A new and unusual procolophonid parareptile from the Lower Triassic Katberg Formation of South Africa

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A NEW AND UNUSUAL PROCOLOPHONID PARAREPTILE FROM THE LOWER TRIASSIC KATBERG FORMATION OF SOUTH AFRICA

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ABSTRACT—A small skull collected from the base of the Katberg Formation of South Africa represents a new Early Triassic procolophonid parareptile. Phonodus dutoitorum, gen. et sp. nov., is diagnosed by a roughly straight ventral temporal margin, prefrontals that contact each other along the dorsal midline, presence of a large posterior maxillary tooth, an edentulous pterygoid, a reduced transverse flange of the pterygoid, and other autapomorphies. A cladistic analysis identifies P. dutoitorum as a basal member of the procolophonid clade Leptopleuroninae. The presence of large maxillary teeth, their position ventrally to strongly developed antorbital buttresses, and the loss of the ventral temporal emargination are suggestive of a durophagous diet. Phonodus dutoitorum is recognized as the oldest known leptopleuronine. Optimization of geographic distributions onto procolophonid phylogeny indicates that the presence of P. dutoitorum in the Karoo Basin of South Africa is explained most parsimoniously as the result of migration from Laurasia. Phonodus dutoitorum is the fifth procolophonid species to be described from the Induan of the Karoo Basin, providing further support for the hypothesis that procolophonid evolution was not greatly perturbed by the end-Permain extinction event.

INTRODUCTION

Parareptiles were the most taxonomically and ecologically diverse reptiles at the end of the Paleozoic Era, but were eclipsed by eureptiles following the end-Permian mass extinction of 252 million years ago (Mundil et al., 2004). Procolophonoids are the only parareptiles that survived this extinction event, and phylogenetic studies suggest that they experienced a reduced extinction level (Modesto et al., 2001, 2003) compared to other tetrapods. Recent field work in South Africa (Botha et al., 2007) indicates that procolophonoids of the earliest Triassic (Induan) appear to have flourished in the wake of the Mother of Mass Extinctions (sensu Erwin, 1993). Indeed, procolophonoid fossils are often locally abundant where they are present (Kitching, 1977; Li, 1983; Botha et al., 2007).

In the course of field work in the Lower Triassic Lystrosaurus Assemblage Zone, Karoo Basin of South Africa, the authors collected the skull of a small tetrapod in a block of intraformational conglomerate from the Lower Triassic Katberg Formation on the Northern Cape farm Bergendal. Little more than the weathered tips of the transverse flanges, quadrate condyles, and the alveolar regions of the maxillae were exposed in ventral aspect. Mechanical preparation revealed the skull of a small reptile of unusual morphology, one characterized by a large tooth in each maxilla, a palate with edentulous palatines and pterygoids, a reduced transverse flange of the palate, and the presence of a small lateral temporal opening. Although most of the skull table, the braincase, and the mandible are missing, the specimen preserves a suite of apomorphies that, among Permo-Triassic reptiles, is known only in procolophonids. We describe the Bergendal specimen as a new genus and species of procolophonid reptile, and discuss its implications for procolophonid evolution.

Institutional Abbreviation—NM, National Museum, Bloemfontein.

