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A taxonomic revision of the genus Procolophon and the phylogenetic relationships of Procolophonoid reptiles

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A procolophonoid reptile with temporal fenestration from the Middle Triassic of Brazil

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The small tetrapod *Candelaria barbouri*, from the Middle Triassic of southern Brazil, is the first example of an owenettid procolophonoid outside Africa and Madagascar. *Candelaria barbouri* was originally described as a primitive procolophonid; however, a re-examination of the holotype, as well as new material, reveals that *C. barbouri* is in fact the youngest member of the Owenettidae, extending the chronological range of the group by more than 10 million years. The recognition of *C. barbouri* as an owenettid points to a broader diversity and distribution for owenettids than hitherto thought. In addition, *C. barbouri* is the first member of the Owenettidae to exhibit temporal fenestrae, a discovery that draws attention to the significance of this feature in 'anapsid' reptiles.

Keywords: owenettid; procolophonoid; anapsids; temporal fenestrae; Triassic

1. INTRODUCTION

The proposed sister-group relationship between turtles and procolophonids (Reisz & Laurin 1991) has generated renewed interest in procolophonoid reptiles. Consequently, much new research has been published in recent years (see references in Modesto & Damiani 2003), increasing substantially our knowledge of this group. The Procolophonoidea was proposed by Romer (1956) to unite the Procolophonidae and Owenettidae. The latter was erected by Broom (1939), who named *Owenetta rubidgei* from the Upper Permian of South Africa. Later, Piveteau (1955) described the owenettid *Barasaurus besairiei* from the Upper Permian Lower Sakamena Formation of Madagascar. No further owenettids were named until the descriptions of *Owenetta kitchingorum* (Reisz & Scott 2002) and *Saurodectes rogersorum* (Modesto *et al.* 2003), both from the Lower Triassic of South Africa.

Candelaria barbouri, from the Middle Triassic Santa Maria Formation of southern Brazil, was the first procolophonoid recorded in South America (Price 1947). Price assigned the holotype to the Procolophonidae, although he recognized some primitive characters that were inconsistent with a Middle Triassic age. These included a large number of marginal teeth, orbitotemporal fenestrae that were not largely expanded and the absence of quadratojugal 'horns'. Until now, the phylogenetic relationships of *Candelaria* have remained uncertain, mostly owing to the poor preservation of the type specimen. Re-examination of the holotype, and the study of new material, leads us to reinterpret *Candelaria* as an owenettid rather than a procolophonid. As such, *Candelaria* represents not only the first record of the Owenettidae outside Africa and Madagascar, but also the geologically youngest owenettid. In addition, the new specimens possess clearly visible temporal fenestrae, making *Candelaria* the first owenettid parareptile known to exhibit this historically important morphological feature. Taken together with the recurrent appearance of temporal fenestrae in parareptiles, this discovery casts further doubt on the utility of temporal fenestration for the classification of 'anapsid' reptiles.

2. MATERIAL AND METHODS

In the holotype of *Candelaria* only the gross morphology is evident because the skull roof and palate are damaged and no sutures are visible. Consequently, most of the information we present is taken from two newly recovered skulls. Like the holotype, these specimens exhibit the typical preservation of Santa Maria Formation fossils, in that recrystallization of permineralized elements has resulted in some relatively minor osteological deformation (Holz & Souto-Ribeiro 2000). Disarticulated postcranial remains were recovered in association with the new skulls and may belong to the same taxon.

Procolophonoids studied for comparative purposes included the holotypes of *Owenetta kitchingorum* (BP/1/4195, Bernard Price Institute for Palaeontological Research, Johannesburg), *Owenetta rubidgei* (RC 50, Rubidge Collection, Graaff-Reinet) and *Coletta seca* (GHG 228, Council for Geoscience, Pretoria) and specimens of *Procolophon* (Bernard Price Institute for Palaeontological Research) and *Barasaurus besairiei* (South African Museum, Cape Town). Information on *Saurodectes rogersorum* and *Sauropareion anoplus* was taken from Modesto *et al.*

