall, Mark J., Modesto, Sean P., and Botha-Brink, Jennifer

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MARK J. MACDOUGALL, SEAN P. MODESTO, and JENNIFER BOTHA-BRINK

The skeletal anatomy of the Early Triassic (Induan) procolophonid reptile *Sauropareion anoplus* is described on the basis of three partial skeletons from Vangfontein, Middelburg District, South Africa. Together these three specimens preserve the large majority of the pectoral and pelvic girdles, articulated forelimbs and hindlimbs, and all but the caudal portion of the vertebral column, elements hitherto undescribed. Our phylogenetic analysis of the Procolophonoidea is consonant with previous work, positing *S. anoplus* as the sister taxon to a clade composed of all other procolophonids exclusive of *Coletta seca*. Previous studies have suggested that procolophonids were burrowers, and this seems to have been the case for *S. anoplus*, based on comparisons with characteristic skeletal anatomy of living digging animals, such as the presence of a spade-shaped skull, robust phalanges, and large unguals.

Mark J. MacDougall [mark.macdougall@utoronto.ca], Department of Biology, Cape Breton University, Sydney, Nova Scotia, B1P 6L2, Canada and Department of Biology, University of Toronto at Mississauga, 3359 Mississauga Road, Ontario, L5L 1C6, Canada;
Sean P. Modesto [sean_modesto@cbu.ca], Department of Biology, Cape Breton University, Sydney, Nova Scotia, B1P 6L2, Canada;
Jennifer Botha-Brink [jbotha@nasmus.co.za], Karoo Palaeontology, National Museum, P.O. Box 266 and Department of Zoology and Entomology, University of the Free State, Bloemfontein, 9300, South Africa.

Introduction

The Parareptilia is one of the great success stories of reptilian evolution during the Palaeozoic. The clade spawned fully aquatic forms (mesosaurs), herbivores (bolosaurids, pareiasaurs, procolophonids), a facultatively bipedal runner (the bolosaurid *Eudibamus*), burrowers (procolophonids), small carnivores (the acleistorhinid *Colobomycter pholeter*), insectivores (the acleistorhinid *Acleistorhinus pteroticus*; millerettids; owenettids), and unusual forms of debatable habitus (the millerosaur *Eunotosaurus africanus*; lanthanosuchids). As the only group of parareptiles to have survived the end-Permian mass extinction, Procolophonoidea has received the most attention in recent years (Modesto et al. 2001, 2003; Tsuji and Müller 2009; Ruta et al. 2011). Recent descriptive work of South African material has importantly expanded the composition of Procolophonoidea (Gow 2000; Modesto et al. 2001, 2003, 2010; Reisz and Scott 2002; Cisneros 2008a), and collecting efforts in the Karoo Basin of South Africa and tree-based studies suggest that this group of reptiles suffered rela-

tively little extinction pressure across the Permo-Triassic boundary (Modesto et al. 2001, 2003; Botha et al. 2007; Tsuji and Müller 2009; Ruta et al. 2011).

Whereas three of the new Karoo procolophonoid species, *Coletta seca* (Gow 2000), "*Owenetta*" *kitchingorum* (Reisz and Scott 2002), and *Kitchingnathus untabeni* (Cisneros 2008a), are based on specimens collected decades earlier, the remaining three, *Sauropareion anoplus* (Modesto et al. 2001), *Saurodektes rogersorum* (Modesto et al. 2003), and *Phonodus dutoitorum* (Modesto et al. 2010), are based on specimens discovered in the course of recent fieldwork. Whereas the cranial anatomy of *S. anoplus* is now well known (Botha et al. 2007; Modesto and Damiani 2007; MacDougall and Modesto 2011), the postcranial skeleton is known primarily from the full description of the holotype (Modesto and Damiani 2007), which preserves only a few vertebrae, associated ribs, and appendicular elements. Botha et al. (2007) announced and briefly described a partial skeleton from a new locality (Vangfontein) in the same farming district (Middelburg) that produced the holotype. That skele-

ton, however, is much smaller and less ossified than the holotype, and is yet to be described. A recent visit to Vangfontein yielded two additional specimens that are assignable to *S. anoplus*. Importantly, one of these is a well-preserved skeleton that is larger than the specimen described by Botha et al. (2007).

The purpose of this paper is to describe the postcranial skeleton of the procolophonid *Sauropareion anoplus* using the new materials from Vangfontein. These specimens preserve considerably more of the postcrania than in the holotype (Modesto and Damiani 2007), and their description will make *S. anoplus* one of the best known procolophonids. The wealth of new information obtained from the description of these specimens justifies the undertaking of a new phylogenetic analysis of the Procolophonidae.

Institutional abbreviations.—BP, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa; NM, National Museum, Bloemfontein, South Africa; SAM, Iziko South African Museum of Cape Town, South Africa.

Material and methods

The new *Sauropareion anoplus* specimens (NMQR 3544 [Figs. 1, 2], NMQR 3556 [Figs. 3, 4], and NMQR 3602 [Figs. 5, 6]) exhibit a few minor differences from the holotype. We attribute the differences that are present to individual variation and to preservational differences. Most autapomorphies that are identified for *S. anoplus* (Modesto et al. 2001; Modesto and Damiani 2007) are preserved in these new specimens. They all lack a supinator process on their humeri, and also exhibit a posteroventral facial process of the quadratojugal, an apomorphy found in other procolophonids; however, *S. anoplus* is the only procolophonid found in the Lower Triassic of South Africa that possesses this feature. Although the specimens do not clearly exhibit deep occipital shelves on the parietals and the supratemporals, the lack of this emargination is likely a result of preservational differences and over-enthusiastic preparation. From this we can conclude that these new specimens can be assigned to *S. anoplus*.

All specimens of *Sauropareion anoplus* described here were originally preserved in nodules of hard mudstone that necessitated mechanical preparation. Initial preparation of the specimens was done by John Nyaphuli and Nthaopa Ntheri at the National Museum in Bloemfontein, South Africa. NMQR 3556 and NMQR 3544 were later further prepared by Jennifer Cooper at Cape Breton University (CBU) in Nova Scotia, Canada. Final preparation of all specimens was done by Nicola Wong Ken at the University of Toronto at Mississauga (UTM) and by the first author at UTM and CBU, respectively. The left humerus of NMQR 3602 was separated from the rest of the skeleton for histological analysis (Botha-Brink and Smith 2012); prior to sectioning, the humerus was partially prepared (a film of matrix was left on

Fig. 1. Procolophonid *Sauropareion anoplus* Modesto, Sues, and Damiani, 2001, from Lower Triassic Katberg Formation, Vangfontein, Middelburg District, South Africa; NMQR 3544. Interpretive drawing of skeleton in dorsal view. Areas without outlines represent impression. Arabic numbers indicate presacral vertebrae.

the distal dorsal surface), cast and duplicated, and a positive resin cast was positioned in place of the original humerus for photography. The prepared specimens were photographed using a digital SLR camera, the images were then imported into Adobe Illustrator CS4, and outline drawings were drafted from the images. The outlines formed the basis of the coquille drawings in Figs. 1–6.

