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SHORT COMMUNICATION

# THE OSTEOLOGY AND AFFINITIES OF *ANOMOIODON LILIENSTERNI*, A PROCOLOPHONID REPTILE FROM THE LOWER TRIASSIC BUNDSANDSTEIN OF GERMANY

LAURA K. SÄILÄ, Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol, BS8 1JU, United Kingdom, Laura.Saila@bristol.ac.uk

The procolophonid reptile *Anomoiodon liliensterni* was found in the Triassic Bundsandstein of Thuringia, Germany, from the lower layers of the *Chirotherium* sandstone horizon in the summer of 1937 by a local bricklayer (Huene, 1939). *Anomoiodon* is represented by a specimen that consists of two closely associated skeletons that are preserved as natural molds in a block of medium-grained sandstone (Fig. 1A). These skeletons were described in 1939 from plaster casts, which revealed little detail (Huene 1939) and subsequently the original specimen was misplaced. This was unfortunate because interest in *Anomoiodon* has been renewed after suggestions that it might be the senior synonym of *Kapes* (Spencer and Storrs, 2002). The latter genus is known from several specimens from the Triassic of both Russia and the United Kingdom, where it has been used as an informal stratigraphic index taxon (Spencer and Benton, 2000; Spencer and Storrs, 2002). Fortunately, the natural molds of the *Anomoiodon* skeletons recently resurfaced in the Museum für Naturkunde, Berlin, and high-fidelity silicone rubber casts of the specimen were produced (Fig. 1B). These reveal the anatomy of *Anomoiodon* in considerably more detail than was available in 1939, allowing a comprehensive comparison with *Kapes* and the inclusion of *Anomoiodon* into a phylogenetic analysis of Procolophonoidea. A formal diagnosis for *Anomoiodon liliensterni* is also provided for the first time.

**Institutional Abbreviations**—**BP**, Bernard Price Institute for Paleontological Research, University of the Witwaterstrand, Johannesburg; **MB.R**, Museum für Naturkunde, Berlin; **PIN**, Paleontological Institute, Russian Academy of Sciences, Moscow; **SAM**, Iziko; South African Museum, Cape Town.

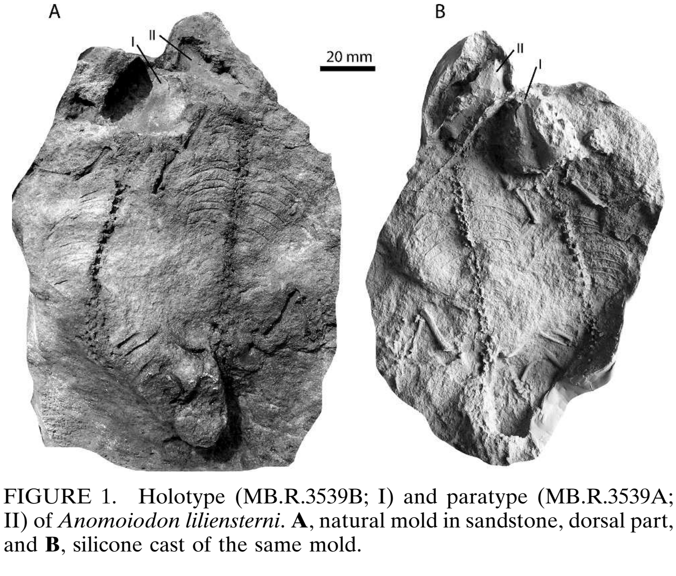

FIGURE 1. Holotype (MB.R.3539B; I) and paratype (MB.R.3539A; II) of *Anomoiodon liliensterni*. **A**, natural mold in sandstone, dorsal part, and **B**, silicone cast of the same mold.

## SYSTEMATIC PALEONTOLOGY

### PROCOLOPHONOIDEA Romer, 1956
### PROCOLOPHONIDAE Cope, 1889
### *ANOMOIODON LILIENSTERNI* von Huene, 1939

**Hypodigm**—MB.R.3539B, holotype, a partial skull and postcrania of a small individual, around 150mm long, preserved as a natural mold in three separate parts; MB.R.3539A, paratype, a partial skeleton, preserved as a natural mold on the same block as the holotype.

**Type Locality and Horizon**—Lowest layer of the *Chirotherium* Sandstone (Middle Bundsandstein) of Reurieth, near Hildburghausen, uppermost Lower Triassic (Olenekian) (Lucas, 2007).

**Diagnosis**—*Anomoiodon* is distinguished by its dentary dentition: the teeth are successively taller and larger posteriorly until the fifth tooth, which is almost double the height of the fourth tooth, whereas the sixth tooth is slightly shorter but the broadest mesodistally.