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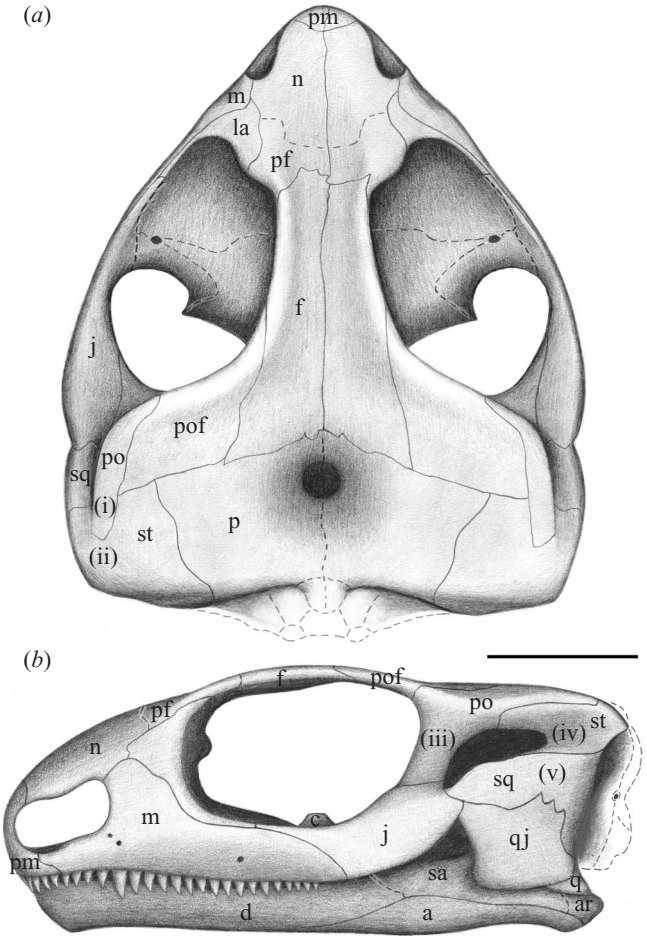

Figure 1. Reconstruction of the skull of the owenettid parareptile *Candelaria barbouri* (Price 1947) from the Middle Triassic of Brazil, based on UFSM 11076, UFSM 11131 and DGM 314R. (*a*) Dorsal view; and (*b*) left lateral view. Characters (i)–(v) relate to the temporal fenestra and are listed in the diagnosis in § 3a. Abbreviations: a, angular; ar, articular; c, coronoid process; d, dentary; f, frontal; j, jugal; la, lacrimal; m, maxilla; n, nasal; p, parietal; pf, prefrontal; pm, premaxilla; po, postorbital; pof, postfrontal; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal; st, supratemporal. Scale bar, 1 cm.

(2001, 2003). Information on the Russian Permian 'nycteroleters' *Nyctiphruretus*, *Nycteroleter*, *Macroleter* and *Tokosaurus* was taken from Tverdokhlebova & Ivakhnenko (1984) and Lee (1997).

3. SYSTEMATIC PALAEONTOLOGY

Parareptilia Olsen, 1947 (*sensu* deBraga & Reisz 1996). Procolophonoidea Romer, 1956 (*sensu* Lee 1995). Owenettidae Broom, 1939 (*sensu* Lee 1995). *Candelaria barbouri* Price, 1947.

(a) *Revised diagnosis*

Candelaria barbouri is distinguished from all other owenettids by its relatively large size (at least 30% larger than all other known owenettid specimens) and by a suite of characters related to the presence of a temporal fenestra (figure 1):

(i) posterior process of the postorbital present, which extends well into the supratemporal;
(ii) lateral notch of supratemporal absent;
(iii) thin concave temporal bar present posterior to the orbitotemporal fenestra;
(iv) supratemporal expanded ventrally;
(v) squamosal dorsoventrally narrow but anteroposteriorly elongate.

(b) *Holotype*

DGM 314R, a poorly preserved skull and mandible in occlusion (Price 1947), which is deposited in the Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil.