Systematic palaeontology

Parareptilia Olson, 1947

Procolophonidae Lydekker in Nicholson and Lydekker, 1889

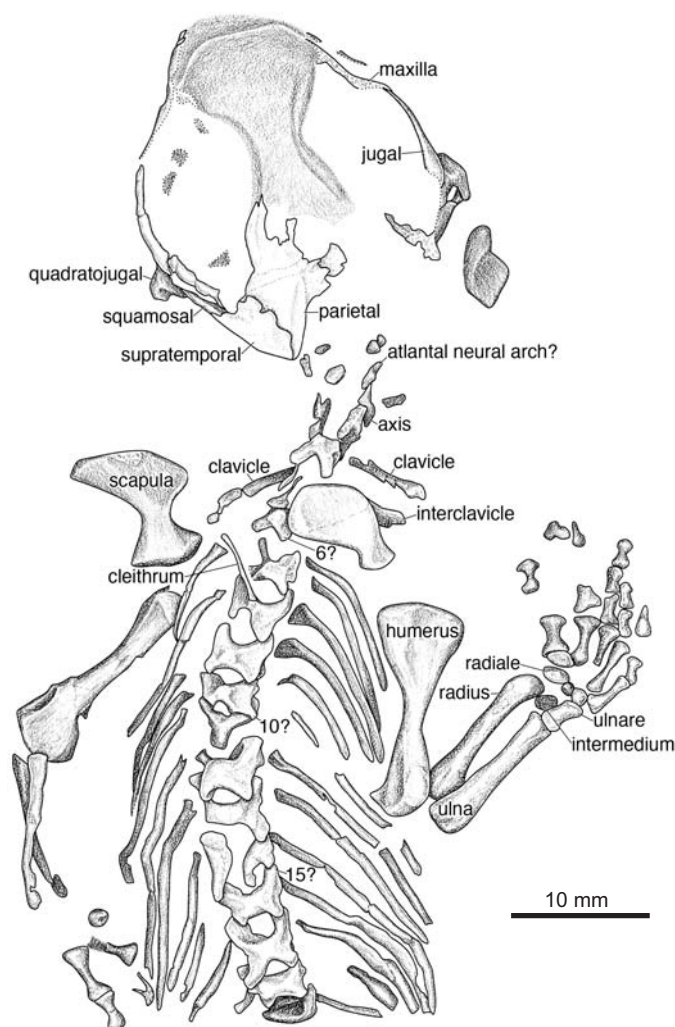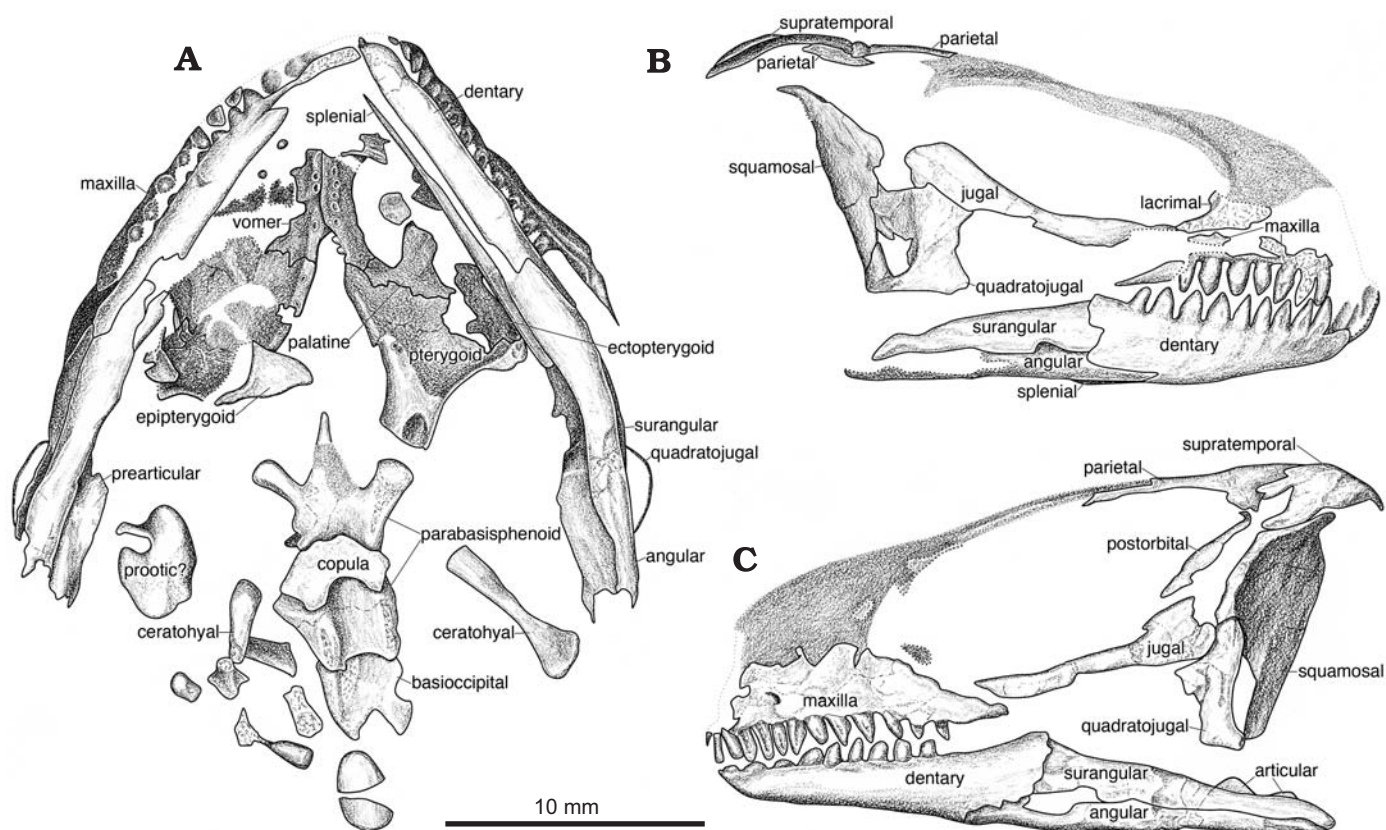Genus *Sauropareion* Modesto, Sues, and Damiani, 2001

Fig. 2. Procolophonid *Sauropareion anoplus* Modesto, Sues, and Damiani, 2001, from Lower Triassic Katberg Formation, Vangfontein, Middelburg District, South Africa; NMQR 3544. Interpretive drawings of skull in palatal (**A**), right lateral (**B**), and left lateral (**C**) views. Areas without outlines represent impression.

Type species: *Sauropareion anoplus* Modesto, Sues, and Damiani, 2001, Barendskraal, Middelburg District, Eastern Cape Province, South Africa; Early Triassic.

Sauropareion anoplus Modesto, Sues, and Damiani, 2001

Figs. 1–7.

Holotype: SAM-PK-11192, a partial skeleton.

Type locality: Barendskraal, Middelburg District, Eastern Cape Province, South Africa (Modesto et al. 2001; Modesto and Damiani 2007).

Type horizon: Uppermost strata of the Palingkloof Member of the Balfour Formation, Beaufort Group, Lower Triassic.

Referred specimens.—BP/1/5779, a partial skull from Barendskraal (MacDougall and Modesto 2011); NMQR 3544 (Figs. 1, 2), a partial, articulated anterior half of a skeleton preserved to the 15th presacral vertebra from Vangfontein, Middelburg District, Eastern Cape Province, South Africa; NMQR 3556 (Figs. 3, 4), partial juvenile skeleton with skull and various disarticulated postcranial elements from Vangfontein; NMQR 3602 (Figs. 5, 6) near complete juvenile skeleton from Vangfontein.

Diagnosis.—From Modesto et al. (2001) and Modesto and Damiani (2007): procolophonid characterized by deep occipital shelves on parietals and supratemporals, resulting in deep median embayment in posterior margin of skull table,

and absence of supinator process on humerus. The presence of a posteroventral facial process on the quadratojugal was identified as an autapomorphy by Modesto et al. (2001), but it may diagnose a more inclusive grouping within Procolophonidae (Modesto and Damiani 2007).

Description

The main focus of the description will be NMQR 3602 (Figs. 5, 6) as it is by far the most complete of the three specimens in this study. The other two specimens, NMQR 3544 (Figs. 1, 2) and NMQR 3556 (Figs. 3, 4), will be used to supplement the description of NMQR 3602 where applicable. Based on comparisons of the humeri, NMQR 3602 is approximately 80% the size of the holotype SAM-PK-11192. The remaining two specimens are considerably smaller than the holotype and NMQR 3602. Most of the centra are inaccessible in NMQR 3602, but the few that are exposed (e.g., presacral 5) are not fused to their respective neural arches, indicating immaturity. Similarly, SAM-PK-11192 was interpreted to be a juvenile by Modesto and Damiani (2007) because it exhibited open neurocentral sutures. Because NMQR 3544 and NMQR 3556 are smaller in size than the holotype, they too can be regarded as immature. The new material has also allowed for a composite skeletal reconstruction to be drafted (Fig. 7).

Skull.—The skull of *Sauropareion anoplus* has been previ-

ously described in detail by Modesto and Damiani (2007) and MacDougall and Modesto (2011). Accordingly, only areas of the skull offering new information will be considered in this study.

