ANATOMY AND PHYLOGENETIC RELATIONSHIPS OF *SCLEROSAURUS ARMATUS* (AMNIOTA: PARAREPTILIA) FROM THE BUNTSANDSTEIN (TRIASSIC) OF EUROPE

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ABSTRACT—We present an anatomical redescription and reassessment of the phylogenetic relationships of *Sclerosaurus armatus* Meyer in Fischer, 1857, a parareptile from the Lower to lower Middle Triassic Buntsandstein of southern Germany and northern Switzerland. This taxon is distinguished from other known parareptiles by the possession of long, posterolaterally projecting spikes formed by supratemporals, posterior dentary teeth with mesiolingually aligned and slightly imbricating crowns, and a narrow band of dorsal dermal armor comprising two or three rows of sculptured osteoderms on either side of the midline. Phylogenetic analysis places *Sclerosaurus* in the Procolophonidae rather than as the sister taxon of Pareiasauria. Furthermore, certain apomorphic character states, particularly the presence of three spines on the quadratojugal, support its referral to the Leptopleuroninae. *Sclerosaurus* resembles pareiasaurs in the presence of an intercondylar canal on the distal end of the femur, the absence of gastralia, and having a short tail. It is possibly the largest procolophonid known to date.

INTRODUCTION

The predominantly clastic strata of the Lower to lower Middle Triassic Buntsandstein Group were deposited in the Germanic Basin, a large, subsiding epicontinental basin that extended from England in the west to Poland in the east and from Switzerland in the south to Denmark in the north (Ziegler, 1982; Paul, 1999). These strata reached a maximum thickness exceeding 1,000 m near the center of the basin. They are divided into Lower, Middle, and Upper Buntsandstein. The Lower and Middle Buntsandstein comprise continental red beds of primarily fluvial origin and also include paleosols as well as lacustrine and eolian deposits, whereas portions of the Upper Buntsandstein, particularly in northern Germany, are marine in origin (Paul, 1999). Although Buntsandstein strata are generally rather unfossiliferous, skeletal remains of temnospondyl amphibians and reptiles have been recovered from a number of localities in the Middle and especially Upper Buntsandstein (Krebs, 1969; Wild, 1998; Fraser and Rieppel, 2006; Schoch et al., 2007). In contrast, tetrapod trackways are diverse and locally abundant, particularly in the upper Middle Buntsandstein (Haubold, 1971).

Most of the known skeletal remains of tetrapods from the Buntsandstein were found and described during the nineteenth and early twentieth centuries (Krebs, 1969) and have subsequently received little attention (Schoch et al., 2007). *Sclerosaurus armatus* was described by Meyer (1859) on the basis of a partial postcranial skeleton from the Upper Buntsandstein near Rheinfelden in Baden (Germany). An earlier report by Fischer (1857), merely intended as an announcement of Meyer's forthcoming account, provided a brief but sufficiently detailed description, accompanied by a photographic illustration of the holotype; thus, the Linnean binomen should be properly attributed

to Meyer in Fischer, 1857. The holotype of *Sclerosaurus armatus* was discovered in 1856 and is housed in the collections of the Geologisches Institut of the Albert-Ludwigs-Universität in Freiburg im Breisgau (Germany). In 1878, Wiedersheim reported a nearly complete, largely undisturbed skeleton of a reptile, preserved as a natural mold, from the upper Middle Buntsandstein of Riehen near Basel (Switzerland). He assigned this specimen, discovered in 1864 and donated by its finder to the collections of the Naturhistorisches Museum Basel, to a new species of labyrinthodont amphibian, *Labyrinthodon Rütimeyeri* (spelling of the specific epithet now emended to *ruetimeyeri*—see below). Wiedersheim studied the skeleton from the cavities that had been left by natural dissolution of the bones prior to its discovery. He removed much of the complex mold of the skull to expose what he misinterpreted as a natural endocranial cast. For example, Wiedersheim mistook the impressions of the large orbitotemporal openings for 'auditory capsules' (Wiedersheim, 1878:pl. II, fig. 3, T). Zittel (1888) subsequently rejected Wiedersheim's classification of *Labyrinthodon ruetimeyeri* as an amphibian and classified this taxon as a reptile, even citing a letter from Wiedersheim in support of this reassignment. Owen (1841) originally substituted *Labyrinthodon* for the generic nomen *Mastodonsaurus* Jaeger, 1828, simply because he disliked the etymological derivation of the latter. He and a number of other nineteenth-century authors subsequently employed this invalid replacement name to refer to a variety of Triassic tetrapods.

Seeley (1896, 1900) was able to borrow Wiedersheim's specimen and carefully studied it by means of rubber impressions made from the molds of individual bones. He concurred with Zittel in interpreting "*Labyrinthodon*" *ruetimeyeri* as a reptile and proposed a new genus, *Aristodesmus*, for its reception. Seeley (1900:644) placed *Aristodesmus ruetimeyeri* "in association with *Procolophon* as a separate [unnamed] family in the tribe Procolophonia" among the Anomodontia (employing an old definition of that name to denote a heterogeneous assemblage of rep-

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tiles and non-mammalian synapsids). Baur (1897) and Huene (1902) independently concluded that *Aristodesmus ruetimeyeri* was, in fact, referable to *Sclerosaurus armatus*. Huene received permission to have a professional sculptor prepare complete casts from part and counterpart of the Basel specimen. This approach yielded a wealth of new anatomical information on *Sclerosaurus*, such as the discovery of long supratemporal spines (Huene, 1902, 1912).

Initially, Huene (1902, 1911, 1912) followed Seeley in classifying *Sclerosaurus* as a procolophonid. Subsequently, however, he compared *Sclerosaurus* to the Pareiasauridae (Huene, 1920, 1932) and later explicitly referred it either to the latter group (Huene, 1943) or to a stem-lineage of pareiasaurs (Huene, 1956). In their synoptic overviews of procolophonoid diversity, Colbert (1946) and Kuhn (1969) retained *Sclerosaurus* in the Procolophonidae, but Kuhn (1969:58) stressed the presence of dermal ossifications and allegedly pareiasaur-like features in the skull. Presumably following Huene, Romer (1956:491) and Wild (1998) placed *Sclerosaurus* in the Pareiasauridae. Following Colbert (1946), Romer and most later authors incorrectly attributed the generic nomen to the Russian naturalist G. Fischer de Waldheim. In his systematic review of Procolophonia, Ivakhnenko (1979) listed a family-level grouping Sclerosauridae Nopsca, 1923, comprising *Sclerosaurus armatus* and the poorly known *Basileosaurus freyi* Wiedersheim, 1879 (incorrectly cited as 1870 by Ivakhnenko) from the Buntsandstein of Riehen near Basel. The holotype and only known specimen of *B. freyi* apparently was lost long ago (Huene, 1932), and thus the affinities of this taxon cannot be resolved.

Whereas the parareptilian affinities of *Sclerosaurus armatus* are no longer subject to debate, its phylogenetic position within Parareptilia has remained contentious. Recent studies discussing the relationships of *Sclerosaurus* have relied on the often-conflicting accounts in the older literature, with additional information gleaned from old casts of inferior quality. Since Huene's work at the beginning of the twentieth century, apparently no further investigation of the original fossils was undertaken. Lee (1995) placed *Sclerosaurus* as the sister taxon to a clade comprising pareiasaurs and turtles (Pareiasauria sensu Lee, 1995), but explicitly cautioned that "the possibility that *Sclerosaurus* is an aberrant procolophonid that has convergently acquired pareiasaurian characters as a consequence of large size cannot be dismissed" (Lee, 1995:515). DeBraga (2003) assigned *Sclerosaurus* to the Procolophonidae, and specifically the Leptopleuroninae, based on brief inspection of the new casts assembled by us. Most recently, drawing on the character-taxon matrix published by Lee (1997), Jalil and Janvier (2005) again placed *Sclerosaurus* as the sister taxon to Pareiasauria, but noted potential issues with this phylogenetic position.

We have restudied the holotype of "*Labyrinthodon*" ruetimeyeri (Naturhistorisches Museum Basel, Bs. 28) using excellent new silicon-rubber casts of part and counterpart of the entire skeleton as well as a separate cast of the skull. In addition, R.R.R. prepared latex peels of the part and counterpart of the holotype of *Sclerosaurus armatus*. This approach has enabled us to document the skeletal structure of *Sclerosaurus* in greater detail than has been attempted before and to reassess the phylogenetic relationships of this taxon.

Spencer and Storrs (2002) compared the anterior end of a tooth-bearing left dentary from the Anisian-age Otter Sandstone Formation of Devon (England) to *Sclerosaurus*. Although the presence of *Sclerosaurus* in the Otter Sandstone Formation is not unexpected in view of other tetrapod taxa shared with the Upper Buntsandstein (Milner et al., 1990), the specimen is too poorly preserved to allow taxonomic identification. Indeed, Spencer and Storrs (2002:458) referred to the jaw fragment only as "?Parareptilia *incertae sedis*."

SYSTEMATIC PALEONTOLOGY

PARAREPTILIA Olson, 1947, sensu Laurin and Reisz, 1995
PROCOLOPHONOIDEA Lydekker in Nicholson and
Lydekker, 1889, sensu Lee, 1997
PROCOLOPHONIDAE Lydekker in Nicholson and
Lydekker, 1889, sensu Modesto and Damiani, 2007
LEPTOPLEURONINAE Ivakhnenko, 1979, sensu Modesto,
Damiani, and Sues, 2002
SCLEROSAURUS ARMATUS Meyer in Fischer, 1857

Sclerosaurus armatus Meyer in Fischer, 1857:136.
Labyrinthodon ruetimeyeri Wiedersheim, 1878:12 (with the original spelling of the specific epithet *Rütimeyer*i emended to *ruetimeyer*i in accordance with Articles 28 and 32.5.2.1 of the International Code of Zoological Nomenclature, Fourth Edition [International Commission for Zoological Nomenclature, 1999])
Aristodesmus ruetimeyeri (Wiedersheim, 1878) Seeley, 1896:167.

Holotype—Collections of the Geologisches Institut of Albert-Ludwigs-Universität in Freiburg im Breisgau, counterpart blocks with a partial postcranial skeleton (Fig. 1). Upper Buntsandstein, talus of quarry at Warmbach near Rheinfelden, Baden, Germany.