GEOLOGICAL SETTING

The skull described in this paper (NMQR 3564) was collected as part of a small block of conglomerate found ex situ atop the first major sandstone exposed on the Northern Cape farm Bergendal. The block appeared to have been ‘calved’ from a sandstone layer that lies less than 1 m above the lowermost sandstone. Collecting at the locality yielded numerous specimens of the genus Lystrosaurus attributable to L. murrayi and possibly L. declivis, and a single specimen of a small therocephalian attributable to Tetracyodon dartii (NMQR 3597). The specimens of the former genus indicate that the Lystrosaurus Assemblage Zone (AZ) broadly crops out on Bergendal. Tetracyodon dartii is known from Lystrosaurus-AZ localities in both the northern and southern portions of the Karoo Basin: the holotype is from the farm New Castle (formerly an annex of the farm Admiralty Estates) in KwaZulu-Natal Province (Sigogneau, 1963; Kitching, 1977), for which an exact placement of the fossiliferous strata in the Lystrosaurus AZ has not been determined. All referred specimens of T. dartii have been collected from localities in the southern part of the Karoo Basin, and have been positioned in the Triassic portion of the Palingkloof Member of the Balfour Formation (Damiani et al., 2004; Botha and Smith, 2006). The specimen of T. dartii collected at Bergendal was found in situ approximately 1 m below the first major sandstone. We infer that this sandstone marks the base of the Katberg Formation on Bergendal, and that NMQR 3564 comes from the base of this formation.
FIGURE 1. *Phonodus dutoitorum*, gen. et sp. nov., NMQR 3564. Photographs of skull in (A) left lateral, (B) palatal, (C) oblique posterolateral, and (D) occipital views.

MATERIAL AND METHODS

NMQR 3564 is preserved ventral up in the conglomerate (Fig. 1). As preparation progressed dorsally, up the lateral surfaces of the skull roof, we realized that not only was the braincase missing, but the skull table (consisting of the frontals, the parietals, the postfrontals [if present as distinct elements], the postorbitals, the supratemporals, and the postparietals) was lost prior to burial as well. In order to ensure the integrity of the snout and temporal regions, we decided not to remove the skull completely from the block, but to leave it attached via the dorsolateral surface of the right side; only the left side together with the dorsal surface of the snout of the skull roof is revealed for the following description.

SYSTEMATIC PALEONTOLOGY

**PARAREPTILIA Olson, 1947**

**PROCOLOPHONIDAE Lydekker in Nicholson and Lydekker, 1889**

**LEPTOPLEURONINAE Ivachnenko, 1979**

**PHONODUS DUTOITORUM**, gen. et sp. nov. (Figs. 1, 2)

**Diagnosis**—Small procolophonid characterized by the following autapomorphies: ventral temporal roughly straight with contact between maxilla and quadratojugal; bifurcated maxillary process of premaxilla; relatively large posterior-most maxillary tooth; prefrontal-prefrontal dorsal midline contact; lateral temporal fenestra present; vomer with two large conical teeth; pterygoid edentulous; transverse process of pterygoid relatively small; and small accessory process present medially on quadrate.

**Holotype**—NMQR 3564, a partial skull.

**Locality and Horizon**—A locality on the farm Bergendal in Noupooort District, Northern Cape Province, Republic of South Africa. Katberg Formation, Beaufort Group, Karoo Supergroup. NMQR 3564 is positioned low stratigraphically in the Katberg Formation and, thus, low in the *Lystrosaurus* Assemblage Zone (Groenewald and Kitching, 1995). Lower Triassic; Induan Stage. Detailed locality data are available from the Department of Karoo Palaeontology of the National Museum, Bloemfontein, to qualified researchers.

**Etymology**—From *phonos* and *odus*, Greek for ‘murderous’ and ‘tooth’ respectively, gender masculine. The specific epithet honors Jan and Susan du Toit, owners of the farm Bergendal, for their hospitality and interest in our work.
DESCRIPTION

The holotype and only known specimen of *Phonodus dutoitorum* preserves little more than half of the skull roof. The premaxillae have been eroded away almost entirely, and the alveolar portions of both maxillae are heavily weathered. The palate, including both quadrates, is preserved in articulation with the skull roof, but the transverse flanges and condyles of both quadrates are weathered to varying degrees. The braincase, the mandible, and the skull table are not preserved.

The skull is 25 mm long, a length that falls in the range of juvenile skulls of *Procolophon trigoniceps* (Carroll and Lindsay, 1985) and *Hypsognathus fenneri* (Sues et al., 2000). The deeply serrate dorsal midline suture formed by the nasals suggests, however, that the skull is that of an adult individual. We use this criterion of ontogenetic age from the cranial description of *H. fenneri* by Sues and colleagues, which documents a straight internasal contact in a juvenile specimen (Sues et al., 2000:fig. 3a) and an interfingering suture in an adult (Sues et al., 2000:fig. 2a).