Skull roof: The posterior emargination of the parietals that was described in the holotype (Modesto and Damiani 2007) is not present in NMQR 3602 (Figs. 5, 6) or NMQR 3556 (Figs. 3, 4) to the degree that it is in the holotype (the posterior of the skull in NMQR 3544 [Figs. 1, 2] is not informative, because a large majority of it is not preserved). This lack of emargination may be attributable to ontogenetic changes, as the largest of the new specimens (NMQR 3602) is approximately 80% the size of the holotype. It is also possible that this difference is attributable to individual variation and preservational artefacts. The difference between NMQR 3602 and the holotype is most likely the result of preservational factors affecting both specimens. The posterior-most portion of the skull in NMQR 3602 appears to be crushed. The posterior of the skull in the holotype is also considerably damaged and this most likely makes the emargination appear more pronounced than it actually is. Additionally, there seems to be no emargination of the parietals in NMQR 3556, but it appears that the posterior of the skull roof of this specimen also suffers from preservational damage.

Braincase: The palatal view of NMQR 3544 (Fig. 2A) reveals that the parabasisphenoid and the basioccipital are preserved. The ventral surface of the parabasisphenoid (a fusion of the basisphenoid and the parasphenoid) can be clearly seen posterior to the elements of the palate. The parabasisphenoid is a large robust element that is partially obscured by the copula resting on its ventral surface. The anterior-most portion of the parabasisphenoid exhibits the cultriform process located medially. It is triangular in shape, being broad posteriorly and tapering off anteriorly as a sharp tip, extending forward into the interpterygoid vacuity to the level of the posterior portion of the pterygoid. The cultriform process found in *Sauropareion anoplus* is considerably longer than the very short processes of *Hypsognathus fenneri* (Sues et al. 2000) and *Leptopleuron lacertinum* (Säilä 2010a). Located on either side of the base of the cultriform process are the two blunt, basipterygoid processes, which extend anterolaterally. The posterior portion of the parabasisphenoid exhibits the cristae ventrolaterales, two ventral ridges that run anteroposteriorly along the dorsal surface; between the ridges is a smooth curved depression. Posterior to the parabasisphenoid is the basioccipital, which does not exhibit any areas of interest due to its poor preservation.

Mandible: MacDougall and Modesto (2011) estimated that the (complete) dentary of BP/1/5779 exhibited 12 or 13 tooth positions. The left mandible of NMQR 3556 (Fig. 4B) clearly shows that there are 15 tooth positions, all of which are occupied by conical homodont teeth. NMQR 3602 and NMQR 3544 do not offer any new substantial information about the mandible.

Hyoid apparatus: Of the three Vangfontein specimens, only the skull of NMQR 3544 has been prepared in ventral aspect and reveals the hyoid apparatus (Fig. 2A). The preserved hyoid apparatus offers some new information that differs slightly from what was found in the holotype (Modesto and Damiani 2007). The central element of the hyoid apparatus, the copula (Carroll and Lindsay 1985) or corpus hyoideum (Reisz and Scott 2002), is a boomerang-shaped element in ventral aspect, and on each side of the corpus hyoideum, curving laterally and posteriorly, are two processes. This shape differs from the bowtie-shaped corpus hyoideum described in the holotype (Modesto and Damiani 2007), probably because this specimen is smaller and thus likely to be ontogenetically younger than the holotype. The ceratohyal of *Sauropareion anoplus* was described as being asymmetric in the holotype, with the posterior end of the bone being a distinctly different shape from the anterior (Modesto and Damiani 2007); the left ceratohyal of NMQR 3544 (the right is missing its posterior end) is fully preserved and is indeed asymmetric. It exhibits a broad flat posterior end and a considerable narrower anterior end, similar in structure to the ceratohyal of "*Owenetta*" *kitchingorum* (Reisz and Scott 2002). This suggests that Modesto and Damiani (2007) were correct in proposing that the ceratohyal of the holotype may not have been completely ossified or was damaged during preparation, because the holotypic ceratohyal (Modesto and Damiani 2007: fig. 4) does not exhibit the broad posterior end seen in NMQR 3544.

Postcranial axial skeleton.—NMQR 3602 exhibits an articulated vertebral column consisting of a string of 27 vertebrae that begins with the axis and runs to the pelvic girdle (Fig. 5). Of these 27, six appear to be cervical vertebrae, although due to preservation and supportive matrix this number is tentative. The first 25 vertebrae are presacral, and the last two in the articulated series are sacral. It is likely that a third sacral is either obscured by overlying bone or not preserved, because procolophonids and owenettids possess three sacral vertebrae (Ivakhnenko 1979; Reisz and Scott 2002; deBraga 2003). Both the axis and atlas are present, but the atlas is not fully exposed, being partly obscured by the supportive matrix of the skull. The atlas brings the presacral vertebrae count up to 26, which is comparable to the 27 presacral vertebrae present in *Procolophon trigoniceps* (deBraga 2003). The remaining two posterior-most articulated vertebrae are clearly sacral based on the short, partially damaged sacral ribs, which can be seen on the left side. Near the pelvis there are also two disarticulated caudal vertebrae partially exposed in either anterior or posterior aspect (exact orientation cannot be determined owing to disarticulation and poor preservation). There also appear to be two partial caudal ribs near the left ischium, but they are disarticulated and damaged. The vertebrae themselves are all similar in structure; they consist of rounded, robust neural spines, which curve dorsally and slightly posteriorly, comprising the dorsal third of the entire vertebrae. The anterior zygapophyses possess facets that are tilted slightly inward, contrary to the posterior zygapophyses, which have facets that are tilted slightly outward. The centrum and transverse processes cannot be seen in most
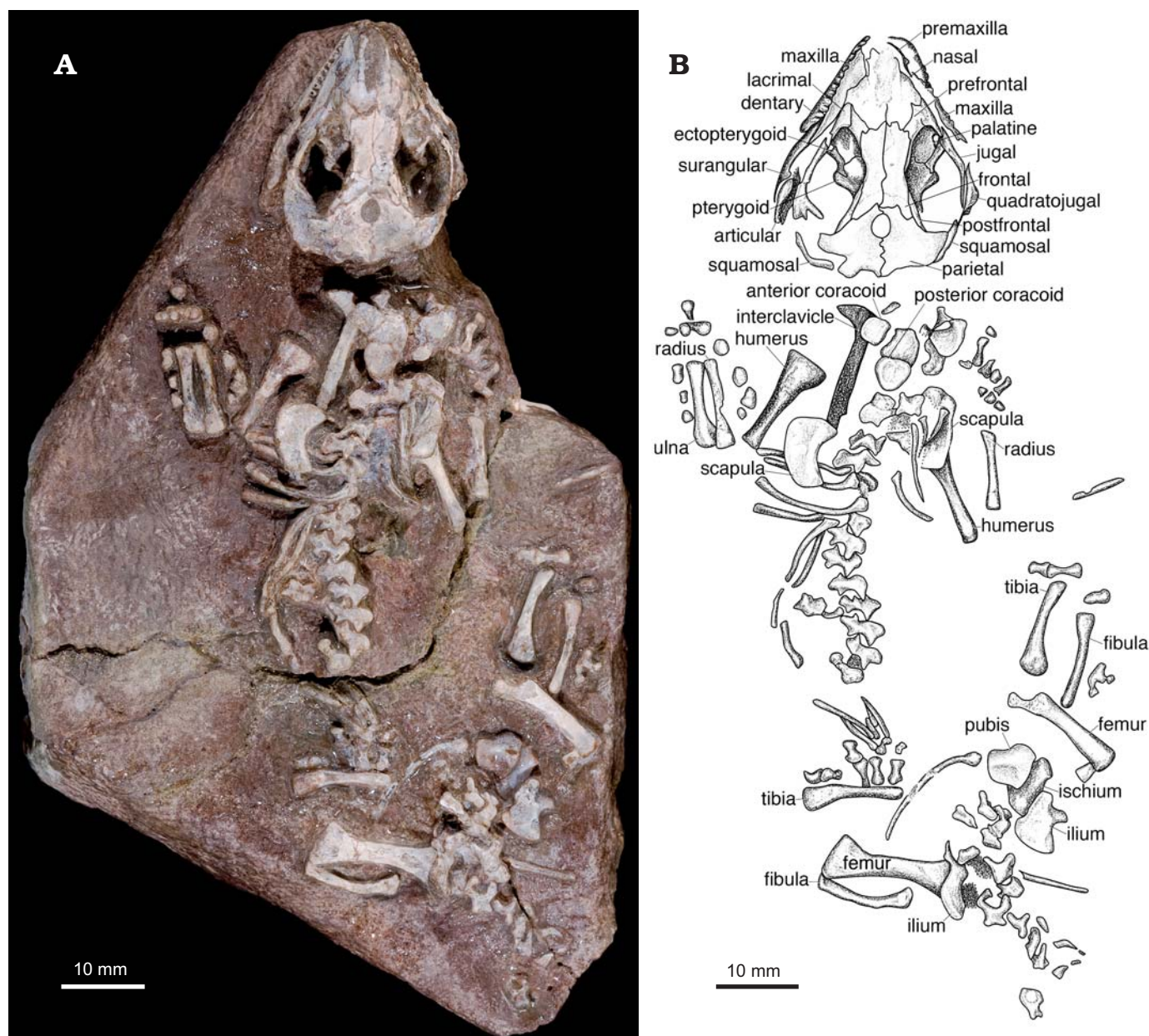
Fig. 3. Procolophonid *Sauropareion anoplus* Modesto, Sues, and Damiani, 2001, from Lower Triassic Katberg Formation, Vangfontein, Middelburg District, South Africa; NMQR 3556. Photograph of skeleton in dorsal view (**A**) and interpretive drawing of skeleton in dorsal view (**B**). Areas without outlines represent impression.