## DESCRIPTION

**Cranium**—Many of the details of the posterior region, lateral side, and palate are not preserved either on the holotype (MB.R. 3539B) or the paratype (MB.R.3539A) but the general shape of the skull, along with several sutures of the skull roof, can be seen in the dorsal view of both specimens (Fig. 2A). The skull, which lacks the quadratojugal horns associated with many procolophonids, measures about 35 mm in length in both specimens and is 30 mm broad at its widest point in the holotype. It is fairly triangular in dorsal view, and lacks sculpturing.

A partial premaxilla is preserved on the left side of MB.R.3539A (Fig. 2A). The premaxillae form a narrow internarial bar between the external nares, which in MB.R.3539A are fairly small and round.

The maxillae are poorly preserved in both specimens but on the right side of MB.R. 3539A the right maxilla can be seen comprising most of the lateral surface of the fairly deep snout (Fig. 3B). Remains of three maxillary teeth are also preserved, illustrating the trend of posteriorly increasing height and size of marginal dentition in *Anomoiodon* (Fig. 3B). Only on the last tooth, possibly the third or fourth on the maxillae (based on the position of the dentary teeth), can the crown be observed. In lateral view, it is pinched-in, making the tooth appear triangular

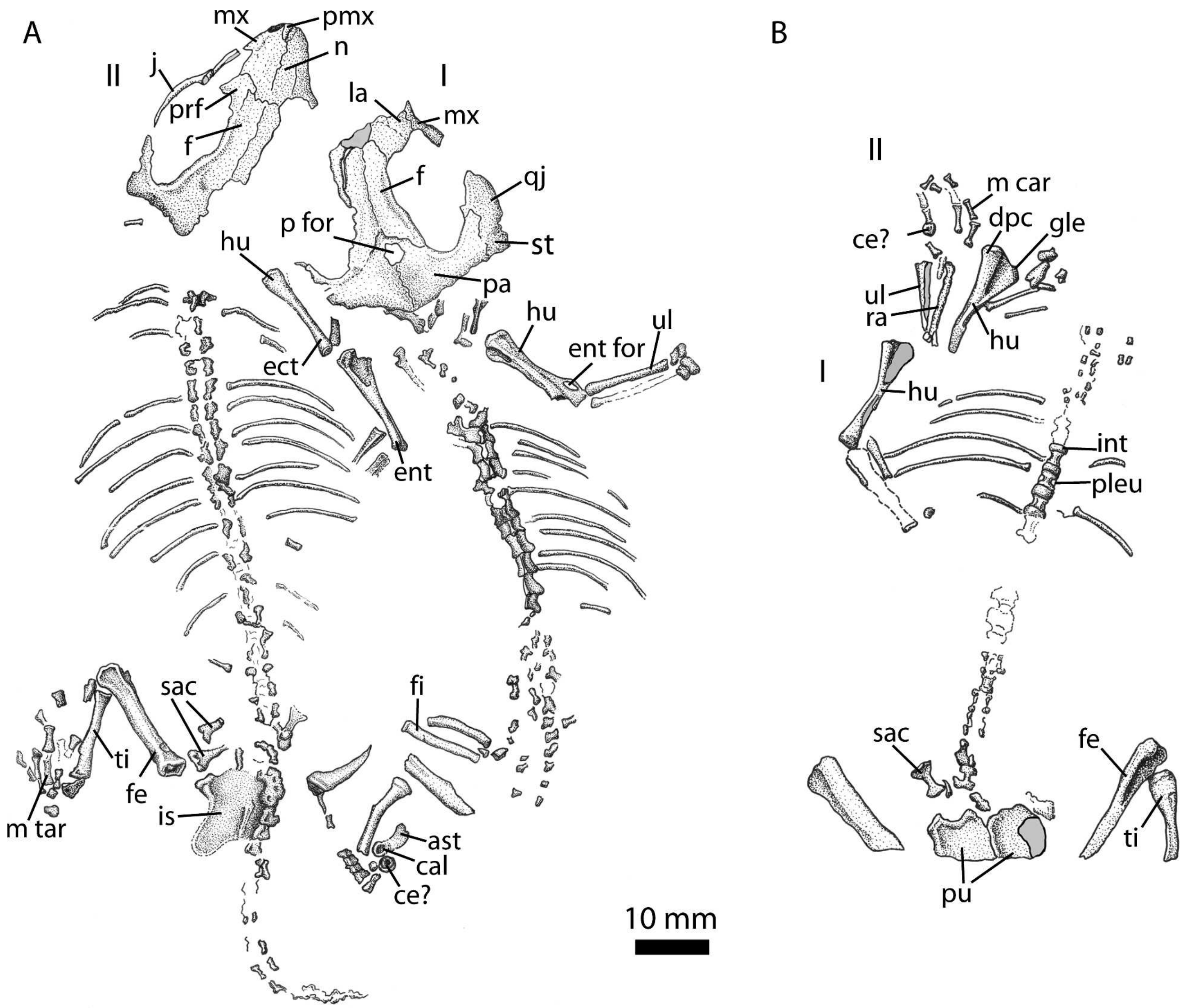

FIGURE 2. Holotype (MB.R.3539B; I) and paratype (MB.R.3539A; II) of *Anomoiodon liliensterni*. **A**, dorsal, and **B**, ventral views of skeletons. **Abbreviations**: **ast**, astragulus; **cal**, calcaneum; **ce**, centrale; **dpc**, deptopectoral crest; **ect**, ectepicondylar region; **ent**, entepicondylar region; **ent for**, entepicondylar foramen; **f**, frontal; **fe**, femur; **fi**, fibula; **gle**, glenoid; **hu**, humerus; **int**, intercentrum; **is**, ischium; **j**, jugal; **la**, lacrimal; **mx**, maxilla; **m car**, metacarpals; **m tar**, metatarsals; **n**, nasal; **pa**, parietal; **p for**, pineal foramen; **pleu**, pleurocentrum; **pmx**, premaxilla; **prf**, prefrontal; **pu**, pubis; **qj**, quadratojugal; **ra**, radius; **sac**, sacral ribs; **st**, supratemporal; **ti**, tibia; **ul**, ulna.

(Fig. 3B) but in posterolateral view the crown can be observed to continue as a narrow ridge transversely towards the lingual side of the maxilla. The ridge was most likely connected to a lingual cusp, although such a cusp cannot be observed in the cast; I infer the teeth were bicuspid, like the molariform teeth of *Procolophon* (Carroll and Lindsay, 1985) and many other procolophonids (sensu Modesto and Damiani, 2007).