Referred Specimen—Naturhistorisches Museum Basel, Bs. 28, holotype of "*Labyrinthodon*" ruetimeyeri Wiedersheim, 1878, counterpart blocks with the natural mold of a nearly complete, largely undisturbed skeleton in dorsal and ventral views (Figs. 2–5). Upper Middle Buntsandstein, abandoned quarry at Riehen near Basel, Switzerland.

Diagnosis—Long, posterolaterally projecting spike on pedicle formed by supratemporal. Quadratojugal with one pair of dorsoventrally flattened spines and an additional spine posteroventral to paired spines. Crowns of posterior dentary teeth aligned mesiolingually, slightly overlapping each other. Narrow band of dorsal dermal armor comprising two or three rows of osteoderms on either side of the midline. Osteoderms with external sculpturing composed of irregular pits. Gastralia apparently absent. Scapula with tall blade and lacking acromion. Distal end of femur with intercondylar canal. Tarsus comprising massive astragalocalcaneum and apparently unossified distal tarsals.

Distribution—Upper Middle to Upper Buntsandstein, southern Germany and northern Switzerland. Age: Early to early Middle Triassic (Olenekian-Anisian; Lucas and Schoch, 2002).

Note—The authorship of the family-level taxon Procolophonidae has been in dispute. Seeley (1888) is often credited as he clearly defined the concept; however, because he only referred to a suborder Procolophonia he is not the author of the family-group name (Article 35.1 of the International Code of Zoological Nomenclature, Fourth Edition). Lydekker (in Nicholson and Lydekker, 1889:1065) and Cope (1889:866) independently first referred to Procolophonidae. Cope cited Procolophonidae as part of his 'Progansauria' [sic] in a list of vertebrate families, whereas Lydekker explicitly recognized the family under the suborder Procolophonia and provides a brief anatomical description. We thus consider Lydekker in Nicholson and Lydekker, 1889, the author of Procolophonidae.

DESCRIPTION

The holotype of *Sclerosaurus armatus* (Meyer, 1859:pl. VI, here reproduced as Fig. 1; Huene, 1902:pl. III) is preserved as part and counterpart on slabs of sandy mudstone. One slab preserves 11 dorsal vertebrae along with 11 or 12 ribs and parts of the pelvic girdle. The other preserves the dorsal dermal armor, the apices of several broken neural spines, eight ribs, indistinct remains of the pelvic girdle, and the complete left and partial right femur in ventral view.
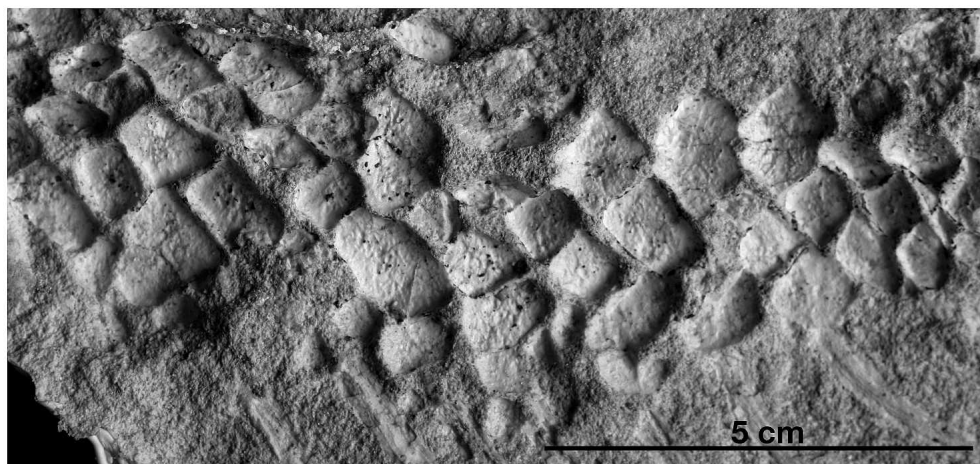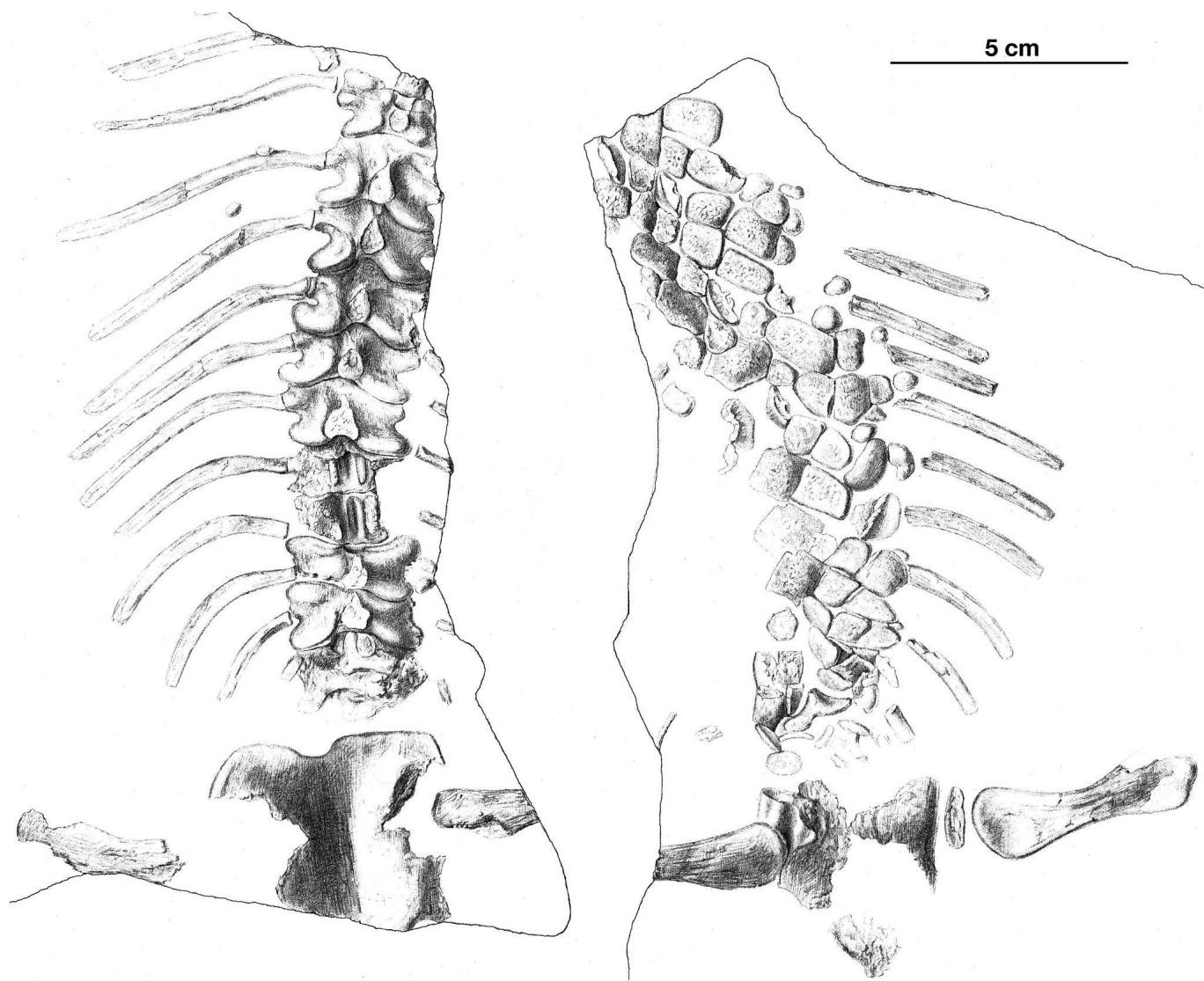
FIGURE 1. Holotype of *Sclerosaurus armatus* Meyer in Fischer, 1857, partial postcranial skeleton preserved on counterpart slabs. Scanned from the original lithograph published by Meyer (1859:pl. VI). Photograph taken from latex mold of holotype.
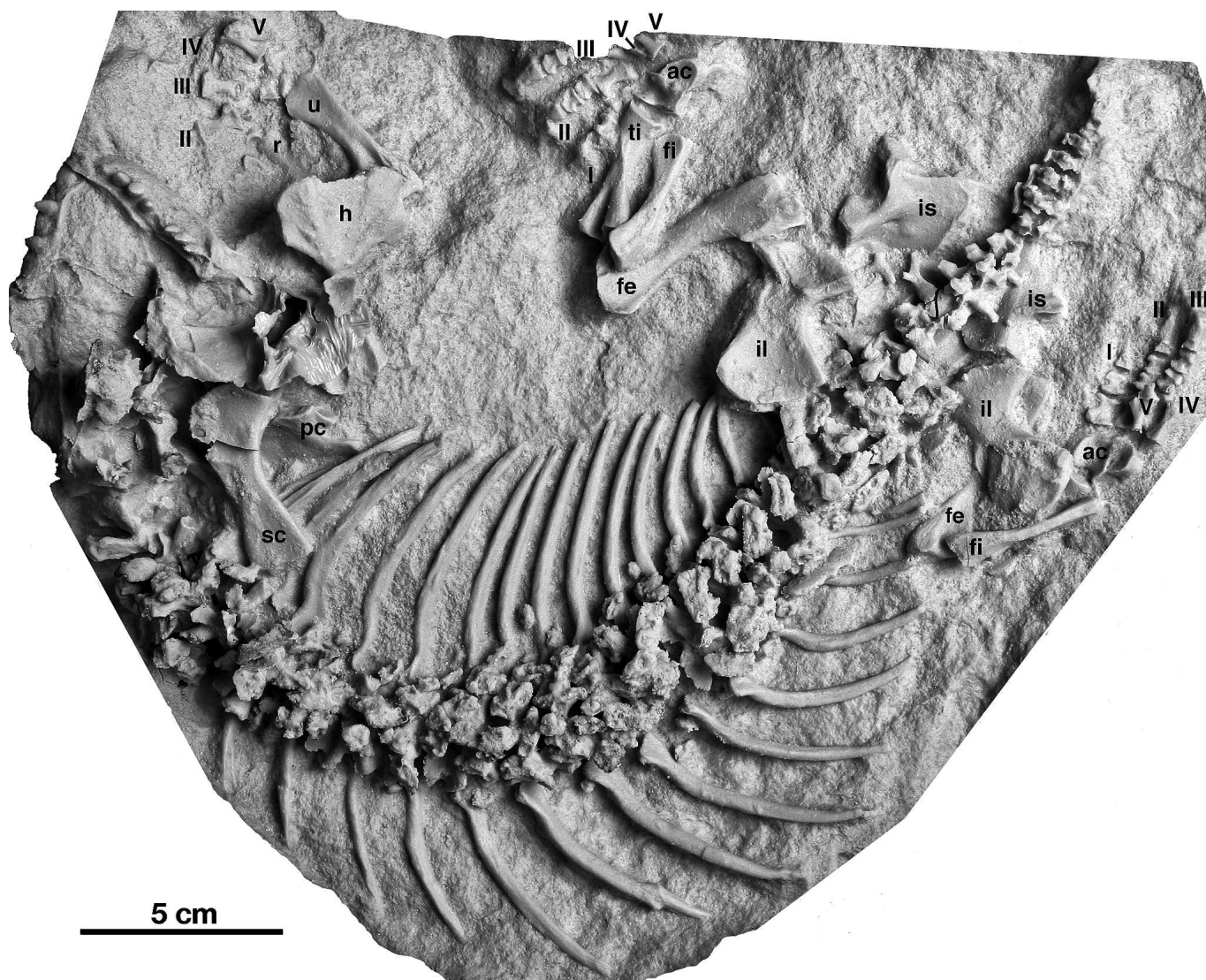
FIGURE 2. *Sclerosaurus armatus*, holotype of "*Labyrinthodon*" *ruetimeyeri* Wiedersheim, 1878 (Bs. 28). Silicon-rubber cast of skeleton in dorsal view. **Abbreviations**: **ac**, astragalocalcaneum; **c**, anterior coracoid; **d**, dentary; **en**, external naris; **fe**, femur; **fi**, fibula; **h**, humerus; **i**, intercentrum; **ic**, interclavicle; **il**, ilium; **is**, ischium; **or**, orbitotemporal opening; **p**, parietal, **p.p**, parietal process; **pc**, posterior coracoid; **pt**, pterygoid; **pu**, pubis; **q**, quadrate; **qj.s1-3**, quadratojugal spines 1-3; **r**, radius; **sc**, scapula; **sp**, splenial; **st.s**, supratemporal spine; **ti**, tibia; **u**, ulna. Roman numerals denote digits or elements of digits.