(c) *Locality and horizon*

Collected in 1942 by an expedition of the Departamento Nacional de Produção Mineral at Sanga Pinheiros (29°46′19″ S, 52°44′54″ W), Candelaria County, Rio Grande do Sul State, Brazil. The sediments belong to the *Dinodontosaurus* Cenozone of the Santa Maria Formation (Paraná Basin) and are of Ladinian (late Middle Triassic) age (Abdala *et al.* 2001).

(d) *Referred material*

UFSM 11076 and UFSM 11131, two complete skulls with mandibles in occlusion and associated postcrania, in the Universidade Federal de Santa Maria (UFSM), Rio Grande do Sul State, Brazil. These materials were collected by UFSM expeditions in 2000 and 2001 at a small outcrop (29°44′55″ S, 53°00′06″ W) 166.5 km along RST 287 Highway, Novo Cabrais County, Rio Grande do Sul State. The sediments pertain to the same horizon as those from which the holotype was recovered.

4. DESCRIPTION

For the sake of brevity, only characters of phylogenetic relevance are reported here. A detailed description of the skulls and postcrania will be provided in a forthcoming publication. We provide a reconstruction of the skull in dorsal and lateral views (figure 1).

The known material of *C. barbouri* indicates that it is a comparatively large owenettid species: the smallest skull (UFSM 11131) measures 39 mm in length, and the largest (UFSM 11076) measures 49 mm. By contrast, the largest previously known owenettid skull, the type specimen of *O. rubidgei*, is 34 mm in length. In lateral view, the skull and mandible (in occlusion) of the holotype of *Candelaria* is 20 mm in height, which is at least twice the average height of the skull and mandible in other owenettids. As in all owenettids, the surface of the cranium lacks complex sculpturing, in contrast to the pitting characteristic of 'nycteroleters' and millerettids, and the bosses and/or projections characteristic of pareiasaurids and some procolophonids.

The premaxilla of *Candelaria* forms the anterior border of the external naris. As in other owenettids, it contributes to only the anterior portion of the ventral margin of the external naris. It bears five conical teeth that are longer than the anterior-most teeth in the maxilla.

The external naris of *Candelaria* is expanded posteriorly and accounts for half of the length of the snout. This is also the condition present in the owenettids *Barasaurus*,

O. rubidgei and *O. kitchingorum* and in the 'nycteroleters' *Nyctiphruretus* and *Tokosaurus*. In procolophonids and most other parareptiles, however, the external naris comprises much less than half of the length of the snout.

As in all parareptiles, the maxilla possesses an anterior dorsal expansion behind the external naris and a large anterolateral foramen (Laurin & Reisz 1995; Lee 1995). A second smaller foramen is adjacent to the anterolateral foramen, and a third is below the margin of the orbitotemporal fenestra, as in all other owenettids in which the area is known, but a feature not seen in procolophonids. The maxilla bears between 21 and 23 teeth, which is close to the numbers present in *O. kitchingorum* (20–21 teeth) and, presumably, *Saurodectes*, judging from the size of the preserved maxillary teeth in the latter. The number of maxillary teeth present in Permian parareptiles (with the exception of pareiasaurids) is higher. For example, *O. rubidgei* bears *ca*. 30 maxillary teeth, a similar number to the 'nycteroleters' *Nyctiphruretus* and *Nycteroleter*. The reduction in dentition in Triassic owenettids is a direct result of the decrease in the length of the maxilla, as first observed in *O. kitchingorum* (Reisz & Scott 2002). This character could represent an apomorphy for these taxa. As in *O. kitchingorum*, the tooth directly below the anterolateral foramen is the largest in the maxilla. It has a wide base, is posteriorly recurved and is followed by a series of progressively smaller caniniform teeth. This caniniform region is absent in all other procolophonoids.