**Skull Roof**

Little more than fragments remain of both premaxillae. The largest fragments are the enlarged maxillary processes and the tips of the palatal processes. The former has an extensive contact with the anterior end of the maxilla and consists of two dorsally extending processes. The anterior process makes contact with the ventral margin of the nasal, thereby excluding the maxilla from the external naris. The posterior ramus overlies the lateral surface of the maxilla and forms the posterior boundary of the maxillary depression (sensu Carroll and Lindsay, 1985). The palatal processes extend slightly farther posteriorly than the maxillary processes. Each appears to contact the anterior end of the vomer via a scarf joint. The dorsal processes of the premaxillae are preserved as tiny fragments in contact with the anterior tips of the nasals. In ventral view the cross-section of each dorsal process is seen to be transversely compressed (i.e., narrow), as in procolophonoids and their close relatives (deBraga and Reisz, 1996).

Septomaxillae are usually prominent elements positioned posteriorly in or along the posterior margin of the external naris, but no such structures are present. A pair of thin, weakly curved bones, exposed in section in palatal aspect immediately postero-medial to the external nares, may be all that remains of the septomaxillae.

The maxilla is a relatively deep, semilunar bone. Its lateral surface is characterized by an extensive anterior fossa, the maxillary depression, and two conspicuous foramina. The maxillary depression is a relatively shallow excavation with a distinct, nearly vertical anteriorly approximately midway along this contact. Anteriorly the jugal contacts the lacrimal and the ectopterygoid, and has a
moderately long overlapping suture with the maxilla. Anterodorsally the jugal forms the gently concave ventral margin of the orbit, and posterodorsally it projects an acuminate process that bears an elongate contact surface for the postorbital. Interestingly, the posterior edge of the posterodorsal end of the jugal forms a free, moderately concave margin, which has its counterpart in a shallow, anteriorly facing emargination in the squamosal. Thus, a small lateral temporal fenestra was present. The dorsal margin of this opening was presumably formed by the postorbital and, as suggested by the extensive contact surface that runs along the entire dorsal edge of the squamosal, possibly by the supratemporal as well, in analogous fashion to the lateral temporal fenestra restored for the owenettid *Candelaria barbouri* (Cisneros et al., 2004).

The quadratojugal forms the ventral margin of the temporal region and the ventral half of the posterior temporal emargination. The latter is defined ventrally by a dorsoventrally deep posteroventral extension of the facial portion of the quadratojugal. The facial portion of the bone is smooth and featureless. The most conspicuous features of the quadratojugal, that it shares an extensive interfingering contact with the jugal and excludes that bone from the ventral margin in making a touch contact with the maxilla, were noted above.

Both squamosals are present and are typically procolophonid in construction. The facial portion of the bone, however, is greatly reduced to a slender, gently curving strip bordering the posterior temporal emargination. The anterodorsal edge of the bone forms the posterior margin of the small, elongate lateral temporal fenestra ventrally and a narrowly quadrangular contact surface for the supratemporal. The squamosal forms the approximate dorsal half of the deep posteroventrally aligned flange within the posterior temporal emargination. This portion extends ventrally to terminate just dorsal to the condylar region of the quadrate. The posterior margin of this region of the squamosal is thickened and has the appearance of a pilaster in occipital view. The squamosal has a deep overlapping contact with the dorsal lamella of the quadrate, and a less extensive overlapping contact with the quadrate process of the pterygoid.
**Discussion**

**Relationships of Phonodus dutoitorum**

Despite the absence of procolophonid hallmarks such as the presence of a ventral temporal margin or quadratejugal spines, NMQR 3564 exhibits apomorphies that are indicative of a phylogenetic placement within Procolophonidae. These include the presence of a maxillary depression, the presence of a large maxillary tooth, and contact between the lacrimal and the ectopterygoid. In addition, the edentulous palatines are suggestive of a close relationship with *Leptopleuron lacertinum* and *Hypsognathus fenneri*.