The block of fine- to medium-grained sandstone containing the holotype of "*Labyrinthodon ruetimeyeri*" (Bs. 28) was split into counterpart slabs. One slab preserves the skull, right forelimb and right scapulocoracoid, pelvic girdle and both hindlimbs, and the dorsal portion of the vertebral column with associated dermal armor and ribs of a nearly complete, largely undisturbed skeleton, mainly in dorsal view (Fig. 2). The other preserves the mandible, the pectoral girdle and right forelimb, the vertebral column back to the first sacral with associated ribs, and part of the proximal end of the right tibia, mostly in ventral view (Fig. 3). Apparently the original bone had already completely disappeared by the time the specimen was discovered (Wiedersheim, 1878). However, almost the entire skeleton is represented by an excellent natural mold; the new silicon-rubber casts often reveal minute detail of the surfaces of individual bones. Bs. 28 is larger than the holotype of *Sclerosaurus armatus*, based on comparison of the lengths of the respective femora (55 mm vs. ca. 45 mm). The following anatomical description is based primarily on the much more complete specimen Bs. 28.

Skull

Due to Wiedersheim's preparation efforts, only portions of the skull of Bs. 28 are still preserved: the ventral surface of much of the skull roof back to the occipital margin, the more ventral portions of the left and right side of the cranium, and the complete mandible. Huene (1902) initially mistook the cast of a complex bone for the basicranial region, but later (Huene, 1912) correctly identified it as the posterolateral portion of the left 'cheek' region of the cranium.

The skull is distinctly wider transversely (ca. 100 mm) at its widest point (across the quadratojugals) than it is long along the midline (ca. 80 mm). It is low dorsoventrally, as in derived procolophonids such as *Hypsognathus*, and its dorsal surface appears to be rather flat. Few cranial sutures are still evident. Anterior to a pair of quadratojugal spines, the sides of the skull converge rapidly toward the blunt tip of the snout. The orbitotemporal openings (sensu Huene [1912]) are large (greatest dimension >30 mm) and face almost directly dorsally. The outline
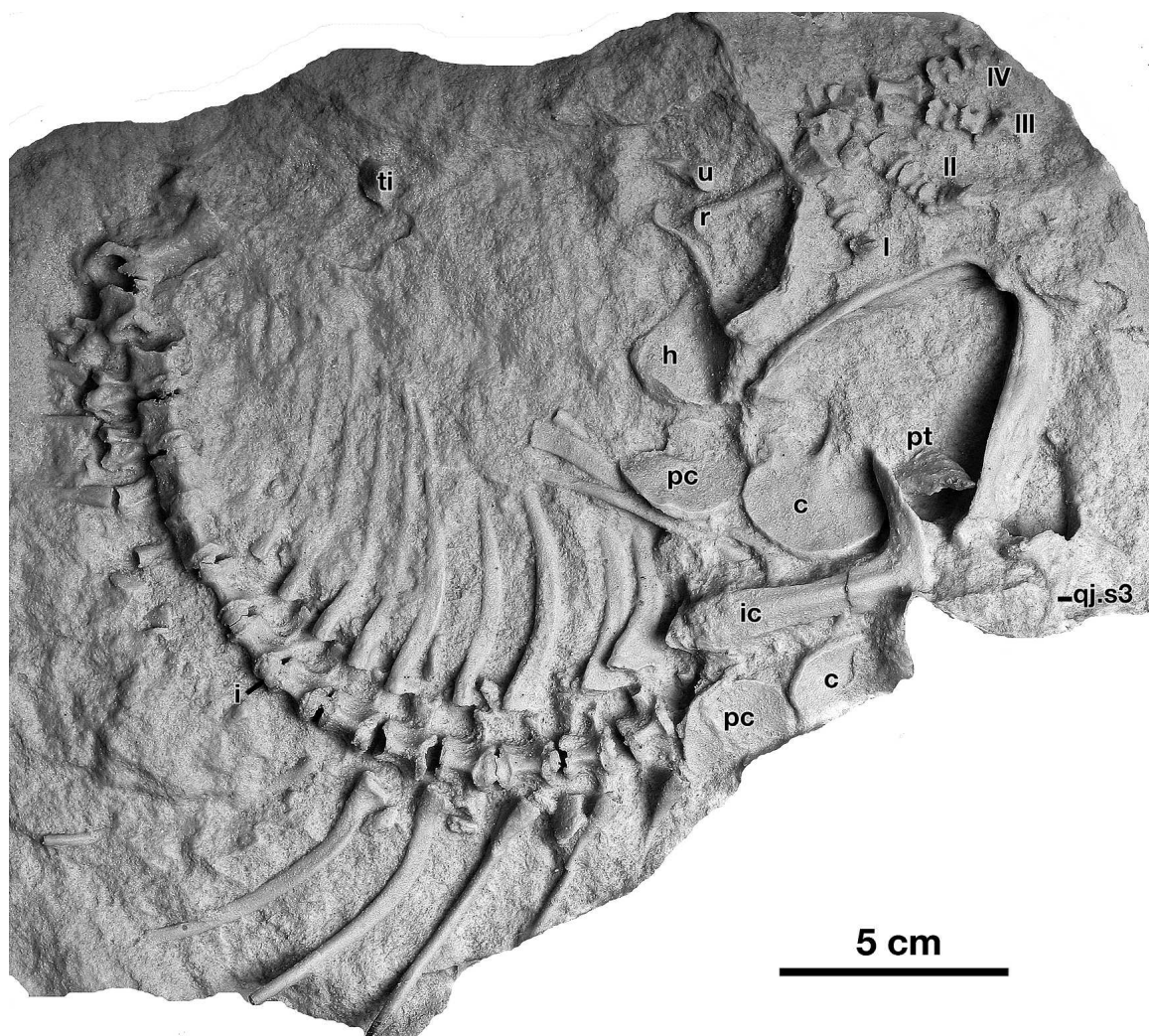
FIGURE 3. *Sclerosaurus armatus*, holotype of "*Labyrinthodon*" *ruetimeyeri* Wiedersheim, 1878 (Bs. 28). Silicon-rubber cast of skeleton in ventral view. Abbreviations as in Figure 2.

of the orbitotemporal opening is broadly rounded anteriorly and somewhat tapered posteriorly (Fig. 4A). Rieth's (1932:fig. 1) diagrammatic interpretation depicting a smaller, more rounded orbit is not supported by the preserved impressions. There is little evidence of external sculpturing on the exposed cranial elements. A long spine projects posterolaterally from what is probably the supratemporal; it presumably corresponds to the acute posterolateral corner of the supratemporal in procolophonids (Fig. 4). It is 22 mm tall, conical, and bears sculpturing composed of longitudinal ridges and grooves. Similar ridging has been observed in *Hypsognathus* (Sues et al., 2000). The spine surmounts a 20 mm tall pedicle and is set off from it by a raised rim, which bears a small dorsal protuberance. A pair of smaller, dorsoventrally flattened spines is present on the presumed quadratojugal; the posterior spine projects posterolaterally and is more conical than the laterally directed anterior spine. An additional conical, posterolaterally projecting spine is situated posteroventral to the posterior of the paired spines, close to the jaw joint; it is clearly visible on the counterslab of Bs. 28. The presence of two or more spines on the quadratojugal is considered diagnostic for leptopleuronines (Modesto et al., 2002).