of the vertebrae, because they are preserved in dorsal view with the ventral portion being embedded in the matrix; however, the fifth presacral vertebra clearly exhibits the anterior portion of the centrum. Additionally, the two disarticulated caudal vertebrae are oriented in a manner that exposes part of either their anterior or posterior surface, allowing for part of their centra to be exposed. The exposed centra are robust, spool-shaped structures with a slight circular depression on their ends.

The majority of the preserved ribs of NMQR 3602 are found articulated with vertebrae; the presacral ribs are slender, pointed elements that possess a posterior curvature. There are 15 ribs preserved on the left side of the vertebral column and

13 ribs on the right; the anterior-most and posterior-most ribs are short, with the ribs between being significantly longer. It appears that most of the cervical ribs are not preserved or are covered by supportive matrix; however, the right anterior-most disarticulated rib would have likely articulated with the seventh presacral vertebra, which is the posterior-most cervical. The large majority of the remaining ribs are associated with dorsal vertebrae. However, the two sacral vertebrae also show their much shorter sacral ribs, which are visible only on the left side. The proximal ends of the presacral ribs are not exposed (being overlapped by the vertebrae or supportive matrix) and cannot be accessed in NMQR 3602; however, NMQR 3556 clearly exhibits the heads of several of its dis-
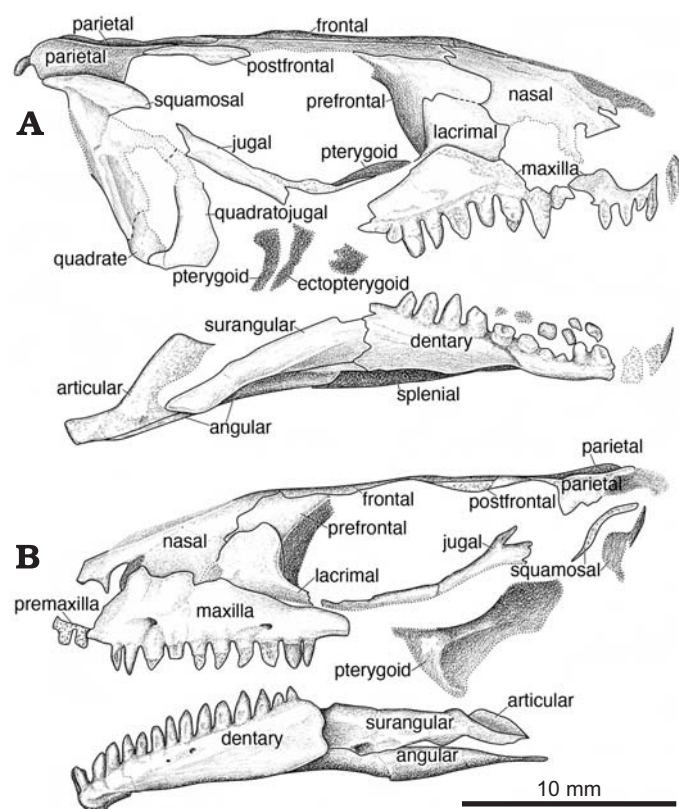
Fig. 4. Procolophonid *Sauropareion anoplus* Modesto, Sues, and Damiani, 2001, from Early Triassic Katberg Formation, Vangfontein, Middelburg District, South Africa; NMQR 3556. Interpretive drawings of skull in right lateral view (**A**) and left lateral view (**B**). Areas without outlines represent impression.

articulated ribs (Fig. 3). Each head is triangular in outline, being most broad proximally and narrowing distally, which eventually transitions to the more gracile body. The head clearly shows that the ribs are holocephalous. The bodies of the ribs possess a gentle posterior curvature that gives the ribs their shape. The sacral ribs are much shorter than even the smallest of the preserved presacral ribs; they are short robust elements fused directly to the sacral vertebrae. In NMQR 3602 the relatively short size of even the longest presacral ribs compared to the glenoid acetabular distance suggests that the trunk of *Sauropareion anoplus* was not as robust as some of its relatives. DeBraga (2003) estimated that *Procolophon trigoniceps* had a body width that was 90% the distance of its glenoid-acetabular length. However, it should be noted that the robust ribcage of *Procolophon trigoniceps* described by deBraga (2003) may not be accurate. Säilä (2010a) points out that deBraga does not justify the unusual attachment of ribs to the vertebral column shown in his reconstruction. *Sclerosaurus armatus*, another procolophonid, also possesses a large ribcage, with a width that is almost equivalent to the length of its glenoid-acetabular distance (Sues and Reisz 2008). In comparison, the rib cage of *S. anoplus* is approximately one third the length of the glenoid-acetabular distance, making it appear to be a rather gracile procolophonid, similar in stature to the

owenettid *"Owenetta" kitchingorum* (see Reisz and Scott 2002).

Pectoral appendicular skeleton.—The pectoral girdles of each specimen offer some unique information and together reveal the structure of this region in *Sauropareion anoplus*. Both scapulae are preserved in NMQR 3602 (Fig. 5); the scapula itself is a tall blade that curves for its entire length. The glenoids of the scapulae cannot be seen beneath matrix. Articulating with the dorsal surface of the right scapula is the clavicle, which is a flat curved element that is broad at its anterior end, becoming slimmer posterodorsally, and eventually terminating with a sharp point. The posterior tip of the clavicle articulates with the cleithrum, which is a narrow bone resembling an elongated grain of rice. Previous to this study the cleithrum has only been described in the Procolophonoidea twice: in the holotype of *S. anoplus* (Modesto and Damiani 2007) and in the owenettid *"Owenetta" kitchingorum* (Reisz and Scott 2002). As concluded by Modesto and Damiani (2007) and confirmed in this study, the cleithrum of *S. anoplus* is relatively shorter than the cleithrum of *"O." kitchingorum*. NMQR 3556 is the only one of the three specimens that has a clearly visible interclavicle (Fig. 3). This element is a T-shaped bone, composed of paired anterolateral processes (the right process is obscured by the overlying anterior coracoid) and a long, flat posterior process. The point at which the posterior process meets the posteromedial margin of the anterolateral processes is a gentle curve, which is common for procolophonoids (Cisneros 2008b). NMQR 3556 also preserves the two anterior coracoids, which are flat subcircular elements, and the posterior coracoid, which is much more triangular.