The nasal is relatively broad and forms the dorsal margin of the external narial opening (Fig. 2A). Parts of the lacrimal have been preserved in both MB.R.3539A and MB.R.3539B, but its dimensions are unclear due to poor preservation of the sutures in this area (Fig. 2A).

The prefrontal forms the anteromedial borders of the orbitotemporal opening. It has an anteromedial portion that extends between the nasal and the frontal but does not reach the midline of the snout (Fig. 2A). It is virtually identical to the anteromedial process of the prefrontal found in *Kapes* cf. *K. majmesculae* (Novikov and Sues, 2004). The prefrontal also has the long posteromedially directed extension seen in most procolophonids.

The frontals are long and narrow, bearing an elevated crest running along the medial margin of the orbitotemporal openings (Fig. 2A). Their overall shape is similar to that of many other procolophonids. The large, elongated orbitotemporal openings are at their widest midway and become quite narrow near the posterior end (Fig. 2A).

The pineal foramen appears slightly triangular in shape, widening posteriorly, and is situated somewhat anterior to the posterior margins of the orbitotemporal openings (Fig. 2A). As far as can be observed, the parietals form most of the posterior skull in dorsal view. They extend posterolaterally around the orbitotemporal openings but it is impossible to say if the anterior extension between the orbitotemporal openings and the frontals is a part of the parietal, as in *Hypsognathus* and *Kapes* (Sues et al., 2000; Novikov and Sues, 2004), or a separate postfrontal bone, as in the owenettids and *Procolophon* (Carroll and Lindsay, 1985).

The sutures between the supratemporal, the postorbital and the quadratojugal have not been preserved, making it impossible to confirm if the postorbitals were missing, like in *Hypsognathus*

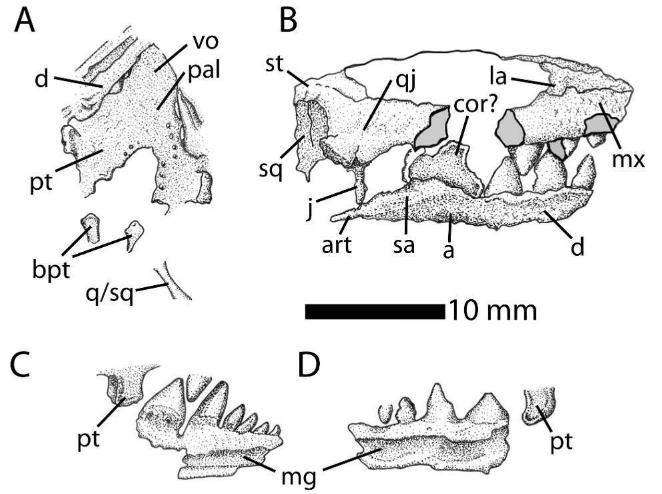

FIGURE 3. Holotype of *Anomoiodon liliensterni*, MB.R.3539B. **A**, palatal and **B**, right lateral view of the skull. **C**, left lower jaw and **D**, right lower jaw in medial view. **Abbreviations**: **a**, angular; **art**, articular; **bpt**, basipterygoid process; **d**, dentary; **cor**, coronoid process; **la**, lacrimal; **mg**, Meckelian groove; **mx**, maxilla; **pal**, palatine; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **sq**, squamosal; **st**, supratemporal; **vo**, vomer. Sutures are not shown between the vomer, the palatine, and the pterygoid or between the dentary, the angular, the surangular, and the articular because sutures cannot be observed; the labels refer to the broad regions in which those elements lay.