Part of the margin of the right external narial fenestra is visible near the tip of the snout and faces anterolaterally. There is no trace of an anterolateral depression on the maxilla posterior to the external naris, as in *Scoloparia*, *Hypsognathus*, and *Leptopleuron*. Each premaxilla has two conical teeth. The right maxilla holds seven bluntly conical teeth; the small seventh tooth is situated at the level of the anterior margin of the orbitotemporal opening. The bases of the teeth are oval in transverse section, with the long axis directed slightly mesiolingually. The lateral margin of the right internal naris indicates that the opening did not curve posteromedially, as it does in pareiasaurs (Lee, 1997). The right jugal has a distinctly concave ventral margin. It contacts the maxilla anteriorly and the broad lateral portion of the ectopterygoid anteromedially. The frontal region is delimited ventrolaterally by distinct cristae cranii, which border the flat ventral surface of the interorbital region of the skull roof and posteriorly extend onto the parietals. The outline of the large pineal foramen, clearly evident in Wiedersheim's (1878:pl. II, fig. 3) illustration, is barely visible now, but the opening is situated at or close to the level of the posterior margin of the orbitotemporal opening and just behind the inferred frontoparietal suture. The posterior margin of the skull roof is gently convex in dorsal view. Occipital flanges, presumably formed by the parietals, are set off from the skull roof by a distinct ridge. A (broken) ventromedial projection of the parietals presumably contacted the
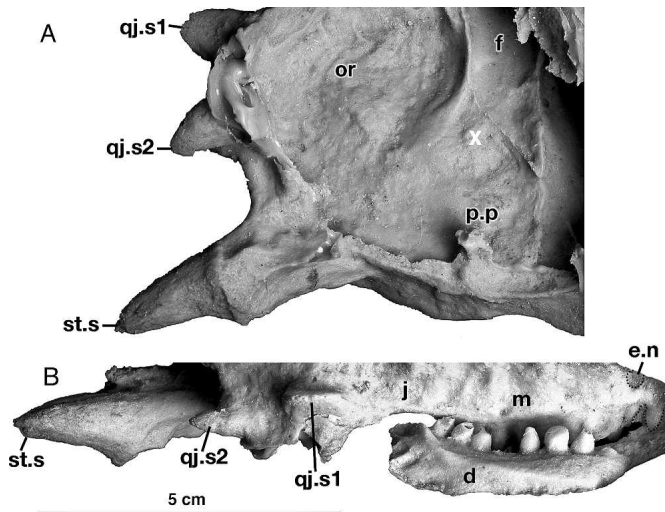
FIGURE 4. *Sclerosaurus armatus*, Bs. 28. Skull in (**A**) ventral and (**B**) right lateral view. X marks the position of the pineal foramen (now barely visible).

supraoccipital anterior to the posterior margin of the skull roof, as, for example, in *Hypsognathus* (Sues et al., 2000). The tapering distal portion of what appears to be the ventrolaterally projecting flange of the left pterygoid is visible near the left mandibular ramus (Fig. 3).

The mandible is shorter than the skull (length of ramus: ca. 60 mm), and the jaw joint is situated anterior to the posterior edge of the skull roof. The lower jaws have been slightly displaced to the right side post mortem, exposing what appears to be the distal articular surface of the left quadrate. In ventral view, the mandible is broadly V-shaped with a blunt, broadly rounded symphysis (Fig. 3). Its rami are not fused to each other. The mandibular symphysis forms a short posteroventral projection, which is evident in lateral view. The dentary (Fig. 5) holds eight teeth. The more complete tooth row of the right element preserves six tooth crowns. The first tooth is represented only by its
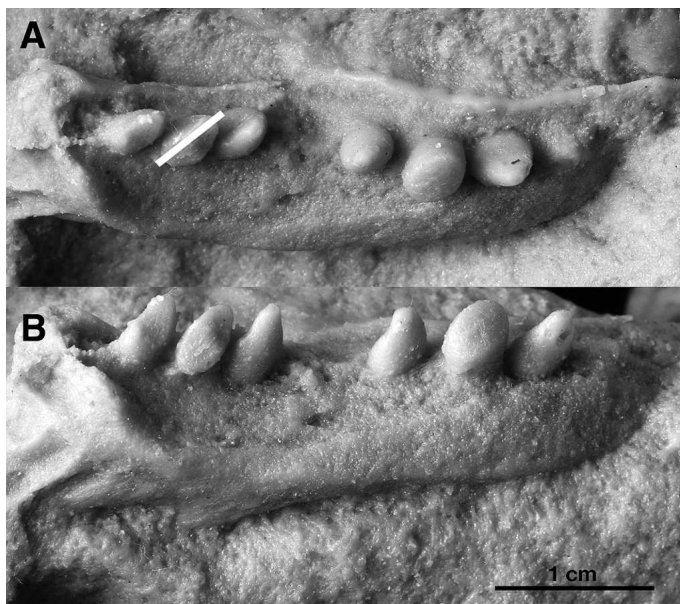

FIGURE 5. *Sclerosaurus armatus*, Bs. 28. Right dentary in (**A**) occlusal and (**B**) lateral view.

base and is followed by a set of three teeth (2–4). This triplet is separated from a posterior set of three teeth (6–8) by the broken base of a tooth (5). The tooth crowns are bluntly conical and slightly labiolingually flattened. No serrations or cusps are visible on the casts of any of the teeth. The posterior three teeth have more distinctly flattened crowns with mesial and distal carinae. The crowns of successive teeth in this part of the tooth row slightly overlap each other in labial view. Their bases are oval in cross-section and have mesiolingually directed long axes. The third, seventh, and eighth tooth crowns have dorsolabially facing, poorly defined wear facets. The lower tooth row is distinctly inset from the lateral edge of the dentary. The lateral surface of the dentary bears a well-developed longitudinal ridge that extends posteriorly to the slightly raised coronoid region. Based on the right mandibular ramus, the dentary does not significantly increase in dorsoventral height posteriorly, unlike in *Hypsognathus* and *Leptopleuron*. The ventral margin of the dentary is gently concave in lateral view. A clearly visible suture on the left mandibular ramus (Fig. 3) establishes that the splenial terminates anteriorly behind the symphysis, unlike in pareiasaurs (Lee, 1997); the anterior portion of the Meckelian groove is exposed on the lingual surface of the jaw. The surangular (visible on the left side) bears a lateral ridge but lacks the distinct lateral process present in *Hypsognathus*. No other sculpturing except for some faint grooves is evident on the external surface of the mandibular ramus. The retroarticular portion of the jaw is short. The articular facet of the jaw joint appears to be situated somewhat below the level of the dentary tooth row. The ventral margin of the angular forms a sharp edge, which, contra Lee (1997: 227), shows no trace of an angular boss. The foramen intermandibularis caudalis is visible at the level of the coronoid process on the right mandibular ramus.

Postcranial Skeleton

Specimen Bs. 28 of *Sclerosaurus armatus* measured about 50 cm from the tip of the snout to the distal end of the tail. It had a stocky overall build, with a broad, barrel-shaped trunk, sturdy limbs, and a short tail. A narrow median band of dorsal dermal armor extends from the posterior cervical region back to the sacrum.

Postcranial Axial Skeleton—It is difficult to determine the precise number of presacral vertebrae in Bs. 28 because the anterior end of the cervical column is not exposed. Counting forward from the first sacral vertebra, we identified 19 presacrals in series, to which the atlas and axis must be added for a total complement of 21. Huene (1902, 1912) assumed the presence of 20 to 22 and 24 presacral vertebrae, respectively. Lee (1995, 1997) counted 21 to 22 and 20 to 21 presacrals, respectively. By comparison, *"Owenetta" kitchingorum* has 26 or 27 presacral vertebrae (Reisz and Scott, 2002) and *Procolophon* has 26 (Broili and Schröder, 1936) or 27 (deBraga, 2003).

The neural spines of the more anterior cervical vertebrae are longer and more slender than those of the dorsals, but there is no obvious structural transition between the cervical and dorsal series. The centra of the dorsal vertebrae are constricted at midlength, with a median ridge separating the ventrolateral depressions ventrally. They are deeply amphicoelous, with almost funnel-shaped anterior and posterior articular surfaces, 10–11 mm long, and 9–10 mm wide at the wider anterior end of the centrum. The ventral margins of the centra are concave in lateral view. The tall neural spines are flattened transversely and have slightly expanded apices. The transverse processes are robust, especially on the more posterior dorsals, and separated from the postzygapophyses by deep lateral notches. The neural arches are robust and wider than long. The pre- and postzygapophyses diverge sharply from the midline in dorsal view and bear large, (where exposed) nearly horizontally oriented articular facets.

Well-developed intercentra are present along the entire dorsal vertebral column; the length of each intercentrum is approximately half that of a pleurocentrum.

The sacrum comprises three vertebrae. The neural arches and spines of the sacrals closely resemble those of the posterior dorsals. The first sacral rib is the most massive and appears to be fused to the transverse process of its vertebra. Its distal end for contact with the medial surface of the iliac blade is expanded. The second sacral rib is similar to the first but more slender in build; its distal end appears to contact that of the first rib.

The short tail (Fig. 2) comprises at least 11 vertebrae, but details of the more distal caudal region are poorly preserved. All caudals have short centra, which further decrease in length toward the distal end of the tail. The more anterior vertebrae have slender, straight transverse processes. A few displaced chevrons are visible.

The maximum width of the ribcage is close to the estimated distance from the scapulocoracoid glenoid to the acetabulum. Ribs extend all the way back along the presacral vertebral column, and there is no distinct 'lumbar' region (Figs. 2, 3). The dorsal ribs each have a single, vertically oriented proximal head and shafts that gently curve ventrally from the proximal ends and taper slightly toward their distal ends. A faint median groove extends along the posterodorsal surface of the rib shaft.

There is no trace of gastralia elements, unlike in *Koiloskiosaurus* and *Leptopleuron* (Huene, 1912) or *Procolophon* (Broili and Schröder, 1936; deBraga, 2003).