Both forelimbs of NMQR 3602 are present (Fig. 5), but the manus of the right forelimb is either not preserved or obscured by supporting matrix (Fig. 6C). The humerus of the left forelimb is a cast, as the original humerus was removed for histological analysis prior to this study (Botha-Brink and Smith 2012). The humerus is a robust element with a particularly stout proximal end and a smaller distal end separated by a hefty shaft. The distal end exhibits a flat trochlea and an ovoid capitulum, which articulate with the ulna and the radius, respectively. The proximal end is set at a distinct angle to the distal end, and clearly exhibits the entepicondylar foramen (or groove). As in the holotype (Modesto and Damiani 2007), there is no supinator process on the humerus.

The radius and the ulna of NMQR 3602 (Figs. 5, 6C) are relatively slender bones that are considerably more gracile and shorter and than the humerus, with the ulna being 20% shorter and the radius being 30% shorter. The ulna is also considerably more robust than the radius, being about twice as wide at the narrowest part of the shaft. The proximal end of the ulna is more expanded in comparison to its distal end because of the olecranon process, distinguishing it from the radius, which possesses proximal and distal ends of similar size. The shaft of the ulna is slightly bowed, unlike the radius, which is relatively straight. The distal ends of the ulna and the radius exhibit smooth, oval facets that articulate with
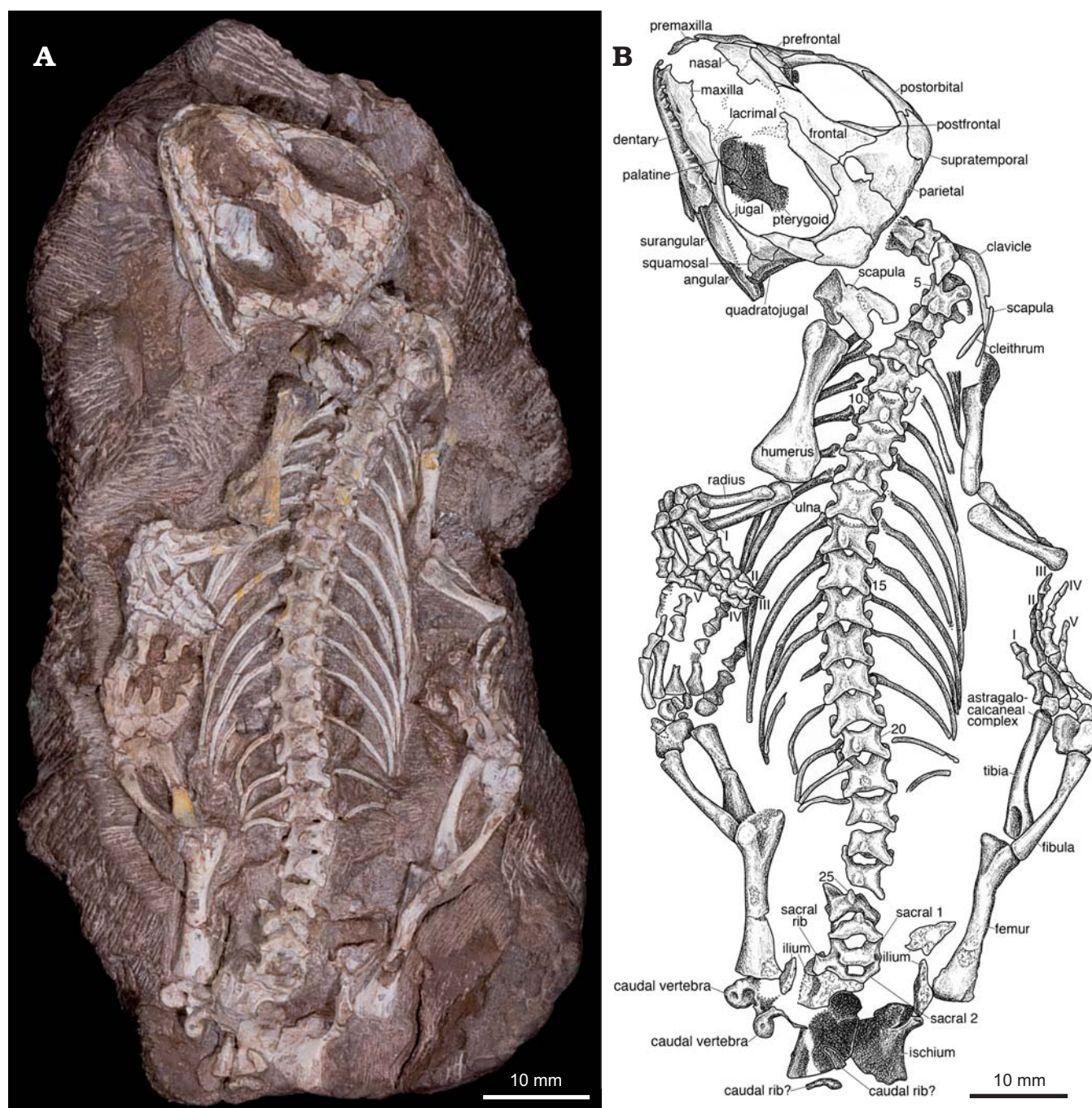
Fig. 5. Procolophonid *Sauropareion anoplus* Modesto, Sues, and Damiani, 2001, from Lower Triassic Katberg Formation, Vangfontein, Middelburg District, South Africa; NMQR 3602. Photograph of skeleton in dorsal view (**A**) and interpretive drawing of skeleton in dorsal view (**B**). Arabic numbers indicate presacral vertebrae. Roman numerals indicate digits.

the proximal carpals; NMQR 3544 clearly shows that the facet on the ulna articulated with the ulnare and the intermedium, and the facet on the radius for the radiale.

The right manus of NMQR 3602 is mostly covered by supportive matrix; only a portion of the intermedium is exposed (Fig. 6C). Fortunately the left manus is extremely well preserved; it lacks only the phalanges associated with digit I, and a few carpals. The carpus is partially obscured by the rest of the manus, which is twisted and preserved in ventral aspect. It

exhibits a distal row of two carpal bones and a proximal row of four elements, which are likely the radiale, the ulnare, the intermedium, and the pisiform, although this is not certain thanks to the manner in which the manus is preserved. The two distal carpals that are present are all that are visible of the five that are normally present. This manus possesses five well-preserved metacarpals; they are the longest bones of the manus, excluding the metacarpal of digit I, which is significantly shorter than the other metacarpals. The metacarpals clearly ar-
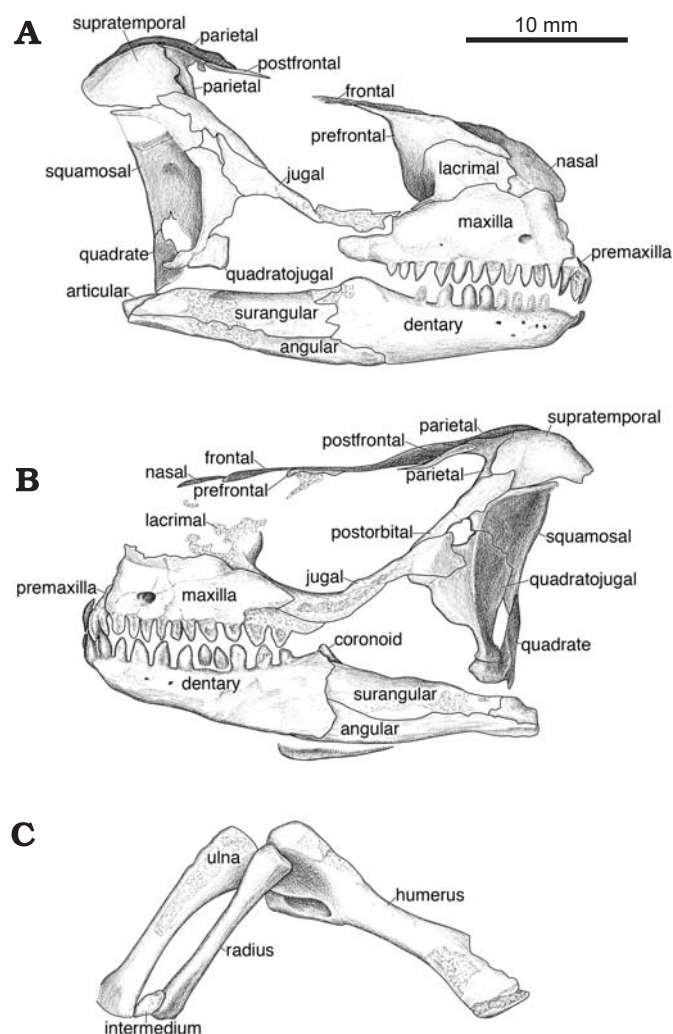
Fig. 6. Procolophonid *Sauropareion anoplus* Modesto, Sues, and Damiani, 2001, from Lower Triassic Katberg Formation, Vangfontein, Middelburg District, South Africa; NMQR 3602. Interpretive drawings of skull in right lateral (**A**) and left lateral (**B**) views, and right forelimb in medial view (**C**).

juvenile specimen. The remaining elements of the girdle are either not preserved, or lie below overlying bone and matrix.