The nasal forms the dorsal margin of the external naris. Its contact with the prefrontal is poorly preserved in all the specimens. However, the anterior edge of the frontal terminates well behind the level of the anterior margin of the orbitotemporal fenestra, as in *O. kitchingorum*. This suggests that the prefrontals are sutured in the midline, separating the nasals from the frontals. In all other procolophonoids, the anterior edge of the frontal is positioned in front of the level of the orbitotemporal fenestra, contacting the nasal and precluding a midline contact between the prefrontals. The condition in *Saurodectes* is uncertain because of poor preservation. The nasals may also have contacted the frontals in *Candelaria*, but this would necessitate an unusual posterior expansion of the nasals.

A prominent crest, formed by the lateral margins of the prefrontal, frontal and postfrontal, borders the medial margin of each orbitotemporal fenestra. This structure, here termed the orbitotemporal crest, is present in all owenettids that we have observed and in the 'nycteroleters' *Nyctiphruretus* and, possibly, *Tokosaurus*. This character could be an apomorphy of owenettids that evolved independently in certain 'nycteroleters' or it could be an apomorphy of a more inclusive group comprising some 'nycteroleters' more closely related to owenettids than to other parareptiles.

The postfrontal contacts the supratemporal, precluding the parietal from contributing to the margin of the orbitotemporal fenestra. This is an owenettid autapomorphy (Reisz & Scott 2002; Modesto *et al.* 2003).

The pineal foramen is located in a shallow fossa within the anterior portion of the parietals and is positioned wholly posterior to the level of the orbitotemporal fenestra, as is characteristic of all other owenettids. Some unidentified elements at the back of the skull of UFSM 11076 could be interpreted as the remains of postparietals. However, the occipital area of each of the three known skulls is badly preserved and the presence of a postparietal cannot currently be assessed.

The most distinctive and unexpected feature of *Candelaria* is the presence of a temporal opening. Accordingly, the morphology of the bones of the cheek region of the skull has been considerably modified (figure 1). The fenestra is bordered by the postorbital anterodorsally, the supratemporal posterodorsally and the squamosal ventrally, with a small contribution from the jugal anteroventrally. In dorsal view, a posterior process of the postorbital extends deep into the supratemporal. The latter is also characterized by being expanded ventrally and lacking the lateral notch characteristic of all other owenettids. The postorbital and the jugal form the narrow anterior temporal bar. This bar is distinctly concave, so that the contact between these bones is not visible in dorsal view. The squamosal is dorsoventrally shallow, but more elongated than in other owenettids.

An acute temporal emargination between the jugal and the quadratojugal is present. This feature is characteristic of owenettids (Reisz & Scott 2002), but occurs to a lesser degree in *Coletta* and *Sauropareion*.

As far as we can determine, the morphology of the palate of *Candelaria* is virtually indistinguishable from that of *O. kitchingorum*. In particular, the length of the palate in these taxa, as in all Triassic parareptiles, is much shorter than in their Permian relatives, judging from the relative distance between the tip of the transverse flange of the pterygoid and the posterior border of the basioccipital. As in all owenettids, *Candelaria* possesses a large number of palatal denticles arranged in long rows. This contrasts with the short rows of enlarged teeth that are characteristic of procolophonids.

The mandible of *Candelaria* cannot be fully described because it remains firmly adducted to the skull in all specimens. However, its visible morphology is similar to that of other owenettids. Presumably the number of dentary teeth is comparable to that of the upper marginal dentition, as suggested by the position of the coronoid process. As in *O. kitchingorum*, the coronoid process is placed more anteriorly than in Permian owenettids. This feature may be related to the reduction in palatal length seen in the Triassic species, because the position of the coronoid process appears to be correlated with that of the transverse flange of the pterygoid.

5. DISCUSSION

To determine the relationships of *C. barbouri* among owenettids, we performed a phylogenetic analysis of all known owenettids and selected well-known procolophonids. The results of this analysis (figure 2) indicate that *Candelaria* is the sister taxon of *O. kitchingorum* within a monophyletic Owenettidae. The Owenettidae can be diagnosed on the basis of four unequivocal synapomorphies (see Appendices A and B): the presence of a large postfrontal that contacts the supratemporal, the absence of an entepicondylar foramen, the presence of orbitotemporal crests and the presence of broad posteriorly expanded nostrils. Other characters typical of though not exclusive to owenettids are also present in *Candelaria* and include the