Dermal Armor—A narrow median band of dorsal dermal armor extends from the posterior cervical region back to the sacrum, where it terminates rather abruptly (Fig. 2). The armor comprises two or three rows of osteoderms overlying the vertebral column on either side of the midline (Figs. 1, 2). On either side of each neural spine, a suboval to subrectangular, thick osteoderm extends posterolaterally over the postzygapophysis. Its dorsal surface bears sculpturing composed of irregular pits, but, unlike in pareiasaurs (e.g., Lee, 1997), it lacks a central boss or keel. Lee's (1997:252) claim that "[m]aterial of *Sclerosaurus* includes both smooth and ornamented osteoderms" is incorrect. Huene (1932:225) extracted an osteoderm from the holotype of *S. armatus* and established that its dorsal surface was sculptured (Huene, 1932:fig. 12). This is also the case for all osteoderms exposed in dorsal view on the referred specimen Bs. 28. Fine wrinkling covers the ventral surfaces of the osteoderms on the holotype. Lateral to each median osteoderm, a smaller, rounded plate overlies the intercostal space in Bs. 28; it also bears dorsal sculpturing. Huene (1902) first observed a third row of more sparsely distributed, small plates. All osteoderms are separated from each other by small gaps. In the holotype of *Sclerosaurus armatus*, details of the arrangement of the armor are more clearly visible than in Bs. 28 (Fig. 1). The holotype differs in having unpaired, more or less rhombic median osteoderms on the more posterior dorsal vertebrae. More anteriorly, however, the large osteoderms lateral to the neural spines are accompanied by one or two smaller plates laterally, as in Bs. 28.

Pectoral Girdle—The blade of the scapula is tall (height: 51 mm) and narrow (Fig. 2). It slightly flares distally and is gently curved along its entire length. An acromion process is absent, but there is a ridge, which Seeley (1900) interpreted as the acromion, near an anterior expansion of the proximal portion of the element. The scapula bears a distinct, posteroventrally facing glenoid facet. The paired coracoids (Figs. 3) are plate-like, the anterior being longer than the posterior (31 vs. 25 mm); together, they are larger than the scapula. The posterior coracoid bears a well-developed glenoid facet. The interclavicle, originally misidentified by Wiedersheim (1878:fig. 1) as the humerus, is T-shaped, with paired anterolateral processes (only the right of which is preserved) and a long posterior process (Fig. 2). The reconstructed width of the element (58 mm) exceeds its length

(52 mm). The anterolateral process of the interclavicle has a vertical anterior surface that is grooved for the reception of the clavicle (which is not preserved); the anteroventral edge of the process is raised along its entire length. The posterior process (stem) of the interclavicle bears a low ventromedial ridge and expands slightly toward its posterior end.

Forelimb—The robust humerus, originally misidentified by Wiedersheim (1878:fig. 1) as the scapula, is 53 mm long (Figs. 2, 3). Its rather narrow proximal end bears a distinct facet for articulation with the scapulocoracoid glenoid. The large deltopectoral crest encloses a wide ventral fossa with the remainder of the proximal portion of the humerus. A short shaft links the expanded articular ends of the humerus. The distal articular end is broad and set at a distinct angle to the proximal end. The entepicondylar foramen is large. There is no trace of an ectepicondylar foramen or groove. The distal end is divided into a flattened trochlea (ulnar condyle) and a slightly convex, dorsoventrally ovoid capitulum (for articulation with the radius), which is situated entirely on the ventral surface of the bone.

The radius and ulna (Figs. 2, 3) are both shorter than the humerus. The ulna is distinctly longer (length: 42 mm) and more robust than the radius (length: 32 mm). Its moderately developed olecranon has a rugose surface texture presumably related to the tendinous insertion of M. triceps. The proximal end of the ulna is more expanded than the distal one, and its articular facet is obliquely inclined relative to the long axis of the bone. The shaft of the ulna is slightly bowed. The radius has an almost straight shaft. Its distal end is more expanded and robust than the proximal end and terminates in a flat, oval articular facet.

The carpus (Figs. 2, 3) comprises a proximal row of two elements and a distal set of four or five bones. Four digits of the right manus are visible in ventral (plantar) view near the right mandibular ramus on the counterslab. Manual digit I has two phalanges and digits II and III each have three; three proximal elements of digit IV are preserved, with the remainder lost along the edge of the cast. Metacarpal IV is the largest. The preungual phalanges are rather short and broad, shorter than the metacarpals. The well-developed ungual phalanges are longer than the penultimate phalanges and gently curved.

Pelvic Girdle—The ilium is tall (height: 43 mm) and oriented vertically (Fig. 2). Both the anterodorsal and posterodorsal edges of the iliac blade are slightly reflected so that its lateral surface is concave anteroposteriorly. The blade flares dorsally and has a modestly developed posterior process. The large acetabulum has a raised dorsal rim, especially anteriorly, but lacks a distinct supra-acetabular buttress. It is separated from the iliac blade by a slight constriction. Most of the medial surface of the blade (exposed on the left ilium; Fig. 2) dorsal to the constriction forms a rugose surface for contact with the sacral ribs, delimited by a weak crista sacralis.

The pubis (partially visible in medial view on the left side; Fig. 2) is anteroposteriorly short. It forms a straight, vertical contact with the ischium.

The ischium (length of right element: 33 mm) forms the posteroventral portion of the acetabulum and is larger than the pubis. The ventromedial margin of the bone forming the symphysis with its fellow is thick. The dorsolateral margin of the ischium is deeply concave anteroposteriorly and forms a laterally directed process at its posterior end (Fig. 2).

Hindlimb—The femur (Fig. 2) is relatively slender and slightly longer than the humerus (55 mm vs. 53 mm), unlike in pareiasaurs, which have broad, massive femora. In lateral view, it has a somewhat sigmoid curvature so that the proximal articular end is slightly deflected dorsally. Based on the holotype of *Sclerosaurus armatus*, the proximal articular surface of the femur is narrow but long anteroposteriorly (Fig. 1). The internal trochanter is separated from the proximal head of the femur but appears to be linked to it by a ridge. Distal to the head, there is a ridge

and associated depression, which may represent the insertion for M. puboischiofemoralis internus, and a short ridge along the posteroventral margin may be related to M. iliofemoralis. The dorsal (extensor) aspect of the distal portion of the femur bears a narrow intercondylar sulcus, which turns into a canal close to the distal articular end, as first noted by Seeley (1900).

The robust tibia (length: 34 mm) bears a prominent cnemial crest, which extends far distally along the lateral aspect of the bone and borders a deep, V-shaped groove on the bowed shaft (Fig. 2). Distally, the crest is continued as a distinct ridge. A second, less prominent ridge forms the medial margin of the groove. The expanded distal articular end of the tibia bears a large facet for contact with the astragalocalcaneum.

The fibula (length: 37 mm) is longer and more slender than the tibia (Fig. 2). It has a bowed shaft, which expands toward the distal end. The slightly expanded proximal end of the fibula bears an obliquely inclined articular facet.

Astragalus and calcaneum form a single massive, more or less triangular element (greatest dimension: 17 mm; Fig. 2). Although a faint suture is still discernable between the two bones on the right side, we can confidently interpret this element as an as-tragalocalcaneum. The element bears well-defined tibial and fibular facets along its proximal edge. Neither pes preserves any distal tarsals, and, in view of the otherwise excellent preservation of Bs. 28, it would appear that these elements were not ossified.

Metatarsals I and II are more robust than the others, which progressively increase in length. Pedal digit I comprises two pha-langes, and digits II and III each have three. According to Huene (1902, 1920), digit IV has four phalanges, but we could not verify this count on the casts used in this study. Pedal digit V is only represented by its metatarsal. The preungual phalanges are short, with length and width being more or less equal. The ro-bust, bluntly conical unguals are almost twice as long as the preungual phalanges. Ventrally, the ungual phalanges bear dis-tinct flexor tubercles close to their proximal articular ends.

PHYLOGENETIC POSITION OF *SCLEROSAURUS ARMATUS*

As noted in the introduction, the phylogenetic relationships of *Sclerosaurus armatus* have long been contentious. Our restudy of the two known specimens of this taxon has now resolved con-flicting interpretations concerning a number of anatomical fea-tures, facilitating reassessment of the phylogenetic position of *Sclerosaurus* in the context of various recent reviews of para-reptilian interrelationships (Lee, 1995, 1997; Laurin and Reisz, 1995; Modesto et al., 2001, 2002; Reisz and Scott, 2002; deBraga, 2003).

We reviewed the character-taxon matrix compiled by deBraga (2003), which drew in part on the aforementioned reviews, and modified it by excluding a number of operationally problemati-cal characters and rescoring others (see Appendices 1 and 2 for further details). Character states for *Sclerosaurus* were coded on the basis of Bs. 28, and several character states for other para-reptilian taxa were reassessed based on first-hand examination of the original fossils or high-quality casts. As an exemplar of Pa-reiasauria, we selected the well-known taxon *Scutosaurus* from the Upper Permian of Russia (Bystrov, 1957; Ivakhnenko, 1987; Lee, 1997). Some character states for *Macroleter* from the Upper Permian of Russia were modified based on the redescription of its skull by Tsuji (2006). As a representative of Owenettidae, we chose the well-documented "*Owenetta*" *kitchingorum* Reisz and Scott, 2002 from the Lower Triassic *Lystrosaurus* Assemblage Zone of South Africa. We did not include *Koiloskiosaurus* from the Middle Buntsandstein of Germany (Huene, 1911, 1912) be-cause we did not examine first-hand casts or specimens of this taxon, which is in need of reassessment. Modesto and Damiani (2003) considered *Thelegnathus* from the Lower to lower Middle

Triassic *Cynognathus* Assemblage Zone of South Africa a nomen dubium, and segregated the various species previously referred to *Thelegnathus* into four new monotypic genera. We could not ascertain which of these genera were coded by de-Braga (2003) for particular characters and thus have deleted *Thelegnathus* from the analysis. We added *Scoloparia* from the Upper Triassic (Carnian) Wolfville Formation of Nova Scotia, Canada, based on the original account by Sues and Baird (1998) and additional specimens currently under study by H.-D.S. Fi-nally, we added character states for *Sauropareion* from the *Lys-trosaurus* Assemblage Zone on the basis of the detailed account by Modesto and Damiani (2007). *Sauropareion* was first hypoth-esized as the sister taxon of Procolophonidae by Modesto et al. (2001), but Modesto and Damiani (2007) included it in their phylogenetically defined taxon Procolophonidae.