The ilium in NMQR 3556 (Fig. 3) consists of a small gracile neck and a large, distinctive hatchet-shaped iliac blade, unlike the fan-shaped iliac blade in *Procolophon trigoniceps* (deBraga 2003). (It should be noted that one of the specimens in deBraga [2003] is not assignable to *Procolophon trigoniceps* [Modesto and Damiani 2007; Cisneros 2008c], and so was not used for comparisons in any part of our study). The portion of the acetabulum on the ilium cannot be seen as the left ilium is embedded in the matrix in its proper position with only its anterior edge visible, and the right ilium is exposed so that only its medial surface can be seen. The ischium of NMQR 3602 (Fig. 5) is a broad fan-shaped element, being most broad posteriorly and becoming smaller anteriorly; it contributes to the pubioischiadic plate of the girdle. It is generally similar in shape to the ischium of *Procolophon trigoniceps* (deBraga 2003) and *Leptopleuron lacertinum* (Säilä 2010a), a shape that is common among early amniotes (Säilä 2010a). The pubis of NMQR 3556 (Fig. 3) is not as well preserved as the ilia, and the only feature that stands out is the edge of the pubis that contributes to the pubioischiadic plate.

NMQR 3602 has extremely well preserved hind limbs (Fig. 5). Both are well articulated, excluding several bones of the left pes that are obscured by other bones or not preserved. The femur is a robust bone that is 9% longer than the humerus. It possesses broad proximal and distal ends, which are moderately expanded in comparison to the shaft. The femur differs from that of *Procolophon trigoniceps* (deBraga 2003) in possessing a smaller, less robust proximal end. The distal end clearly exhibits the medial and lateral condyles, separated by the intercondylar fossa. The proximal end does not appear to possess any informative features.

The tibia and the fibula of NMQR 3602 are not as long as the femur, with the tibia being 23% shorter and the fibula being 27% shorter. The tibia is the more robust of the two epipodials, being approximately twice as wide at the narrowest part of its shaft. The proximal end of the tibia is expanded and is divided into two articular surfaces for the femoral condyles. The more gracile fibula is a bowed element possessing expanded proximal and distal ends. The distal ends of both the tibia and the fibula articulate with the astragalus and the calcaneum.

The tarsus of NMQR 3602 is composed of astragalus, calcaneum, and several other small elements (Fig. 5). The rectangular astragalus and ovoid calcaneum are fused into a single large quadrangular element, separated by only a small line of contact posterior to the perforating foramen, suggesting that, as a juvenile, they were not yet completely fused. This astragalocalcaneal complex is not uncommon among procolophonids and their relatives, and has also been described in *Leptopleuron lacertinum* (Huene 1920; Säilä 2010a), pareiasaurs (Lee 1997), *Barasaurus besairiei* (Ketchum and Barrett 2004), *Sclerosaurus armatus* (Sues and Reisz 2008), *Macroleter poezicus* (Tsuji and Müller 2008), and *Emeroleter levis* (Tsuji et al. 2012).

ticulate with their respective phalanges, excluding the metacarpal of digit I. With the exception of the unguals, the phalanges are all similarly shaped elements, being short and robust with broadened proximal and distal ends; the unguals themselves are broad recurved elements, longer than the penultimate phalanges. NMQR 3602 exhibits a phalangeal formula of ?-3-4-5-3, which is comparable to that of other early amniotes including *Procolophon trigoniceps*, which has a phalangeal formula of 2-3-4-5-3 (deBraga 2003).

Pelvic appendicular skeleton.—The pelvic girdle of NMQR 3602 (Fig. 5) is preserved in such a way that the majority of it is only visible in dorsal aspect; the main portions of the girdle that can be identified are the left ischium, most of the right ischium (some bone is missing from the posterior edge), and the partially exposed left and right ilia. The pubis cannot be seen in NMQR 3602; however, the right pubis is partially preserved in NMQR 3556 (Fig. 3), it is found next to the disarticulated right ischium but is not fused to it, as this is a
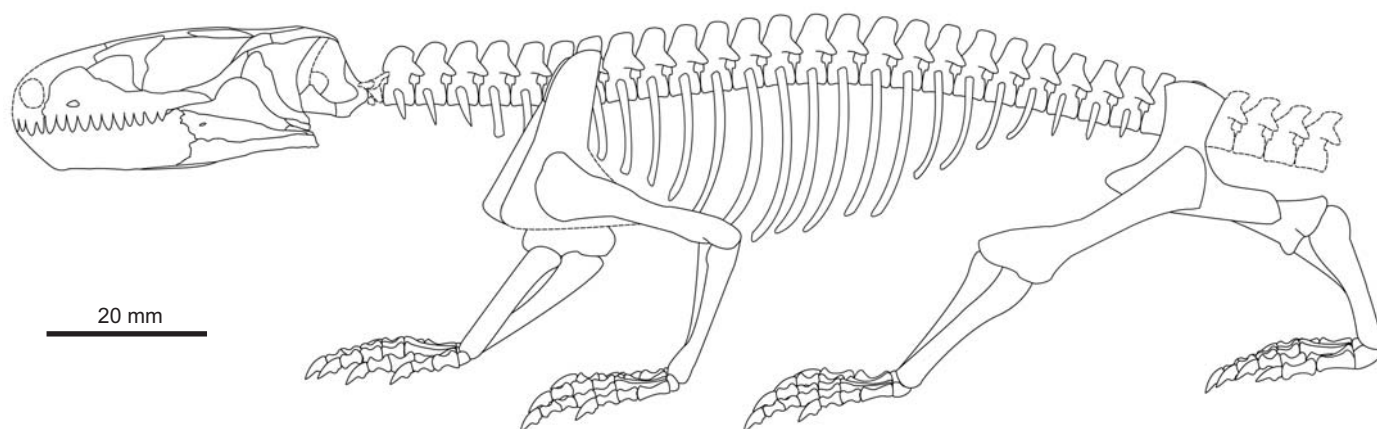
Fig. 7. Procolophonid *Sauropareion anoplus* Modesto, Sues, and Damiani, 2001, from Lower Triassic Katberg Formation, Vangfontein, Middelburg District, South Africa. Reconstruction of skeleton (excluding the unknown caudal vertebrae) based mainly on NMQR 3602, with additional information from BP/1/5779, NMQR 3544, and NMQR 3556.

Distal to the astragalocalcaneal complex are four sub-circular tarsal elements, which articulate with the metatarsals. These are the longest bones of the pes, being relatively long and gracile except for the metatarsal of pedal digit I, which is shorter. The more proximal phalanges are robust, and the more distal phalanges gracile. Each digit terminates with a recurved ungual, and the unguals are 40% longer than the penultimate phalanges. Large unguals have also been reported in other procolophonid taxa. The pedal unguals of *Procolophon trigoniceps* are 50% longer than the penultimate phalanges (deBraga 2003), and those of *Sclerosaurus armatus* almost twice as long (Sues and Reisz 2008). The ventral surface of the ungual bears a relatively prominent flexor tubercle near the proximal end of the bone; this can be seen best on digit III of the right pes. Based on information from both pedes of NMQR 3602, the phalangeal formula is 2-3-4-5-3?. This formula is common for early amniotes, and is the same as the pedal phalangeal count reported by deBraga (2003) for *P. trigoniceps*.