In order to test the hypothesis that *Phonodus dutoitorum* is a leptopleuronine procolophonid, we added this taxon to the data matrix of Cisneros (2008b) and reran the augmented matrix using the line of coding provided by Cisneros (2008c), but changed the codings for characters 1 and 40 to '0' and '2', respectively. We also changed the codings for characters 0, 1, 10, 24, and 37 to '0', '0', '0', '0', '2', '2', '2', '0', '0', '2', '2', '2', '2', respectively, for *Coletta seca* (based on Modesto et al., 2002); the codings for characters 16 and 49 to '0' and '1', respectively, for *Sauropareion anoplus* (based on Modesto and Damiani, 2007); the coding for character 37 to '0' for *Leptopleuron lacertinum* (based on Säilä, 2008a). Whereas Cisneros (2008b) ordered six of his characters, we ran all characters unordered to minimize assumptions of character evolution. A branch-and-bound search discovered 90 optimal trees (each 121 steps in length), the strict consensus of which is shown in Figure 3. Apart from the inclusion of *P.
**N. asiaticus** the least stratigraphic debt positions **P. dutoitorum** species of **Neoprocolophon asiaticus** exact phylogenetic position of sions for two or three leptopleuronine lineages, depending on the The Induan age of this species mandates downward range exten-

short ghost lineage for **P. dutoitorum** requires a long ghost lineage for **P. dutoitorum** of Procolophonidae (whereas only **S. anoplus** forms a clade at the base of Procolophonidae in Cisneros, 2008c) with the exception that **C. seca** is the sister taxon of the least inclusive clade that includes **Sclerosaurus ar-

**Phonodus dutoitorum** is the oldest known leptopleuronine. The Induan age of this species mandates downward range exten-
sions for two or three leptopleuronine lineages, depending on the exact phylogenetic position of **P. dutoitorum**. The topology with the least stratigraphic debt positions **P. dutoitorum** as the sister taxon of the least inclusive clade that contains **Sclerosaurus ar-

and **Hypsognathus fenneri**; in another third it is the sister species of **Neoprocolophon asiaticus** and in the remaining third it is the sister taxon of the least inclusive clade that includes **N. asi-

ticus** and **H. fenneri**. The decay analysis reveals that most clades within Procolophonidae collapse with the addition of a single step, and there is no resolution among procolophonids following two extra steps.

**Phonodus dutoitorum** is a lepto-
pleuronine. In a third of the optimal trees **P. dutoitorum** is a sister taxon of the least inclusive clade that includes **Sclerosaurus ar-

matus** and **Hypsognathus fenneri**; in another third it is the sister species of **Neoprocolophon asiaticus** and in the remaining third it is the sister taxon of the least inclusive clade that includes **N. asi-
ticus** and **H. fenneri**. The decay analysis reveals that most clades within Procolophonidae collapse with the addition of a single step, and there is no resolution among procolophonids following two extra steps.

**Dietary modes in procolophonoid reptiles have been inferred primarily on the basis of the marginal dentition.** Owenettids and basal procolophonids (e.g., **Kitchingnathus untabeni**) are regarded as insectivores because most exhibit numerous, sim-

ple, non-occluding teeth, whereas larger and phylogenetically younger procolophonids, including **Procolophon trigoniceps** and **Hypsognathus fenneri**, are thought to be high-fiber herbivores because they possess a reduced marginal dentition that features rel-
atively large, occluding molariform teeth (Gow, 1978; Reisz and Sues, 2000; Cisneros, 2008c). Sues et al. (2000) cautioned, how-

ever, that the consumption of arthropods with hard exoskeletons in addition to plant matter could not be ruled out for **P. trigoni-

ceps**, **H. fenneri**, and closely related forms.