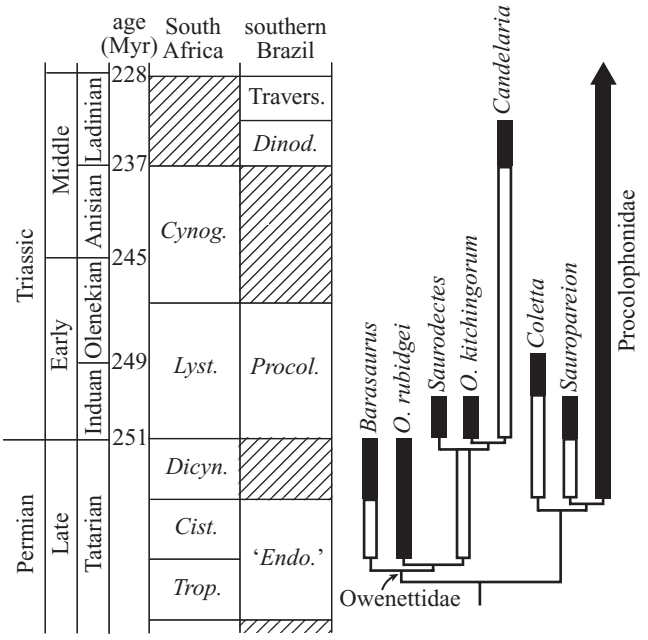

Figure 2. Stratocladogram of procolophonoid interrelationships, including ghost lineages (white extensions of black bars). The Owenettidae is a monophyletic taxon that includes *Candelaria*, while the Early Triassic taxa *Coletta* and *Sauropareion* are transitional forms between the Owenettidae and Procolophonidae. The phylogeny is based on a PAUP 3.1.1 (Swofford 1993) analysis of the data matrix in Appendix B, and represents one of two most parsimonious trees, chosen on the basis of greatest stratigraphic congruence, found using the branch-and-bound algorithm. Tree length, 31 steps; consistency index, 0.81; rescaled consistency index, 0.80. Biostratigraphy of South Africa from Rubidge (1995); southern Brazilian Triassic from Abdala *et al.* (2001); southern Brazilian Permian adapted from Langer (2000) and Malabarba *et al.* (2003). Hatched shading indicates a sedimentary hiatus. Abbreviations: *Cist.*, *Cistecephalus*; *Cynog.*, *Cynognathus*; *Dicyn.*, *Dicynodon*; *Dinod.*, *Dinodontosaurus*; '*Endo.*', '*Endothiodon*'; *Lyst.*, *Lystrosaurus*; *Procol.*, *Procolophon*; Travers., Traversodontid; *Trop.*, *Tropidostoma*.

presence of an acute temporal emargination, a pair of anterolateral foramina on the maxilla and a pineal foramen that is set within a shallow fossa.

The sister-group relationship between *Candelaria* and *O. kitchingorum* is supported by one unequivocal synapomorphy, the presence of posteriorly recurved maxillary teeth. Three further synapomorphies—the presence of a prominent anterior maxillary tooth, a short palate and a midline contact between the prefrontals—also support this relationship but their distribution on the cladogram is equivocal. The long ghost lineage for *Candelaria* suggested by this relationship (figure 2) implies an unknown fossil record for owenettids spanning most of the Early Triassic and the early part of the Middle Triassic. On a local scale this may be partly explained by the sedimentary hiatus during that time in southern Brazil. Our phylogenetic results also support those of Modesto *et al.* (2003) in that *O. kitchingorum* and *O. rubidgei* do not form a monophyletic group. Instead, the Triassic owenettids *Saurodectes*, *O. kitchingorum* and *Candelaria* form a natural group to the exclusion of the Permian owenettids. This tree topology necessitates a ghost lineage in the uppermost Permian for the Triassic owenettid clade (figure 2).