Stratigraphic and geographic range.—Barendskraal and Vangfontein farms in Middelburg District, Eastern Cape Province, Republic of South Africa, Palingkloof Member of the Balfour Formation and lower strata of the Katberg Formation, Beaufort Group, Karoo Supergroup, Induan portion of the *Lystrosaurus* Assemblage Zone, Lower Triassic.

Discussion

Phylogenetic analysis.—Recent studies of procolophonid phylogeny (Modesto et al. 2001; Botha et al. 2007; Modesto and Damiani 2007; Säilä 2008; MacDougall and Modesto 2011) have shown that *S. anoplus* is the sister taxon of a clade consisting of all procolophonids exclusive of *Coletta seca*. Although some studies have offered alternative viewpoints for the relationship of *S. anoplus* (Cisneros 2008a, b), they are a minority.

We were interested in discovering if the postcrania of the three specimens presented enough new anatomical information to help strengthen the phylogenetic position of *S. anoplus*. For this analysis we used the data matrix from MacDougall and Modesto (2011), which was modified from Cisneros' (2008a, b) data matrix. We further augmented this matrix by recoding several characters for *S. anoplus*. Based on NMQR 3602, NMQR 3556, and NMQR 3544, *S. anoplus* is recoded for characters 19, 20, 25, 26, 38, 41, 45, 46, 48, 49, 50, 52, 53, 54, 55 and 56 as 0, 0, 1, 0, 0, 1, 0, 0, 0, 1, 1, 1, 1, 1, 1, and 1, respectively. Following Cisneros (2008b), *Nyctiphruretus acudens* served as the outgroup. However, whereas Cisneros (2008b) originally coded *N. acudens* as having a squamosal that terminated at least as far ventrally as the quadratojugal, newer studies reveal that the squamosal does not extend as far ventrally as the quadratojugal at the tympanic notch (Säilä 2010b; Laura K. Säilä personal communication, 2011). Thus, the polarity of character 14 was reversed. The augmented data matrix is presented in Appendix 1.

The revised data matrix was imported into PAUP 4.0b10 (Swofford 2002) and subjected to a branch-and-bound search. The analysis found 45 optimal trees, each of which is 155 steps in length. In all trees, *Sauropareion anoplus* is the sister taxon of a clade comprising all other procolophonids exclusive of *Coletta seca*; the phylogenetic results are summarized in the strict consensus tree (Fig. 8). This supports previous phylogenetic work by Modesto et al. (2001), Botha et al. (2007), Modesto and Damiani (2007), Säilä (2008), and MacDougall and Modesto (2011) as far as the phylogenetic position of *S. anoplus* within Procolophonidae is concerned. The position of *S. anoplus* is supported unambiguously by character 54 (state 1), unguals that are at least 50% longer than the penultimate phalanges. The results of our analysis, however, are not particularly robust. A decay analysis, conducted using PAUP by relaxing parsimony a single step at a time and generating strict consensus trees until resolution was completely lost in the ingroup, revealed that most of the clades discovered in the analysis collapse with the addition of a single step.
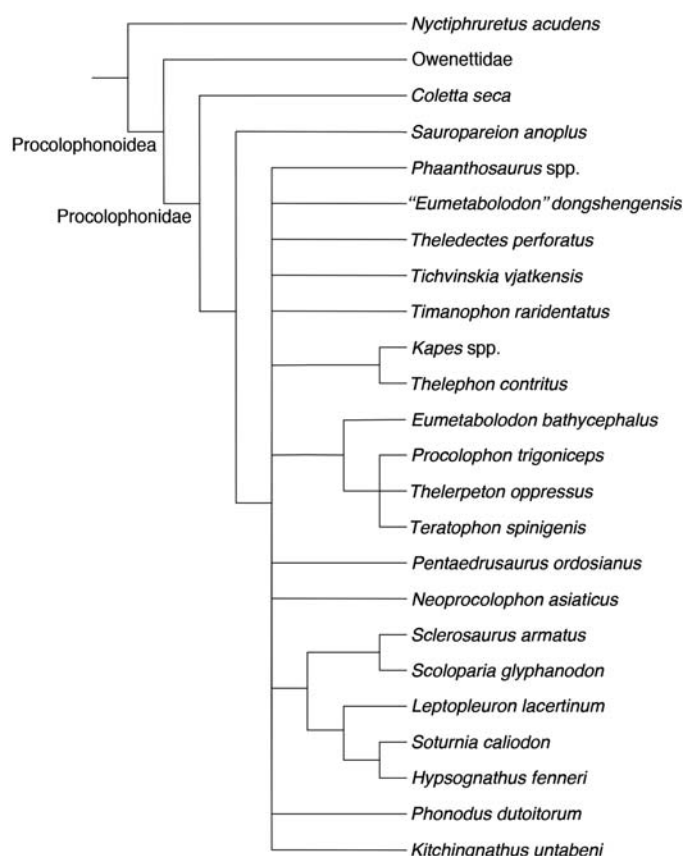
Fig. 8. Strict consensus of 45 optimal trees discovered in PAUP 4.0b10 analysis of a modified version of the data matrix from MacDougall and Modesto (2011). Tree length = 155, consistency index (CI) = 0.72, CI excluding uninformative characters = 0.71, rescaled CI = 0.56.

There is no phylogenetic resolution within Procolophonidae with two extra steps, and no resolution for the entire ingroup with four extra steps. A bootstrap analysis (100 replicates) was also performed; bootstrap support was below 75% for most clades, and was 65% for the clade consisting of *S. anoplus* and all other procolophonid taxa, exclusive of *C. seca*. However, low support values are a common problem in analyses of the Procolophonoidea owing to abundant missing data, and low support values for procolophonoid clades were also reported by Cisneros (2008b), Säilä (2008), Modesto et al. (2010), and MacDougall and Modesto (2011).

Life history interpretation.—Previous studies of *Sauropareion anoplus* (Modesto et al. 2001; Botha et al. 2007; Modesto and Damiani 2007; MacDougall and Modesto 2011) did not attempt to offer any interpretations on its possible lifestyle because of the former paucity of postcranial remains. However, the new specimens permit this to be rectified.

A common life history hypothesis in the literature (Groenewald 1991; Sues et al. 2000; deBraga 2003; Botha-Brink and Modesto 2007; Säilä 2010a) is that procolophonids were burrowers. This was first suggested when remains found within a burrow-cast were attributed to *P. trigoniceps* (James W. Kitching personal communication to Groenewald, 1991).

Hypsognathus fenneri was described as lacking cranial kinesis, a characteristic that may reflect a burrowing lifestyle (Sues et al. 2000). Burrowing behaviour was suggested for *Koiloskiosaurus coburgensis* by Botha-Brink and Modesto (2007), because the only three known specimens of this species are preserved together, dorsal up and in the same orientation, which led to the hypothesis that the arrangement makes sense if the three individuals were occupying a burrow. Lastly, *Leptopleuron lacertinum* possesses several morphological traits that are associated with a burrowing mode of life (Säilä 2010a).

The suggestion by Groenewald (1991) that *Procolophon trigoniceps* led a burrowing lifestyle was examined by deBraga (2003), who compared this procolophonid to a genus of living facultative burrowers, *Phrynosoma* (horned lizards). *Phrynosoma* is a genus of iguanid lizard, and although its members do not have a truly fossorial mode of life, they are capable of burrowing when threatened (Presch 1969). Several cranial and postcranial features of species of *Phrynosoma* were interpreted by deBraga (2003) as adaptations to burrowing: the skull is spade-shaped when viewed from above; it possesses a slight concavity dorsally, and a tendency to develop horns; the unguals are at least 33% longer than the penultimate phalanges; the broad rib cage is 50% of glenoid acetabular length.