The severe weathering sustained by the marginal dentition of NMR 3564 greatly complicates an assessment of the diet of **Phonodus dutoitorum**. Only the relatively enormous posterior maxillary teeth remain of the marginal dentition. Although some procolophonid taxa possess relatively large posterior maxillary teeth (e.g., **Anomomoidon iliensterni**: Säilä, 2008b; **Thelephon op-

pressus**: Modesto and Damiani, 2003), only **Haligonia bolodon**, from the Norian of Nova Scotia (Sues and Baird, 1998), has a posterior maxillary tooth of such relative enormity. The remains of a comparably small alveolus immediately anterior to the left maxillary tooth in NMR 3564 suggests that the maxilla supported at least one much smaller tooth anterior to the large bulbous tooth, akin to the condition seen in **Ha. bolodon** (Sues and Baird, 1998:fig. 2). The large maxillary tooth of **Ha. bolodon** displays a small lingual wear facet on its apex. Sues and Baird (1998:527) remark that this wear facet is poorly defined, and inferred that occlusion between upper and lower dentitions in **Ha. bolodon** was not developed to the degree seen in **P. trigoniceps** and **H. fenneri**. Possibly the occlusal condition seen in **Ha. bolodon** also pertained to **P. dutoitorum**, but the utter absence of crown apices in the latter precludes any inference into occlusion in that species.

Despite the lack of information on the crown morphology of the large maxillary teeth, certain aspects of the general skull mor-

phology suggest that **P. dutoitorum** was durophagous: the largest maxillary teeth are positioned ventral to well-developed antor-
bital buttresses and, apart from the presence of a small lateral

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**FIGURE 3.** Strict consensus of 90 optimal trees discovered in a PAUP* 4.0b10 analysis of a modified version of the data matrix from Cisneros (2008b). Tree length = 121, consistency index (CI) = 0.67, CI excluding uninformative characters = 0.66, rescaled CI = 0.53. We have condensed nine of the terminal taxa into more inclusive taxa for this figure, as follows: Theledeca
tinae (*Eumetabolodon* dongshengensis, *Theledectes perforatus*), Procolophoninae (*Eumetabolodon bathycepha
lus*, *Kapes* spp., *Procolophon trigoniceps*, *Teratophon spinigenis*, *Thelephon conditris*, *Thelepton oppres
sus*, *Timanophon raridentatus*). *Phonodus dutoitorum* is coded for the 58 characters of Cisneros (2008b) as follows: 17A1111?? 0000??1 ??0??0010 000??011 ??0??0?? ??0??000 ????0000 00000011 where ‘A’ and ‘B’ indicate uncertainty for states 1 and 2 and for states 3 and 4, respectively.
FIGURE 4. Stratigraphically calibrated trees illustrating the implications of the three possible phylogenetic positions of Phonodus dutoitorum within Leptopleuroniinae for leptopleuroniine diversity during the Olenekian. A, topology with the least stratigraphic debt. B–C, topologies with greater debt. The black bars indicate known ranges, the gray bar indicates uncertainty in the placement of the stratigraphic range of Pentaeodratus (following Casier, 2008b), and open bars indicate ghost lineages and ghost taxa. Clade ‘N’ refers to the clade of leptopleuroniines identified in Figure 3. Numerical dates from Mundil et al. (2004) and Lehmehr et al. (2006).

temporal fenestra, the temporal region is entirely roofed over in bone and there is no ventral emargination. The deeply interdig-
itating suture between the jugal and the quadratojugal presumably served to resist the tensile forces that would have manifested between the alveolar region and the jaw articulation when the large maxillary teeth were engaged during feeding. Our tree topology indicates that the temporal morphology seen in P. du-
toitorum is clearly a secondary condition, one that is derived from the ventrally emarginated temporal condition retained in such taxa as Neaprocolophion asiaticus and Procolophon trigoniceps. The closure of the ventral temporal emargination in P. dutoi-
torum is analogous to the closure of the lateral temporal fenestra in the diapsid genus Araeoscelis, which was inferred by Reisz et al. (1984) to be an adaptive response to a durophagous diet of invertebrates. In P. dutoitorum, however, the ventral margin appears to have been closed by extensions of both the jugal and the quadra-
tojugal, resulting in a deeply interfingering contact. Given the uncertain relationship of P. dutoitorum to phylogenetically younger taxa such as Scoloparia glyphanodon and Leptopleu-
ron lacertinum, it is unclear whether the condition seen in P. du-
toitorum is ancestral to the condition seen in those younger leptopleuroniines, in which a ventral emargination is also absent but the ventral margin of the temporal region is markedly convex.