The presence or absence of temporal fenestrae has long played a major role in the classification of amniotes (e.g. Romer 1956; Gauthier *et al.* 1989). Historically, four major types of temporal fenestration were recognized for systematic purposes: synapsid, diapsid, euryapsid and anapsid conditions. The Parareptilia is generally recognized to be a group that is characterized in part by an anapsid temporal morphology. Indeed, the term Anapsida has been applied to the clade that includes parareptiles and mesosaurids (Modesto 1999; Reisz & Scott 2002). However, the significance of temporal fenestrae in anapsid phylogeny is questionable because of its repeated occurrence across several lineages (cf. Hamley & Thulborn 1993), as shown in figure 3. Temporal fenestration is absent in the most primitive anapsids, the Mesosauridae, but is present in all members of the Millerettidae (*Millerosaurus*, *Milleropsis* and young individuals of *Millereta*; Gow 1972), all lanthanosuchoids (*Acleistorhinus*, *Lanthanosuchus*, *Lanthaniscus*; deBraga & Reisz 1996), at least one 'nycteroleter' (*Tokosaurus*; Tverdokhlebova & Ivakhnenko 1984), at least one procolophonid (*Procolophon laticeps*; Hamley & Thulborn 1993) and at least one owenettid (*Candelaria*). Briefly, temporal fenestration is present in the most basal parareptiles, the millerettids, and in all other lineages except for pareiasaurids. This distribution implies that temporal fenestration has arisen independently in most parareptile lineages, but a more intriguing possibility is that it is a synapomorphy of Parareptilia. The latter possibility will be explored in a forthcoming publication. For the moment, the recognition of temporal fenestrae in *Candelaria* may be viewed as further evidence for the independent development of temporal openings in different parareptile lineages. We conclude that the absence of temporal fenestration may be of limited taxonomic significance for those amniotes traditionally perceived as 'anapsids'.

The presence of temporal fenestrae in tetrapods has been explained as a means of reducing the weight of the skull in areas experiencing little or no stress, expanding the jaw adductor musculature and/or increasing the area for muscle attachment (Frazetta 1968; Tarsitano *et al.* 2001). Interestingly, Colbert (1946) suggested that the progressive enlargement of the orbitotemporal fenestrae within procolophonids, culminating in the leptopleuronines, may have been correlated with expansion of the adductor musculature. While there is no direct evidence for muscular expansion in derived leptopleuronines, we may speculate that the true temporal openings of *Candelaria* were functionally analogous to the enlarged orbitotemporal fenestrae in leptopleuronines.

Until now, owenettids were known only from the Upper Permian and lowermost Triassic of South Africa and the Upper Permian of Madagascar. The recognition of *Candelaria* as an owenettid extends the known stratigraphic range of this group to Middle Triassic times, which significantly increases the entire chronological range of the Owenettidae. Biogeographically, it expands the known distribution of owenettids from what was then central Gondwana (South Africa and Madagascar) to western Gondwana (Brazil). Therefore, future discoveries of