(Sues et al., 2000), or present like in most procolophonoids. The supratemporals have pointed corners that form the posterolateral corners of the skull table (Fig. 2A). The squamosal is situated underneath the supratemporal, and makes broad contact with the quadratojugal in MB.R.3539B (Fig. 3B), although these two bones are poorly preserved. A narrow sliver of bone, tentatively identified as part of the jugal, but possibly including the lacrimal and the maxilla as well, outlines the lateral margin of the orbit on the right side of MB.R.3539A (Fig. 2A). This area is mostly missing from MB.R.3539B.

Some imprints of the palate of MB.R.3539B have been preserved on a separate part of the natural mold (Fig. 3A). No suture lines are visible. The shape of the vomers and the palatines is unclear, and no vomerine or palatal dentition is preserved. The interpterygoid vacuity is oval-shaped and has a row of teeth around its edges on the pterygoid (Fig. 3A). Another row of teeth, aligned anteromedially, is also preserved on the left prerygoid but it is unclear whether the row continued onto the palatine anteriorly, due to the lack of suture lines. The transverse flanges of the pterygoid extend ventrally just below the level of the marginal dentition (Fig. 3D). These extended flanges are also present in leptopleuronine procolophonids and in *Tichvinskia* and *Kapes* (Ivachnenko, 1979; Novikov and Sues, 2004). Presence or absence of a tooth row on the flange cannot be verified due to incomplete preservation. The flanges were presumably formed together with the ectopterygoid as in other procolophonids. The only other element of the skull preserved in palatal view is a pillar-like quadrate/squamosal process on the left side of MB.R.3539B (Fig. 3A), which makes broad contact with the posterior extent of the pterygoid in most procolophonoids. Additionally, paired appendages resembling the basipterygoid processes of the braincase of *Leptopleuron* (Spencer, 2000) and *Contritosaurus/Phaanthosaurus* (pers. obs. of PIN 2482/1) are preserved in the space that would have been occupied by the braincase in life (Fig. 3A).

**Mandible**—The partial mandibular rami of MB.R.3539B can be observed in lateral (Fig. 3B) and medial views (Fig. 3C–D). The anterior-most portion of the dentary is not preserved in lateral view and the rest of the dentary is also damaged (Fig. 3B). In medial aspect, a distinct Meckelian groove is present (Fig. 3C–D). The more posterior parts of the mandible, including the surangular, the angular, the articular, and a possible coronoid process, are visible in lateral view. Preservation is poor, however, and no sutures between these elements can be observed (Fig. 3B). The mandible is quite shallow, becoming slightly deeper towards the end of the tooth row. This is most clear on the medial side of the right mandible of MB.R.3539B, which is otherwise much more poorly preserved than the medial side of the left mandibular ramus (Fig. 3D).

The dentary dentition, which is somewhat inset from the lateral margin, is quite well preserved. There are six teeth that increase in height and size posteriorly until the fifth tooth, which is nearly twice the height of the preceding tooth (Fig. 3C–D). The sixth tooth is slightly shorter than, but twice as broad mesodistally as the fifth (Fig. 3C–D). Only the most medial aspect of the crowns of the first four teeth can be seen but the crown of the fifth tooth is transversely broadened, whereas the apex of the crown of the sixth tooth appears quite pinched-in transversely. This, however, does not mean there is only one cusp, because some procolophonids, including *Kapes* (Novikov and Sues, 2004; Spencer and Benton, 2000; Spencer and Storrs, 2002), possess posterior dentary teeth with two cusps that are situated next to each other near the middle of the crown. The three posteriormost teeth can also be seen in lateral view on the right dentary of MB.R.3539B (Fig. 3B), but the crowns are obscured by the maxillary dentition.

**Postcrania**—The predorsal region of the vertebral column has not been preserved in either specimen. Several dorsal vertebrae are well preserved in dorsal view in MB.R.3539B (Fig. 2A), whereas some dorsal pleuro- and intercentra are preserved in MB.R.3539A (Fig. 2B). The zygapophyseal regions of the vertebrae are swollen but lack the groove that separates the anterior and posterior zygapophyses in *Procolophon* (deBraga, 2003). The neural spines lean backwards (Fig. 2A), a character shared with *Kapes* (pers. obs. of the undescribed postcrania of PIN 4365/40) and the leptopleuronine procolophonids *Soturnia, Hypsognathus,* and *Leptopleuron* (Cisneros and Schultz, 2003; Colbert, 1946; Säilä, unpublished data). The dorsal pleurocentra are hourglass-shaped in ventral view, with a high central ridge and deep grooves on both sides (Fig. 2B). The intercentra are large and wedge-shaped (Fig. 2B). The sacral and caudal vertebrae are very poorly preserved, and no details are visible. However, an outline of the caudals has been preserved in MB.R.3539A, indicating the minimum length of the tail (Fig. 2A).