The evidence marshaled above for the hypothesis of durophagy in P. dutoitorum is seemingly at odds with the observation that the walls of the large maxillary teeth appear relatively thin: the thickness of the tooth wall ranges 0.2–0.3 mm, forming roughly 8–12% of crown basal diameter (measured transversely across the right tooth). To our knowledge, no histological work has been published on procolophonoid dentition, but the work of Riehlès and Bolt (1983:fig. 15) on the Early Permian eureptile Captorhinus aguti (a durophagous captorhinid according to Hot-
ton et al., 1997) documents that the crown walls of the labial-most tooth in the multiple-rowed portion of the maxilla are 0.23–0.27 mm thick and form 33–44% of the basal diameter of the crown. Thus, the crown walls of P. dutoitorum are approximately the same absolute thickness as those of C. aguti, but they are thin relative to overall tooth size. At first glance, this suggests that the teeth of the former taxon were structurally weaker than those of the former. However, Evans and Sanson (1998) remark that teeth of the same shape but of different sizes require different forces to penetrate food items. A direct comparison of tooth efficiency between P. dutoitorum and C. aguti is complicated by the damage to those of the former taxon and minor shape differences, but a corollary of Evans and Sanson’s (1998) observation on tooth efficiency is that one needs to be mindful of the absolute size of the animal. It follows that it is possible that the smaller size of P. dutoitorum, with a skull length of 25 mm, could account for the absence of expected modifications for strengthening the walls of its teeth, because this procolophonid was probably not able to generate the jaw adductor forces that individuals of C. aguti, which attained skull lengths of 80 mm (Seltin, 1959), would have by virtue of their larger size. Pursuant to Evans and San-
son’s (1998) statement on the relationship between tooth scale and tooth efficiency, it is interesting that the largest teeth of the apleistorhinid parareptile Colobomycter pholeter are characterized by folding of the relatively thin tooth walls (Modesto, 1999; Modesto and Reisz, 2008). Modesto and Reisz (2008:677) suggested that this folding may have served to strengthen the largest teeth in C. pholeter. In this respect, we note that the skull of C. pholeter is estimated to have attained at least 50 mm in length (Vauhn, 1958), thereby reaching twice the size of the skull of P. dutoitorum. The walls of the large maxillary teeth of the latter parareptile may not have required either thickening or mechanical support in the form of tooth folding because of the tiny size of its skull.

Finally, clues to the diet of Phonodus dutoitorum may be drawn from the palatal dentition. The palate of this species is nearly edentulous apart from the presence of two pairs of vomerine fangs. In addition to their conspicuous size, what is remark-
able about the vomerine teeth is that they extend ventrally directly between the large, bulbous maxillary teeth. It is difficult to dismiss this organization of the marginal and palatal teeth as coincidental, but given the incomplete crown morphology of the
large maxillary teeth, it would be premature to draw conclusions on the purpose of this dental organization. The vomerine teeth do not exhibit distinct facets or other conspicuous wear, so it seems likely that they were used to pierce or to hold food items. Pursuant to this observation, the apices of these fangs are directed slightly posteriorly, which suggests that they served to keep food from moving (or slipping) anteriorly. We know of no herbivorous tetrapods with remarkably few and relatively large palatal teeth with this orientation, so it seems plausible to us that *P. dutoitorum* preyed on small invertebrates. We hope that future material will preserve more of the dentition than is present in the holotype and only known specimen, to test these inferences.

**Origins of the Karoo Procolophonid Fauna**

Our description of *Phonodus dutoitorum* adds a new element to the procolophonid assemblage of the Induan part of the *Lystrosaurus* Assemblage Zone of South Africa. Previously we (Botha et al., 2007) reported a modest diversity of Induan procolophonids that spanned the uppermost strata of the Balfour Formation and lowermost strata of the Katberg Formation, and formed part of a Permo-Triassic recovery fauna (sensu Smith and Botha, 2005), and suggested that procolophonids were not greatly disturbed by the mass extinction of 252 million years ago.