However, there are some problems with deBraga's (2003) discussion of burrowing. For example, he is the only author to mention a broad rib cage as a characteristic of burrowers, whereas most discussions of postcranial digging adaptations make reference only to the girdles and the limbs (Hildebrand 1985; Lagaria and Youlatos 2006; Kley and Kearney 2007). Further, deBraga (2003) mentions that horns have some bearing on digging behaviour, but he does not say why. It has been reported that species of *Phrynosoma* use their horns as a predator deterrent (Presch 1969), and at least one species has been shown to develop elongated horns as a result of predation (Young et al. 2004). Thus, it seems unlikely that the horns of *Phrynosoma* are adaptations for burrowing. Lastly, the other problem with deBraga's (2003) comparison is that species of *Phrynosoma* live in desert environments, and they use many of the described skeletal characteristics for sand burrowing, which is different from burrowing in firmer soil (Mosauer 1932). In order to better determine if procolophonids were capable of burrowing, it is better to examine a wider range of extant digging reptiles and mammals.

Burrowing mammals and reptiles are characterized by various cranial modifications, and these depend on whether the skull is used for tooth digging or head-lift digging (Wake 1993; Samuels and Van Valkenburgh 2009). Tooth digging is associated with elongated procumbent incisors, deep skulls, short nasals, and massive, reinforced maxillae and dentaries (Wake 1993; Samuels and Van Valkenburgh 2009). These adaptations allow the teeth, particularly the incisors, to be used as the primary tool for digging through soil. Head-lift digging animals are characterized by elongated nasals, triangular spade-shaped skulls, and deep, anterodorsally slanted occipi-

tal regions (Wake 1993; Samuels and Van Valkenburgh 2009). These modifications allow the head to be used as a shovel, for lifting and packing down soil. Other animals use limb-based digging, in which the skull and the teeth usually play a supporting role. Postcranial adaptations of limb-based diggers are not always present; scratch-digging mammals often exhibit few, if any, adaptations (Hildebrand 1985), and the same proves true for limb-based digging reptiles (Kley and Kearney 2007). However, some digging mammals, such as moles, ground squirrels and aardvarks, possess extensive postcranial adaptations (Hildebrand 1985; Lagaria and Youlatos 2006), including enlarged unguals, a stout humerus shorter than the femur, an elongated acromion process of the scapula, and an elongated olecranon process on the ulna (Hildebrand 1985; Kley and Kearney 2007). These enlarged processes provide a larger area for muscle attachment, which aids in increasing the mechanical advantage of the limb and increases digging efficiency (Hildebrand 1985; Kley and Kearney 2007). Furthermore, some digging reptiles, such as the gopher tortoise, have short, robust phalanges, which helps to rigidify the manus, protecting it from the resulting forces of digging (Kley and Kearney 2007).

Sauropareion anoplus exhibits some of the above-mentioned skeletal modifications. Most noticeable is the prominent spade-shaped skull, clearly seen in NMQR 3602 (Fig. 5). This shape would make the skull of *S. anoplus* suitable for moving and packing soil, as accomplished by various extant mammals, such as the golden mole, marsupial mole, and mole-rat (Hildebrand 1985; Wake 1993). All of the teeth of *S. anoplus* are similar in size and shape, but the incisors are not enlarged, suggesting that it is unlikely *S. anoplus* practiced tooth digging. The limbs of *S. anoplus* are not heavily modified for digging, possessing none of the modifications that would increase the mechanical advantage of the limb, such as elongated acromion and olecranon processes. *Sauropareion anoplus* does, however, possess unguals that are relatively large (Fig. 5), being 40% longer than the penultimate phalanges, making them large enough for digging (Hildebrand 1985). The non-terminal phalanges are short and robust, a morphology that acts to rigidify both manus and pes and help them to endure the forces while digging (Kley and Kearney 2007). Although not exhibiting the extreme limb modifications seen in some mammals, this does not preclude burrowing abilities for *S. anoplus*, as many extant digging mammals and reptiles do not have extensively modified limbs.

The possibility that *S. anoplus* could burrow has implications for the clade as a whole; mapping burrowing behaviour onto the phylogeny of the Procolophonidae (Supplementary Online Material at http://app.pan.pl/SOM/app58-MacDougall_etal_SOM.pdf, SOM: fig. 1S) suggests that the most parsimonious origin for burrowing is one in which procolophonids evolved from a burrowing ancestor or developed burrowing behaviour early in their evolution (i.e., in the sister species of *Coletta seca*), rather than the less parsimonious suggestion that burrowing arose multiple times within the Procolophonidae.

Conclusions

We describe three specimens of the procolophonid *Sauropareion anoplus* from the Lower Triassic of South Africa, with focus on the postcranial region, which has never been thoroughly described. The new information gained from the description allowed us to update a recent procolophonoid data matrix from the literature, and to perform a new phylogenetic analysis of the Procolophonidae. This yielded 45 optimal trees, in each of which *S. anoplus* was found to be the sister taxon of all procolophonids except for the basal procolophonid *Coletta seca*, a topology consonant with the results of several recent studies. The new morphological information also allowed us to infer details about the possible palaeobiology of *S. anoplus*. As suggested for other procolophonids, *S. anoplus* was most likely a burrowing animal based on its spade-shaped skull, robust phalanges, and enlarged unguals.

Acknowledgements

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Appendix 1

Data matrix used in phylogenetic analysis. Uncertainty for character states is coded as follows: A = 0/1; B = 1/2; C = 0/2; D = 3/4; E = 2/3.

Nyctiphruretus	00000 00000 00000 0000? 00000 00000 000?0 00000 00000 00000 00000 0000
Owenettidae	00000 00000 10100 AA00? 00000 00000 010?0 00000 00100 00010 01001 0000
Coletta	00100 10000 00100 ???0? ???0? 10100 020?1 1??0? 0???? ????? ????? ????
Pintosaurus	20??? ????? ????? ???0? ???0? 20100 020?1 11??1 0???? ????? ????? ????
Sauropareion	????0 10100 20201 00000 ?1100 10000 020?1 11010 01??? 00?01 10111 11?1
Phaanthosaurus	10101 100?? B0??? ???1? ????0 20110 020?1 01?01 0???? ????? ????? ????
Eumetabolodon dongshengensis	????? 11??? ?0??? ???1? ????? ??000 030?1 ?1??0 0???? ????? ????? ????
Theledectes	????? ?1210 3020? 11??? ???0? 21010 030?? ??000 0???? ????? 00??? ????
Tichvinskia	10100 10210 30201 11010 00000 21110 13101 01?01 21?0? 0???1 101?0 1101
Timanophon	????? 10201 20211 0101? 010?0 2?110 13?01 01001 2???? ????? ????? ????
Kapes	1111? 11201 30201 1111? ??00 211B0 13101 0100C 1???? ????? ????? ???1
Thelephon	????? ?1201 2020? 111?? ???0? ??B10 1D101 ?10?? ????? ????? ????? ????
Eumetabolodon	21111 10210 20211 ??21? ?1000 21110 13101 01001 2?1?? ????? ????? ????
Procolophon	21111 10110 20211 11210 01000 21B00 B3101 A1001 21010 10111 10110 1101
Thelerpeton	2?111 ?0110 20211 1121? ?1?00 21110 1D101 01001 ????? ?011? ??11? ????
Teratophon	21111 1A110 E0211 1121? 01000 21110 13101 0100? ?1??? 10111 10??? ??01
Pentaedrusaurus	B1111 10212 30211 1111? ???11 21110 131?1 11001 B11?0 ?1111 1010? 110?
Neoprocolophon	??111 1?21C ?021? 21B1? ????1 ??B?? 1D1?1 1?0?? ????? ????? ????? ????
Sclerosaurus	????? ??310 ??32? 2????? ????? 3?B1? B31?? ????? ??110 10??1 1?101 111?
Scoloparia	????? 0031 3232? ??1?? ???1? 31100 2D10? ??01 2???? ????? ????? ??1?
Leptopleuron	?1100 02210 3132? 21211 1?111 3?111 B41?1 1201? 1??0? 1???? ????? ??0?
Soturnia	10??? 0???? ????? ???1? ???11 31111 24112 ??12 001?1 ????? ?0??? ????
Hypsognathus	?01A0 02310 32320 B1211 11111 31111 14112 1211? ??1?1 1???? ?0??? ??0?
Phonodus	1?111 11??? ?0000 ???1? ????? ??10 ?D0?1 121?? ????? ????? ????? ???1
Kitchingnathus	B0??0 10?00 C020? 110?? ???00 B0100 1200? ????1 2???? ????? ????? ????