The revised character-taxon matrix, comprising 12 taxa of Pararcptilia and 51 characters (Appendix 2) was compiled in MacClade 4.0 (Maddison and Maddison, 2000) and analyzed us-ing parsimony analysis with the heuristic search algorithm in PAUP* 4.0b10 (Swofford, 2002). All characters were treated as unordered in the analysis, and no character weighting was used.

We discovered two most parsimonious trees (MPTs), each with a tree length of 75 steps, a Consistency Index (CI) of 0.720 (CI excluding uninformative characters: 0.691), a Retention In-dex (RI) of 0.792, and a Rescaled Consistency Index (RC) of 0.570. *Sclerosaurus* is clearly placed among Procolophonidae, as first suggested by Seeley (1900), and, more specifically, with Lep-topleuroninae, as argued by deBraga (2003) based on brief in-spection of the casts prepared for our study. The MPTs only differ in the placement of the four OTUs (*Hypsognathus, Lep-topleuron, Sclerosaurus*, and *Scoloparia*) relative to each other. A strict consensus tree is presented in Figure 6. Bootstrap analy-sis with 1,000 replicate runs (with TBR branch swapping and MULPARS in effect) found 88% support for a clade comprising *Hypsognathus, Leptopleuron, Sclerosaurus*, and *Scoloparia* and 58% support for a previously recognized grouping comprising *Hypsognathus* and *Leptopleuron* (Colbert, 1946; Sues et al., 2000). For both trees, the only unambiguous synapomorphies for Leptopleuroninae are character states 15.2, presence of two or more spines on the quadratojugal, and 28.1, transverse flange of pterygoid extending well below marginal dentition. The only un-ambiguous autapomorphy for *Sclerosaurus* found for both trees is character state 48.1, presence of an intercondylar canal on the femur; this feature is elsewhere present only in pareiasaurs (Lee, 1995, 1997). Several additional apomorphic character states,
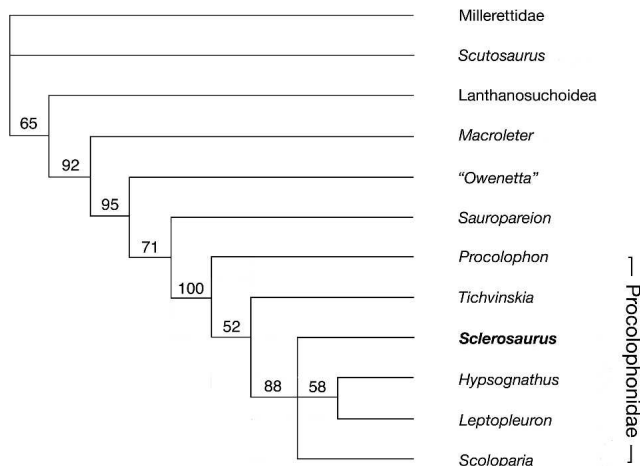

FIGURE 6.   Strict consensus tree derived from parsimony analysis of 12 taxa of Parareptilia and 49 characters (for further details see Appendices 1 and 2). For each node, the percentage of support found by the boot-strap analysis is given.

however, clearly distinguish *Sclerosaurus* from *Hypsognathus, Leptopleuron*, and *Scoloparia*. Although *Sclerosaurus* and *Scoloparia* share the presence of dorsal dermal armor, the osteoderms in *Sclerosaurus* form a narrow median band along the back whereas they form a nuchal shield in *Scoloparia* (to date observed only in the holotype of *S. glyphanodon*) and other dorsal armor is absent in the latter (H.-D. S., unpublished data). *Sclerosaurus* is further distinguished from other known leptopleuronines by its dentition, particularly the obliquely set, labiolingually flattened crowns of the more posterior dentary teeth. Mesiodistal rather than labiolingual alignment of the cutting edges is elsewhere present on the posterior dentary and maxillary tooth crowns of the poorly known procolophonid *Acadiella* from the Upper Triassic Wolfville Formation of Nova Scotia (Sues and Baird, 1998). Pareiasaurs have mesiodistally expanded, leaf-shaped tooth crowns with distinctly cuspidate cutting edges (Lee, 1997). *Sclerosaurus* is less derived than *Hypsognathus* and *Leptopleuron* in lacking an anteroventrally facing ventral margin of the jugal, lacking the broad distal expansion of the transverse flange of the pterygoid, and having more than one anterior dentary tooth (Sues et al., 2000).

Sclerosaurus is readily distinguished from all other known pareptiles by the presence of long, posterolaterally directed supratemporal spines. Huene (1920, 1956) noted a resemblance between these spines and the prominent supratemporal projections in the small pareiasaur *Elginia mirabilis* Newton, 1893 from the Upper Permian Cutties Hillock Sandstone Formation of Scotland, but no other features support a closer relationship between *Elginia* and *Sclerosaurus* (Lee, 1997; Jalil and Janvier, 2005). In addition to sharing the presence of an intercondylar canal on the distal end of the femur, *Sclerosaurus* resembles pareiasaurs and differs from other known procolophonids (e.g., *Leptopleuron*) in the apparent absence of gastralia and in the possession of a short tail.

With a total length of about 50 cm, Bs. 28 is the largest procolophonid skeleton found to date. Dias-da-Silva et al. (2007) recently referred to *Procolophon* vertebrae from the Lower Triassic Sanga do Cabral Formation of Rio Grande do Sul (Brazil), which are comparable in size to those of Bs. 28. DeBraga (2003) stated that total length in *Procolophon trigoniceps* ranges from 15 to over 30 cm. However, the latter figure was based on a large, headless skeleton from the *Cynognathus* Assemblage Zone of South Africa that is probably not referable to *Procolophon*, which is otherwise known only from the underlying *Lystrosaurus* Assemblage Zone (Cisneros, in press). *Leptopleuron lacertinum* from the Upper Triassic Lossiemouth Sandstone Formation of Scotland can reach a length of up to 25 cm (Säilä, 2006). Judging on the basis of its dentition and its broad, barrel-shaped trunk, *Sclerosaurus* was probably herbivorous, much as inferred for other derived procolophonids (Reisz and Sues, 2000).

Referral of *Sclerosaurus* to the Procolophonidae is consistent with recent observations that the diversity of Early Triassic procolophonoid pareptiles was significantly greater than previously assumed (Modesto et al., 2001). It also lends further support to previous suggestions that the stratigraphic range of the Pareiasauria did not extend across the Permo-Triassic boundary (Cisneros et al., 2005). This leaves a significant gap in the fossil record between the stratigraphically youngest known pareiasaurs from the latest Permian and their putative descendants, turtles, which date back to the Late Triassic.

ACKNOWLEDGMENTS

LITERATURE CITED

Baur, G. 1897. Pareiasauria Seeley (Cotylosauria Cope) from the Triassic of Germany. Science (n.s.) 5:720–722.

Broili, F., and J. Schröder. 1936. Beobachtungen an Wirbeltieren der Karrooformation. XXI. Über *Procolophon*. Sitzungsberichte der Bayerischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Abteilung 1936:239–256.

Bystrov, A. P. 1957. Cherep pareiazavra. Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR 68:3–18.

Cisneros, J. C. In press. Taxonomic status of the reptile genus *Procolophon* from the Gondwanan Triassic. Palaeontologia Africana.

Cisneros, J. C., F. Abdala, and M. C. Malabarba. 2005. Pareiasaurids from the Rio do Rasto Formation, southern Brazil: biostratigraphic implications for Permian faunas of the Paraná Basin. Revista Brasileira de Paleontologia 8:13–24.

Colbert, E. H. 1946. *Hypsognathus*, a Triassic reptile from New Jersey. Bulletin of the American Museum of Natural History 86:225–274.

Cope, E. D. 1889. Synopsis of the families of Vertebrata. American Naturalist 23:849–877.

deBraga, M. 2003. The postcranial skeleton, phylogenetic position, and probable lifestyle of the Early Triassic reptile *Procolophon trigoniceps*. Canadian Journal of Earth Sciences 40:527–556.

Dias-da-Silva, S., S. P. Modesto, and C. L. Schultz. 2007. New material of *Procolophon* (Parareptilia: Procolophonidae) from the Lower Triassic of Brazil, with remarks on the ages of the Sanga do Cabral and Buena Vista formations of South America. Canadian Journal of Earth Sciences 43:1685–1693.

Fischer [L. H.] 1857. Über *Sclerosaurus armatus* Meyer, eine neue Saurier-Gattung aus dem Bunten Sandstein bei Warmbach gegenüber Rheinfelden. Neues Jahrbuch für Mineralogie, Geologie, Geognosie und Petrefakten-Kunde 1857:136–140.

Fraser, N. C., and O. Rieppel. 2006. A new protorosaur (Diapsida) from the Upper Buntsandstein of the Black Forest, Germany. Journal of Vertebrate Paleontology 26:866–871.

Gauthier, J. A., A. G. Kluge, and T. Rowe. 1988. The early evolution of the Amniota; pp. 103–155 in M. J. Benton (ed.), The Phylogeny and Classification of the Tetrapods. Vol. 1: Amphibians, Reptiles, Birds. Systematics Association Symposium Volume 35A. Clarendon Press, Oxford.

Haubold, H. 1971. Die Tetrapodenfährten des Buntsandsteins in der Deutschen Demokratischen Republik und in Westdeutschland und ihre Äquivalente in der gesamten Trias. Paläontologische Abhandlungen, Abteilung A: Paläozoologie 4(3):397–548.

Huene, F. von. 1902. Übersicht über die Reptilien der Trias. Geologische und Palaeontologische Abhandlungen, N. F. 6(1):1–84.

Huene, F. von. 1911. Ueber die Procolophoniden, mit einer neuen Form aus dem Buntsandstein. Centralblatt für Mineralogie, Geologie und Paläontologie 1911(3):78–83.

Huene, F. von. 1912. Die Cotylosaurier der Trias. Palaeontographica 59:69–102.

Huene, F. von. 1920. *Sclerosaurus* und seine Beziehungen zu anderen Cotylosauriern und zu den Schildkröten. Zeitschrift für induktive Abstammungs- und Vererbungslehre 24:163–166.

Huene, F. von. 1932. Ein neuartiger Stegocephalen-Fund aus dem oberhessischen Buntsandstein. Palaeontologische Zeitschrift 14:200–229.