Cervical ribs and gastralia are not preserved. The preserved dorsal ribs are fairly long and slightly recurved (Fig. 2A–B). There are at least two pairs of sacral ribs; three is typical for most procolophonoids. They are somewhat flared at both ends (Fig. 2A–B) but are not as massive as the sacrals of *Procolophon* (deBraga 2003). No caudal ribs are preserved.

A few unidentifiable bone fragments is all that has been preserved of the shoulder girdle (Fig. 2A–B). The forelimb of *Anomoiodon* is similar to, but slightly less robust than, that of SAM-PK-7711, a specimen that was assigned to *Procolophon* by deBraga (2003), but is now regarded as an indeterminate procolophonid (Modesto and Damiani, 2007) or possibly referable to the taxon *Teratophon spinigenis* (Cisneros, 2008a). A large entepicondylar foramen is present on the right humerus of MB.R.3539B (Fig. 2A), and there appears to be no ectepicondylar foramen in the ectepicondylar region. In lateral view, the glenoid, the deltopectoral crest, and the deep sulcus between these elements can be observed on the right humerus of MB.R.3539A (Fig. 2B). The ulna and the radius both appear slender (Fig. 2B). Only one circular element of the wrist, possibly a centrale or a large distal carpal, has been preserved. The metacarpals are fairly long and slender (Fig. 2B).

Little is visible of the pelvic girdle. A partial outline of the ischium is visible on the left side of MB.R.3539A in dorsal view (Fig. 2A), and the anterior edges of the paired pubes can be seen in ventral view (Fig. 2B). The shapes of these elements are very similar to those of *Procolophon* (deBraga, 2003). The femur, the tibia, and the fibula are virtually indistinguishable from those in SAM-PK-7711 (deBraga, 2003) and the astragalus and the calcaneum appear to be fused together (Fig. 2A). The number of ankle elements is uncertain but the metatarsals, like the metacarpals, are slender (Fig. 2A).

## PHYLOGENETIC ANALYSIS

In order to identify the phylogenetic position of *Anomoiodon* within the Procolophonidae, a phylogenetic analysis of 12 well-known procolophonid taxa was conducted. The following taxa (with sources) formed the ingroup: *Anomoiodon liliensterni* (this study), *Coletta seca* (Modesto et al., 2002), *Sauropareion anoplus* (Modesto and Damiani, 2007), *Procolophon trigoniceps* (Carroll and Lindsay, 1985; deBraga, 2003), *Thelerpeton oppressus* (Modesto and Damiani, 2003; pers. obs. of BP/1/4586), *Teratophon spinigensis* (Modesto and Damiani, 2003; pers. obs. of SAM/PK/10192 and BP/1/4300), *Hypsognathus fenneri* (Colbert, 1946; Sues et al., 2000), *Leptopleuron lacertinum* (Spencer, 2000; Säilä, unpublished data), *Scoloparia glyphanodon* (Sues and Baird, 1998), *Kapes* cf. *K. majmesculae* (Novikov and Sues, 2004; pers. obs. of PIN 4365/40), *Tichvinskia vjatkensis* (Ivachnenko, 1979; pers. obs. PIN 954/1), and *Contritosaurus simus* (Ivachnenko, 1979; pers. obs. PIN 3355/1). The parareptiles *Macroleter poezicus* (Tsuji, 2006) and *Nyctiphruretus acudens* (Lee, 1997; Tsuji, 2006; pers. obs. PIN 158/4, 162/1 and 4659/1) and the more basal procolophonoid clade Owenettidae (represented by '*Owenetta' kitchingorum*, Reisz and Scott, 2002, and *Barasaurus besairei*, Ketchum and Barrett, 2004; Cisneros, 2008b; pers. obs. SAM-PK-K8282) served as outgroups. The 44 characters used in this analysis were mainly taken from previously published analysis but several characters were modified and three new characters were added (for complete list of characters and data matrix see Supplementary data; Appendices 1 and 2, www.verpalaeo.org/jvp/JVPcontents.html). Characters were un-weighted and un-ordered. A branch-and-bound search using Acctran optimization in PAUP* 4.0b10 (Swofford, 2002) found three most parsimonious trees (tree length = 81, consistency index = 0.70, retention index = 0.84, homoplasy index = 0.3, rescaled consistency index = 0.59). A strict-consensus of these trees is shown in Figure 4. The overall tree topology agrees with previous studies (Modesto et al., 2001, 2002; Cisneros et al., 2004; Modesto and Damiani, 2007) but differs from the results of Cisneros (2008b) in the position of *Kapes*. *Anomoiodon* forms a sister-group relationship with *Kapes* and the *Anomoiodon-Kapes* clade is at the base of Leptopleuroninae (Fig. 4). Bootstrap support (1000 replicates) was over 80% for most clades, and 90% for the *Anomoiodon-Kapes* clade (Fig. 4). Decay values varied between 1 and 5; the *Anomoiodon-Kapes* clade and the Leptopleuroninae both had a decay value of 2 (Fig. 4). One unambiguous synapomorphy (prefrontal bone with anteromedial flange that does not reach the midline of the snout; #16:1), and one ambiguous synapomorphy (the increased height and size of lower marginal dentition in lateral view; #12:1), support the *Anomoiodon-Kapes* clade. In addition, *Anomoiodon* and *Kapes* share the same codings (except for unknown ones) for all characters.