This small assemblage of Induan-age Karoo procolophonids now comprises two owenettids ("Owenetta" *kitchingorum* and *Saurodekes rogersorum*), two basal procolophonids (*Coletta seca* and *Sauropareion anoplus*), and a basal leptomeline procolophonid (*Phonodus dutoitorum*). It exceeds the taxonomic and morphological diversity of procolophonids from the Laurasian Induan, represented by *Contritosaurus convector*, *C. simus*, and *Phaanthosaurus ignatjevi* from the Russian Platform. These Laurasian taxa were thought to be so similar that Spencer and Benton (2000) regarded the former genus to be a junior synonym of *Phaanthosaurus*.

The owenettid and procolophonid members of the Karoo Induan fauna are probably endemic forms (Modesto et al., 2002). Optimization of Laurasian and Gondwanan distributions onto the tree seen in Figure 3 (Fig. 1S, Supplementary Data 2002) increases the number of Karoo Induan procolophonids to five, and it supports the hypothesis that *P. dutoitorum* was a leptomeline procolophonid from the Lower Triassic Katberg Formation of South Africa. *Phonodus dutoitorum*, gen. et sp. nov., is an unusual leptomeline procolophon because it lacks quadratojugal processes and a ventral temporal emargination, but exhibits a lateral temporal fenestra. It is diagnosed also by the presence of a single large maxillary tooth, midline dorsal contact between the prefrontals, reduced pterygoid flanges, and several other autapomorphies. The damage to the marginal dentition and the nearly edentulous palate together preclude a definitive statement on the probable diet of *P. dutoitorum*, but the presence of large marginal teeth is suggestive of durophagy, and the presence and the morphology of well-developed vomerine fangs suggest that this leptolepine preyed on invertebrates. A phylogenetic analysis positions *P. dutoitorum* basally in Leptomelinae. The precise relationship between *P. dutoitorum* and the other leptolep- ronines cannot be determined with the available evidence, but the new species does not appear to be the most basal leptolep- ronine. Each one of the three possible phylogenetic positions for *P. dutoitorum* suggests that the early evolutionary history of Lep- tomelinae is poorly recorded in the Lower Triassic. The description of *P. dutoitorum* increases the number of Karoo Induan procolophonids to five, and it supports the hypothesis that procolophonid evolution was not greatly affected by the Permo-Triassic mass extinction.

**CONCLUSIONS**

We describe the anatomy of a new genus and species of leptomelaneous procolophon from the Lower Triassic Katberg Formation of South Africa. *Phonodus dutoitorum*, gen. et sp. nov., is an unusual leptomeline procolophon because it lacks quadratojugal processes and a ventral temporal emargination, but exhibits a lateral temporal fenestra. It is diagnosed also by the presence of a single large maxillary tooth, midline dorsal contact between the prefrontals, reduced pterygoid flanges, and several other autapomorphies. The damage to the marginal dentition and the nearly edentulous palate together preclude a definitive statement on the probable diet of *P. dutoitorum*, but the presence of large marginal teeth is suggestive of durophagy, and the presence and the morphology of well-developed vomerine fangs suggest that this leptolepine preyed on invertebrates. A phylogenetic analysis positions *P. dutoitorum* basally in Leptomelinae. The precise relationship between *P. dutoitorum* and the other leptolep- ronines cannot be determined with the available evidence, but the new species does not appear to be the most basal leptolep- ronine. Each one of the three possible phylogenetic positions for *P. dutoitorum* suggests that the early evolutionary history of Lep- tomelinae is poorly recorded in the Lower Triassic. The description of *P. dutoitorum* increases the number of Karoo Induan procolophonids to five, and it supports the hypothesis that procolophonid evolution was not greatly affected by the Permo-Triassic mass extinction.

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