Huene, F. von. 1943. Zur Beurteilung der Procolophoniden. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Monatshefte 1943:192–198.

Huene, F. von. 1956. Paläontologie und Phylogenie der niederen Tetrapoden. Gustav Fischer Verlag, Jena, 716 pp.

International Commission for Zoological Nomenclature. 1999. International Code of Zoological Nomenclature. Fourth Edition. The International Trust for Zoological Nomenclature, London, 306 pp.

Ivakhnenko, M. F. 1979. Permskiye i triasovyye prokolofony Russkoy platformy. Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR 164:1–80.

Ivakhnenko, M. F. 1987. Permskiye parareptilii SSSR. Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR 223:1–160.

Jaeger, G. F. von. 1828 Ueber die fossile [sic] Reptilien welche in Würtemberg aufgefunden worden sind. Metzler, Stuttgart, 48 pp.

Jalil, N.-E., and P. Janvier. 2005. Les pareiasaures (Amniota, Parareptilia) du Permien supérieur du Bassin d'Argana, Maroc. Geodiversitas 27:35–132.

Krebs, B. 1969. *Ctenosauriscus koeneni* (v. Huene), die Pseudosuchia und die Buntsandstein-Reptilien. Eclogae geologicae Helvetiae 62:697–714.

Kuhn, O. 1969. Cotylosauria. O. Kuhn (ed.), Handbuch der Paläoherpetologie, Teil 6. Gustav Fischer Verlag, Stuttgart, 89 pp.

Laurin, M., and R. R. Reisz. 1995. A reevaluation of early amniote phylogeny. Zoological Journal of the Linnean Society 113:165–223.

Lee, M. S. Y. 1995. Historical burden in systematics and the interrelationships of 'parareptiles'. Biological Reviews 70:459–547.

Lee, M. S. Y. 1997. Pareiasaur phylogeny and the origin of turtles. Zoological Journal of the Linnean Society 120:197–280.

Lucas, S. G., and R. R. Schoch. 2002. Triassic temnospondyl biostratigraphy, biochronology and correlation of the German Buntsandstein and North American Moenkopi Formation. Lethaia 35:97–106.

Maddison, D. R., and W. P. Maddison. 2000. MacClade 4: Analysis of Phylogeny and Character Evolution. Sinauer Associates, Inc., Sunderland, MA.

Meyer, H. von. 1859. *Sclerosaurus armatus* aus dem bunten Sandstein von Rheinfelden. Palaeontographica 7:35–40.

Milner, A. R., B. G. Gardiner, N. C. Fraser, and M. A. Taylor. 1990. Vertebrates from the Middle Triassic Otter Sandstone Formation of Devon. Palaeontology 33:873–892.

Modesto, S. P., and R. J. Damiani. 2003. Taxonomic status of *Thelegnathus browni* Broom, a procolophonid reptile from the South African Triassic. Annals of Carnegie Museum 72:53–64.

Modesto, S. P., and R. Damiani. 2007. The procolophonoid reptile *Sauropareion anoplus* from the lowermost Triassic of South Africa. Journal of Vertebrate Paleontology 27:337–349.

Modesto, S. P., R. J. Damiani, and H.-D. Sues. 2002. A reappraisal of *Coletta seca*, a basal procolophonoid reptile from the Lower Triassic of South Africa. Palaeontology 45:883–895.

Modesto, S. P., H.-D. Sues, and R. J. Damiani. 2001. A new Triassic procolophonoid reptile and its implications for procolophonoid survivorship during the Permo-Triassic extinction event. Proceedings of the Royal Society of London B 268:2047–2052.

Newton, E. T. 1893. On some new reptiles from the Elgin sandstones. Philosophical Transactions of the Royal Society of London B 184:431–503.

Nicholson, H. A., and R. Lydekker. 1889. A Manual of Palaeontology For the Use Of Students. Third Edition. Volume II. William Blackwood and Sons, Edinburgh and London, 735 pp. (numbered as pp. 889–1624).

Nopsca, F. 1923. Die Familien der Reptilien. Fortschritte der Geologie und Palaeontologie 2:1–210.

Olson, E. C. 1947. The family Diadectidae and its bearing on the classification of reptiles. Fieldiana: Geology 11:1–53.

Owen, R. 1841. On the teeth of species of the genus *Labyrinthodon* (*Mastodonsaurus salamandroides*, and *Phytosaurus* (?) of Jäger) from the German Keuper and the sandstone of Warwick and Leamington. Proceedings of the Geological Society of London 3:357–360.

Paul, J. 1999. Fazies und Sedimentstrukturen des Buntsandsteins; pp. 105–114 in N. Hauschke and V. Wilde (eds.), Trias—Eine ganz andere Welt. Verlag Dr. Friedrich Pfeil, Munich.

Reisz, R. R., and D. Scott. 2002. *Owenetta kitchingorum*, n. sp., a small parareptile (Procolophonia: Owenettidae) from the Lower Triassic of South Africa. Journal of Vertebrate Paleontology 22:244–256.

Reisz, R. R., and H.-D. Sues. 2000. Herbivory in late Paleozoic and Triassic tetrapods; pp. 9–41 in H.-D. Sues (ed.), Evolution of Herbivory in Terrestrial Vertebrates: Perspectives from the Fossil Record. Cambridge University Press, Cambridge.

Rieth, A. 1932. Schädelstacheln als Grabwerkzeuge bei fossilen und rezenten Reptilien. Palaeontologische Zeitschrift 14:182–193.

Romer, A. S. 1956. Osteology of the Reptiles. The University of Chicago Press, Chicago and London, 772 pp.

Säilä, L. 2006. New information on the Late Triassic reptile *Leptopleuron lacertinum* and its implications for the phylogeny of procolophonoid parareptiles. Journal of Vertebrate Paleontology 26(3, Supplement): 118A.

Schoch, R. R., M. Fastnacht, J. Fichter, and T. Keller. 2007. Anatomy and relationships of the Triassic temnospondyl *Sclerothorax*. Acta Palaeontologica Polonica 52:117–136.

Seeley, H. G. 1888. Researches on the structure, organization, and classification of the fossil Reptilia. Part VI. On the anomodont Reptilia and their allies. Proceedings of the Royal Society of London B 44:381–383.

Seeley, H. G. 1896. Researches on the structure, organization, and classification of the fossil Reptilia. Part X. On the complete skeleton of an anomodont reptile (*Aristodesmus Rütimeyeri*, Wiedersheim) from the Bunter Sandstone of Riehen, near Basel, giving new evidence of the relation of the Anomodontia to the Monotremata. Proceedings of the Royal Society of London B 59:167–169.

Seeley, H. G. 1900. On an anomodont reptile, *Aristodesmus Rütimeyeri* (Wiedersheim), from the Bunter Sandstone near Basel. Quarterly Journal of the Geological Society of London 56:620–645.

Spencer, P. S., and G. W. Storrs. 2002. A re-evaluation of small tetrapods from the Middle Triassic Otter Sandstone Formation of Devon, England. Palaeontology 45:447–467.

Sues, H.-D., and D. Baird. 1998. Procolophonidae (Reptilia: Parareptilia) from the Upper Triassic Wolfville Formation of Nova Scotia, Canada. Journal of Vertebrate Paleontology 18:525–532.

Sues, H.-D., P. E. Olsen, D. M. Scott, and P. S. Spencer. 2000. Cranial osteology of *Hypsognathus fenneri*, a latest Triassic procolophonid reptile from the Newark Supergroup of eastern North America. Journal of Vertebrate Paleontology 20:275–284.

Swofford, D. 2002. PAUP*: Phylogenetic Analysis Using Parsimony (*And Other Methods). Version 4.0b10. Sinauer Associates, Inc., Sunderland, MA.

Tsuji, L. A. 2006. Cranial anatomy and phylogenetic affinities of the Permian parareptile *Macroleter poezicus*. Journal of Vertebrate Paleontology 26:849–865.

Wiedersheim, R. 1878. *Labyrinthodon Rütimeyeri*. Ein Beitrag zur Anatomie von Gesammtskelet und Gehirn der triassischen Labyrinthodonten. Abhandlungen der Schweizerischen Paläontologischen Gesellschaft 5:1–56.

Wiedersheim, R. 1879. Ueber einen neuen Saurus aus der Trias. Abhandlungen der Schweizerischen Paläontologischen Gesellschaft 6(2):1–6.

Wild, R. 1998. Leben in der Flusslandschaft des Buntsandsteins; pp. 37–44 in E. P. J. Heizmann (ed.), Vom Schwarzwald zum Ries. Erdgeschichte mitteleuropäischer Regionen, Vol. 2. Verlag Dr. Friedrich Pfeil, Munich.

Ziegler, P. A. 1982. Geological Atlas of Western and Central Europe. Shell International Petroleum Maatschappij B.V., The Hague, 130 pp.

Zittel, K. A. von. 1888. Ueber "*Labyrinthodon Rütimeyeri* Wiedersheim." Neues Jahrbuch für Mineralogie, Geologie und Palaeontologie 1888(2):257–258.

APPENDIX 1.   Character list for phylogenetic analysis of selected parareptilian taxa.

Character numbers used by deBraga (2003) are indicated in brackets; where possible, the original source for the character has been cited in parentheses.

1[2].   Premaxillary teeth: equal in size (0); first two teeth enlarged (1).

2.   Premaxillary tooth count: four or more (0); two or three (1). (Modified from Modesto et al. [2001]).

3[4].   Lacrimal-narial contact: lacrimal reaching posterior margin of external naris (0); lacrimal excluded from posterior border of external naris (1).

4[5].   Maxilla lateral depression: maxilla behind posterior margin of external naris without any significant changes to surface (0); anterolateral depression present (1). (Modified from Modesto et al. [2002]).

5[6].   Maxillary tooth row: extending well posterior to level of anterior margin of orbit (0); terminating at about level of anterior margin of orbit (1). (Modified from Gauthier et al. [1988]).

6.   Maxillary teeth: flush with labial surface of maxilla (0); inset (1). (Modesto et al., 2001).

7[7]. Caniniform region: distinct (0); absent (1). (Gauthier et al., 1988).

8[8]. Maxilla-quadratojugal contact: present (0); absent (1). (Gauthier et al., 1988).