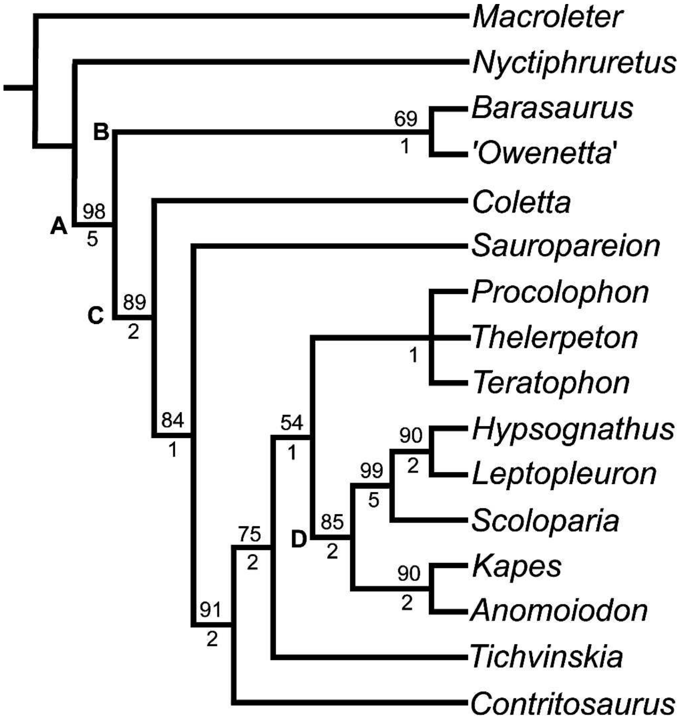

FIGURE 4. Strict consensus of three most parsimonious trees from an analysis of procolophonid interrelationships. The three trees differ only in the positions of *Procolophon, Teratophon*, and *Thelerpeton* in relation to each other, shown here as a polytomy. Bootstrap values of above 50% are indicated above and decay values below each node. A = Procolophonoidea, B = Owenettidae, C = Procolophonidae, D = Leptopleuroninae. See text for tree statistics and discussion.

## DISCUSSION

The results of the phylogenetic analysis show that *Anomoiodon* and *Kapes* form a clade within the Leptopleuroninae (Fig. 4). The similarities, and possible synonymy, between *Anomoiodon* and *Kapes* were first noted by Spencer and Storrs (2002). At the time, *Kapes* was only known from jaw material and the *Anomoiodon* specimens were unaccounted for, and the observed similarity between *Kapes* and *Anomoiodon* was the number and increasing height of the dentary teeth on the lower jaw (Spencer and Storrs, 2002). Since then, more complete material of *Kapes* has been found and described (Novikov and Sues, 2004), and with the new silicone casts of *Anomoiodon*, a proper comparison can finally be made. *Anomoiodon* and *Kapes* cf. *K. majmesculae* (Novikov and Sues, 2004) share many characters, but only two were found to be synapomorphies of the *Anomoiodon-Kapes* clade reported here. The posteriorly increasing height and size of the lower marginal dentition in lateral view has been considered an autapomorphy of the genus *Kapes* (Spencer and Storrs, 2002; Novikov and Sues, 2004), but is found to be an ambiguous synapomorphy of the *Anomoiodon-Kapes* clade because it is also shared with the genus *Thelerpeton*. It is also present in many other genera known from fragmentary or incomplete material (Modesto and Damiani, 2003; Sues and Baird, 1998).

The other, and only unambiguous, synapomorphy of the *Kapes-Anomoiodon* clade is a prefrontal bone that has an anterodorsal portion with a posteromedial process that extends to, but does not reach, the midline. This kind of prefrontal is found in *Kapes* cf. *K. majmesculae* (Novikov and Sues, 2004) but it is indeterminable in other species of *Kapes* because they are only known from fragmentary jaw parts (Spencer and Benton, 2000; Spencer and Storrs 2002). Additionally, this character might be present in some undescribed SAM material attributable to the South African procolophonid *Thelephon contritus* (Cisneros, 2008b; S. P. Modesto, pers. comm.). However, because this material has not been described and only the poorly preserved holotype (BP/1/3512) was available for personal observations, *Thelephon* was not included in this phylogenetic study. Nevertheless, *Thelephon* forms a sister-group relationship with *Kapes* in the phylogenetic analysis of Cisneros (2008b), and as this was mostly because of the shape of the prefrontal bone, this remains a valid synapomorphy for the clade that includes *Kapes* and *Anomoiodon* in this study, and *Kapes* and *Thelephon* in Cisneros (2008b). However, the *Kapes-Thelephon* clade was found to be more closely related to *Procolophon* than to *Leptopleuron* in Cisneros (2008b), a result markedly different from the position of the *Anomoiodon-Kapes* clade within the leptopleuroninae in this study.