9[9]. Prefrontal anterior extent: not extending past anterior limit of frontal (0); extending past anterior limit of frontal (1). Character state 1 appears to be present in all procolophonoids.

10[10]. Prefrontal dorsomedial process: absent (0); present (1). (Lee, 1995). Contra deBraga (2003), the process cannot be described as "bulbous" in most procolophonoid taxa.

11[12]. Postfrontal: present (0); absent (1). The postfrontal is probably fused to the parietal rather than absent in various procolophonid taxa (e.g., *Hypsognathus*; Sues et al., 2000).

12[13]. Jugal anterior extent: extending beyond anterior orbital margin (0); terminating prior to reaching anterior orbital margin (1). (Laurin and Reisz, 1995). DeBraga (2003) incorrectly coded the condition in leptopleuronines, where the jugal extends well beyond the anterior margin of the orbit anteriorly (e.g., *Hypsognathus*; Sues et al., 2000).

13[14]. Jugal embayment: absent (0); V-shaped ventral embayment formed between jugal and quadratojugal (1); jugal with smooth concave ventral margin (2).

14[15]. Quadratojugal dorsal extent: restricted to ventral margin of posterior cheek region (0); dorsally expanded (1). (Laurin and Reisz, 1995).

15[16]. Quadratojugal, ornamentation of lateral surface: spine absent (0); single posterodistally directed spine (1); two or more diverging spines (2). (Modesto et al., 2002).

16[17]. Pineal foramen position: located at about mid-point of interparietal suture (0); located close to frontoparietal suture (1). (Lee, 1995).

17[19]. Supratemporal posterolateral process: forming smooth border along posterolateral corner of skull (0); developing sharp, posterolaterally directed, spine-like process (1).

18[20]. Postparietal: present (0); absent (1). (Laurin and Reisz, 1995).

19[22]. Posterior margin of skull: smoothly contoured posterior edge of skull roof (0); with occipital shelf (1).

20[24]. Orbit posterior extent: orbit generally circular in outline (0); elongated posteriorly to reach level of anterior margin of pineal foramen (1); reaching posterior margin of pineal foramen or extending beyond (2).

21[27]. Lateral temporal fenestra: present (0); absent (1). *Procolophon* is polymorphic for this character (Cisneros, in press).

22[28]. Choana orientation: parallel to lateral margin of skull (0); deflected posteromedially and bordered by the palatine posteriorly (1). (Lee, 1995).

23[29]. Interpterygoid vacuity: elongate, anterior margin tapering to point (0); shorter, anterior margin rounded (1). The size and shape of the interpterygoid vacuity varies considerably, but the opening is shorter, broader, and more or less crescentic in derived procolophonids such as *Hypsognathus* (Sues et al., 2000).

24[30]. Cranioquadrate space: small (0); quadrate ramus of pterygoid and paroccipital process parallel (1) (Laurin and Reisz, 1995). In character state 0, the two structures converge distally, and, contra deBraga, most procolophonoids retain this character state.

25[31]. Pterygoid anterior limit: reaching posterior end of choana (0); not reaching posterior limit of choana (1). In deBraga's (2003: 554) description, his character states 0 and 1 appear to be identical; therefore, they are combined here and deBraga's state 2 is redesignated as state 1.

26[32]. Pterygoid transverse flange: directed posterolaterally (0); directed anterolaterally (1).

27[33]. Pterygoid transverse flange dentition: single row of teeth present (0); teeth absent (1). (Gauthier et al., 1988).

28[34]. Pterygoid transverse flange and marginal dentition: dentition at same level as flange (0); flange extending well below marginal dentition (1).

29[37]. Splenial anterior extent: extending to mandibular symphysis (0); excluded from mandibular symphysis (1). (Modified from Laurin and Reisz [1995]).

30[38]. Coronoid process: short (0); rising above mandibular ramus, composed only of coronoid (1). We have slightly modified the description of character state 1 because the process cannot be properly characterized as "tall" in any known procolophonoid.

31[39]. Surangular anterior extent: elongate, extending anterior to coronoid eminence (0); short, terminating behind coronoid eminence (1). (Laurin and Reisz, 1995).

32[40]. Retroarticular process configuration: absent or narrow (0) or transversely broad and dorsally concave (1). (Laurin and Reisz, 1995).

33[42]. Lower jaw position: no overbite (0); distinctive overbite (1). Based on deBraga's character description, most pararreptiles have character state 1.

34[43]. Jaw joint: more or less aligned with dentary tooth row (0); situated well below dentary tooth row (1). (Modesto et al., 2002).

35[44]. Dental configuration: maxillary and posterior dentary teeth transversely narrow (0); transversely broad, molariform (1).

36[45]. Tooth count in lower jaw: 15 or more teeth (0); nine or fewer teeth (1). DeBraga distinguished a second derived character state ("no more than six teeth"), but this only applies to *Hypsognathus* among the taxa analyzed here and thus is phylogenetically uninformative.

37[46]. (Dorsal) dermal armor: absent (0); present (1). (Gauthier et al., 1988).

38[47]. Presacral vertebral count: more than 20 (0); no more than 20 (1). (Laurin and Reisz, 1995).

39[48]. Sacral vertebral count: two (0); three or more (1). (Lee, 1995).

40[49]. Interclavicle configuration: rhomboidal (0); T-shaped (1). (Lee, 1995).

41[50]. Cleithrum: present (0); absent (1). (Gauthier et al., 1988).

42[51]. Scapula: short, broad blade (0); tall, more gracile blade (1). (Lee, 1995).

43[52]. Ectepicondylar foramen: present (0); absent (1). (Laurin and Reisz, 1995).

44[53]. Entepicondylar foramen: present (0); absent (1). (Laurin and Reisz, 1995).

45[54]. Olecranon configuration: large (0); small or absent (1). (Laurin and Reisz, 1995).

46[55]. Acetabular buttress of ilium: very weak (0); heavy, triangular (1). (Lee, 1995).

47[56]. Femoral proximal articulation: width less than half length of articular surface (0); width exceeding length (1).

48[57]. Femoral intercondylar fossa: large (0); flange and foramen present (1).

49[58]. Astragalus and calcaneum: separate elements (0); fused (1). (Gauthier et al., 1988).

50[59]. Astragalus relationship to distal tarsal 4: astragalus extending distally to same level as calcaneum (0); astragalus shortened distally to accommodate fourth distal tarsal (1).

51[60]. Ungual to penultimate phalangeal length ratio: unguals no longer than penultimate phalanges (0); terminal unguals nearly 50% longer than penultimate phalanges (1).

Operationally problematical characters removed from the analysis

1. Premaxilla posterodorsal extent: distinct dorsal exposure (0); no dorsal exposure (1). Some pareiasaurs have a short posterodorsal process, whereas it is fully visible in dorsal view in some procolophonoids. Coding of this character also depends on the orientation of the skull.

3. Narial shelf: smooth nasal surface directly above external naris (0); nasal thickened above naris, forming distinct shelf (1). Contra deBraga (2003), the derived character state is not present in most procolophonoids.

11. Frontal configuration: parallel margins of the frontal (0); margins converge anteriorly (1). The angle of the margin varies along the length of the frontal.

18. Supratemporal size: large (0); small (1). DeBraga's (2003) coding of this character is problematical. There is little difference in the relative size of the supratemporal in *Hypsognathus* and *Procolophon*. The supratemporal in *Tichvinskia* (Ivakhnenko, 1979) is intermediate in size rather than "very small" as scored by deBraga.

21. Tabular: present (0); absent (1). Lee (1997) argued that pareiasaurs have a supernumerary bone rather than a tabular.

23. Skull height to length ratio: height at least 40% length of skull (0); skull height not more than 25% of its length (1). This is not an operationally useful character because the point of maximum skull height differs in relative position among the various taxa.

25. Skull girth: skull elongate (0); length equal to or less than greatest skull width (1). This character is not useful for the same reasons given for deBraga's character 23.

26. Supraoccipital: plate-like and without tall medial crest (0); pillar-like supraoccipital (1). Although the supraoccipital forms a dorsal process in a number of procolophonoid taxa it cannot be characterized as "pillar-like" in any taxon examined by us.
35. Cultriform process: long (0); short (1). Due to postmortem and/or preparation damage, this character cannot be confidently coded in most specimens.
36. Basipterygoid tubera orientation: directed largely laterally (0); directed mainly anteriorly (1). The structure of the basipterygoid tubera in *Lanthanosuchus* is different from that in Millerettidae, and thus deBraga's coding of character state 0 for both taxa is misleading.
41. Retroarticular process composition: composed of articular (0); composed of articular, prearticular, angular, and possibly surangular (1).

APPENDIX 2.   Character-taxon matrix (12 taxa and 51 characters) for selected parareptiles used in the phylogenetic analysis.

Millerettidae
01000 0?100 00000 00000 ?0000 00000 00000 00000 0000? 0000? 0

Lanthanosuchoidea
00100 000?0 01000 ?0000 1000? 000?? 10000 0?0?1 ?0?0? ????? ?

Scutosaurus
01001 00010 0?000 0000? 01001 00000 00110 01111 11000 1011? 1

Macroleter
00100 00010 01000 00001 01011 0001? ?1000 ?0011 ?1100 00?10 0

"O." kitchingorum
00100 00111 01110 10001 00011 11011 01000 00011 01??1 0?0?? ?

Sauropareion
??1?0 0?11? 01110 10011 11011 111?? 11?00 ?0??? 0?10? ????? ?

Procolophon
00110 11111 01211 11112 00112 11011 11101 10011 11101 11011 1

Tichvinskia
01110 01111 11210 11112 00112 11011 11101 1?011 1?101 ??0?? 1

Sclerosaurus
01?00 11??? ??2?2 11?12 00??? ??111 ??1?1 11011 ?1101 1?11? 1

Scoloparia
11100 11110 11212 11112 0???? ???11 11111 11??? ???01 ?10?? ?

Hypsognathus
11101 11110 11212 11112 0011? ?1111 11111 100?? ?11?1 ????? ?

Leptopleuron
11101 111?0 01212 11112 00112 11111 11111 100?? ?1??? ??01? ?

Modified from deBraga (2003); see text and Appendix 1 for further discussion.