The present phylogenetic study found no differences between *Anomoiodon* and *Kapes*. However, of the autapomorphies of *Kapes* listed by Spencer and Storrs (2002) (excluding the height and size of lower marginal dentition, shared with several other genera), all are indeterminable or can be disputed in *Anomoiodon* because of the incomplete preservation of specimens assigned to both genera. Additionally, the dentary dentition of *Anomoiodon* differs from the dentition of all species of *Kapes* to some degree. In *Kapes*, the tallest tooth is also the broadest one (Spencer and Storrs, 2002), whereas in *Anomoiodon* the tallest tooth precedes the broadest one (Fig. 3C). This dental pattern of *Anomoiodon* is actually more similar to *Acadiella psalidodon*, a poorly known small procolophonid from the Late Triassic of Nova Scotia (Sues and Baird, 1998), than to *Kapes*. However, the tallest and broadest teeth of *Acadiella* have mesodistally aligned apical crests with several denticles (Sues and Baird, 1998), a dental organization not seen in *Anomoiodon*. It is also worth noting that in the genus *Procolophon* replacement teeth are added to the back of the tooth row without resorption pits (Gow, 1977), and if this type of tooth replacement was present in *Anomoiodon*, it is possible that the last, broadest dentary tooth might not be fully erupted and would have eventually become taller than the preceding tooth. However, this possibility can be rejected because the last tooth is of similar height on both dentaries of MB.R.3539B (Fig. 3C-D), a highly unlikely condition in the case of posterior tooth replacement. Furthermore, the last teeth on both sides have identical bone attachment with the preceding teeth, indicating they were fully attached and not in the process of erupting further. Additionally, the tallest tooth in the dentary of *Anomoiodon* is nearly twice the height of the preceding tooth (Fig. 3C-D). This dental pattern is considered a valid autapomorphy of the genus *Anomoiodon* because it has not been observed in any other procolophonoid. Thus, although *Anomoiodon* and *Kapes* form a well-supported clade in this phylogenetic analysis, with all material considered, there is not enough evidence to support the synonymy of these two genera.

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APPENDIX 1. Description of characters used in the phylogenetic analysis. Characters mostly from Modesto et al., 2001 (MOD), but also added from Modesto et al., 2002 (MDS), Modesto and Damiani, 2007 (MDA), Cisneros et al., 2004 (CIS) and deBraga, 2003 (DEB). Character numbers from the original analysis follow the abbreviations, and an asterisk (*) indicates a character has been modified. Characters 12, 41, and 44 are new characters.

1. Premaxillary nasal process extends posterodorsally (0) or anterodorsally (1). MOD 1
2. Premaxillary teeth number: five or more (0), four (1), three (2), two (3). MOD 2*
3. Premaxillary tooth size: fairly subequal in size (0), first tooth considerably larger than the following tooth/teeth (1). DEB 2*
4. Maxilla premaxillary (subnarial) process present (0) or absent (1). MOD 3
5. Laterally visible maxillary depression absent (0) or present (1) on maxilla and nasal. MOD 4
6. Maxillary teeth number: 12 or more (0), nine or less (1). MOD 5
7. Prominent anterior maxillary teeth present (0) or absent (1). CIS 15*
8. Maxillary teeth in basal cross-section: subcircular (0), labiolingually expanded (1). MOD 6
9. Maxillary teeth crowns subcircular (0) or labiolingually expanded (1). MOD 7
10. Maxillary tooth row extends well beyond the anterior margin of the orbit (0) or the maxillary tooth row terminates anterior to or at the level of the anterior margin of the orbit (1). DEB 6*
11. Dentary incisiform tooth number two or more (0) or one (1). MDS 24
12. Height and size of lower marginal dentition stays fairly constant (0), or increases significantly posteriorly (1) in lateral view.
13. Lateral marginal teeth bases mesodistally narrow (0) or mesodistally broad (1). MOD 8
14. Marginal 'cheek' teeth not inset (0) or inset (1) from lateral surfaces of the cheek and jaws. MOD 9
15. Lacrimal separated from (0) or contacts (1) ectopterygoid. MOD 10
16. Prefrontals: medial borders straight, no midline contact (0), approach each other medially but no midline contact (1), midline contact present (2), do not extend anterodorsally between frontal and lacrimal (3). CIS 18*
17. Prefrontal 'spur' or 'bulbous process': absent (0), or present (1). DEB 10
18. Orbits terminate before or at the level of the anterior margin of the pineal foramen (0), extend posteriorly to the level of the posterior margin of the pineal foramen (1), or extend posteriorly well beyond the pineal foramen (2). MOD 11*
19. Pineal foramen flush with the dorsal surface of the skull table (0) or positioned in a shallow fossa (1). MOD 12
20. Postfrontal in contact with the postorbital (0), in contact with supratemporal also (1), separated from both elements (2), postfrontal absent and area occupied by parietal (3). MOD 13
21. Squamosal ventral margin terminates dorsal to (0) or extends at least as far ventrally as (1) that of the quadratojugal in the tympanic notch. MOD 14
22. Supratemporal longer anteroposteriorly than broad transversely (0), or vise versa/equal in dimensions (1). MOD 16 / CIS 7
23. Postparietal present (0) or absent (1). MOD 18
24. Tabular: present (0) or absent (1). DEB 21
25. Posterior margin of skull: entirely dorsal (0), with occipital shelves (1). DEB 22
26. Jugal virtually excluded from the ventral margin of lateral skull (0), jugal contributes to the ventral embayment of the posterior cheek (1) or has a convex, anteroventrally-facing ventral margin (2). MDS 9*
27. Quadratojugal lateral surface spineless (0), with single, large-based and posteriorly directed process (1) or with two or more radiating spines with bases circumscribed with distinct sulci (2). MDS 14
28. Quadratojugal anteroposteriorly narrow (0) or broad, extending anteriorly as far as the frontal contribution to the orbit (1). MOD 24
29. Temporal ventral margin roughly straight (0), acutely emarginated with no contribution from maxilla (1), broadly embayed with contribution from maxilla (2). MDA 25
30. Vomerine dentition consisting of shargreen of small denticles (0), consisting of two or three rows of larger parachoanal teeth instead of denticles (1) or dentition entirely absent (2). MOD 19
31. Suborbital foramen formed ventrally by palatine and ectopterygoid alone (0) or by palatine, ectopterygoid and maxilla (1). MOD 20
32. Pterygopalatine teeth present and aligned anterolaterally (0), present and aligned anteromedially (1) or absent (2). MOD 21
33. Marginal dentition at the same level as the ventral limit of the transverse flange of the pterygoid (0) or a pronounced ventral expansion of the transverse flange of the pterygoid so that it descends below the ventral limit of the marginal dentition (1). DEB 34
34. Pterygoid dentition on transverse flange: present (0), or absent (1). DEB 33
35. Pterygoid quadrate process extends posterodorsally to but does not contact (0) or makes broad contact with (1) the occipital flange of the squamosal. MOD 22
36. Epipterygoid columella ends freely (0) or in contact with dorsally with prootic and supraoccipital (1). MDS 20
37. Parasphenoid cultriform process absent/short vertical pillar (0), or directed anteriorly and tapers to a sharp tip (1). MDS 21*
38. Supraoccipital dorsally expanded (0), or reduced to a sagittal pillar (1) in posterior view. MDS 22
39. Basioccipital fused indistinguishably to exoccipitals (0) or sutures between these elements persist so that tripartite structure of the condyle evident (1). MDS 23
40. Jaw articulation roughly in line with (0) or positioned well below level of marginal dentition (1). MDS 25
41. Depth of dentary: shallow, stays constant (0), deepens gradually (1) or dentary very deep, deepening substantially after the caniniform region (2).
42. Entepicondylar foramen on the humerus present (0) or absent (1). MOD 25
43. Ectepicondylar foramen: present (0), or absent (1). DEB 52
44. Neural spine of dorsal vertebrae pillar-like and aligned vertically (0) or leans posteriorly (1).

APPENDIX 2. Data matrix used in the phylogenetic analysis. Missing data coded as '?'.

*Macroleter*
0000000000 0000000000 0000000000 0000000000 0000

*Nyctiphruretus*
0000000000 0000000010 0100000000 ?0000?10?0 00?0

*Barasaurus*
0000001000 0000?0?0?1 0111110010 ?00?0?1??0 0110

'*Owenetta*'
0000000000 0000021011 0101110010 0001001000 01?0

*Coletta*
0100101000 0000?0?010 0???10011 0201?????0 0???

*Sauropareion*
??0???1000 ?00010?112 1001110011 ?101?????0 001?

*Contritosaurus*
0201111100 0010101??? ?????????1 1101?????0 0???

*Tichvinskia*
0201111110 0010101203 ?011010021 1111?0?110 1010

*Procolophon*
1101111110 0001101102 1011111121 1101101110 1010

*Thelerpeton*
?200?11110 ?111?0?103 ?011101101 ?101?????0 1???

*Teratophon*
?20??11110 ?01113?103 ?011?11121 1101?????0 1??0

*Hypsognathus*
1311011111 1011?30203 0011122122 1211110111 20?1

*Leptopleuron*
1311011111 1011?00203 1111122121 ?211110111 2011

*Scoloparia*
1311011111 0011?0?203 ?0?1112?2? ????1????1 2???

*Kapes*
1211111110 0111111203 1111110121 ?1100????1 1?11

*Anomoiodon*
????11110 ?111?1?20? ??111?0??? ?11??????1 1011