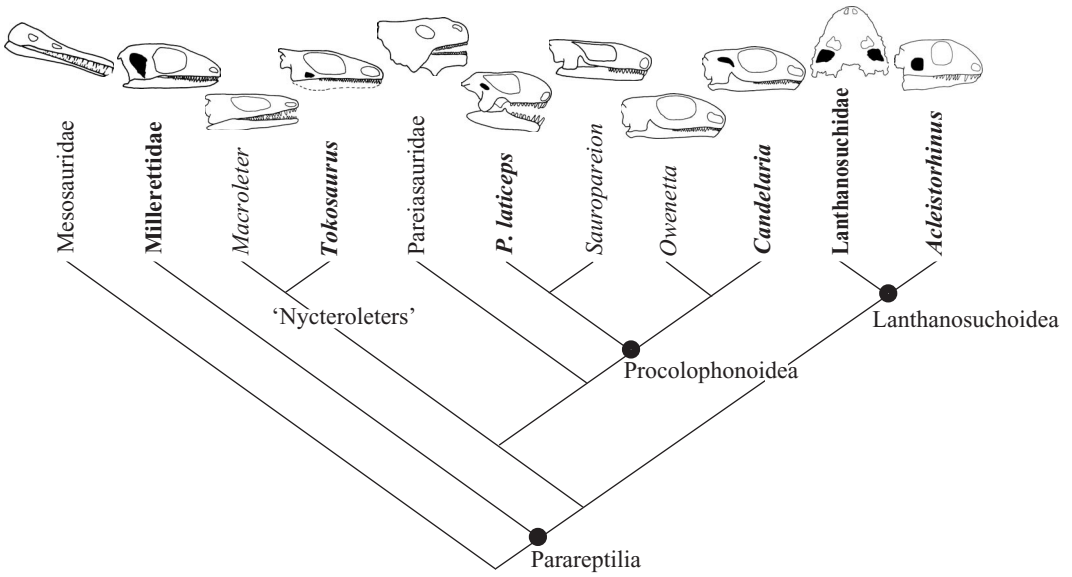

Figure 3. Simplified cladogram of 'anapsid' reptiles, showing distribution (in bold face) of all known taxa that possess temporal fenestrae (see § 4). Skull outlines, from left to right, are: *Stereosternum tumidum*, *Millerosaurus nuffieldi*, *Macroleter poezicus*, *Tokosaurus perforatus*, *Bradysaurus baini*, *Procolophon laticeps*, *Sauropareion anoplus*, *Owenetta kitchingorum*, *Candelaria barbouri*, *Lanthanosuchus watsoni* and *Acleistorhinus pteroticus*; temporal fenestrae are shaded in black. Phylogeny adapted from Reisz & Scott (2002). Drawings not to scale.

owenettids in Triassic sediments elsewhere in Gondwana could be expected.

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APPENDIX A: PHYLOGENETIC CHARACTERS

Characters (i)–(xiv) are taken from Modesto *et al.* (2003), with slight modifications to characters (i), (iv), (viii) and (xiii). Characters (xv–xxi) are new characters.

(i) Premaxillary teeth number: five or more (0); fewer than five (1).
(ii) Maxillary fossa: absent (0); present (1).
(iii) Lacrimal: separated from ectopterygoid (0); contacts ectopterygoid (1).
(iv) Orbit posterior margin: anterior to or level with anterior margin of pineal foramen (0); posterior to it (1).
(v) Pineal foramen: flush with skull roof (0); set within shallow fossa (1).
(vi) Postfrontal: large and contacts postorbital (0); large and contacts supratemporal (1); splint-like and separated from postorbital (2).
(vii) Squamosal ventral point: ends dorsal to ventral margin of quadratojugal (0); extends as far ventrally as quadratojugal (1).
(viii) Supratemporal: broader than long (0); approximately as broad as long (1); longer than broad (2).
(ix) Supratemporal lateral margin: straight (0); with lateral notch (1).
(x) Postparietal: present (0); absent (1).
(xi) Vomerine dentition: present as small denticles (0); present as larger teeth (1).
(xii) Pterygo-palatine dentition: 'continuous' (0); stops in the middle of the palatine (1).
(xiii) Temporal emargination: roughly straight (0); forms acute angle (1); broadly excavated (2).
(xiv) Entepicondylar foramen: present (0); absent (1).
(xv) Prominent anterior maxillary tooth: absent (0); present (1).
(xvi) Maxillary dentition formed by: straight conical teeth (0); posteriorly recurved teeth (1); conical and transversely widened teeth (2).
(xvii) Orbitotemporal crests: absent (0); present (1).
(xviii) Prefrontals: midline contact absent (0); midline contact present (1).
(xix) Nostril shape: subcircular, unexpanded posteriorly (0); broadly expanded posteriorly (1).
(xx) Maxillary tooth count: greater than 24 (0); fewer than 24 (1).
(xxi) Palate length (i.e. distance between tip of transverse flange and basioccipital): long (0); short (1).

APPENDIX B: DATA MATRIX

Character states for eight procolophonoid taxa and the outgroup taxon *Nycteroleter*. Character polarity denoted as follows: primitive state = 0; derived states = 1 and 2; state unknown = ?; inapplicable character = -.

Nycteroleter	00?00	00000	00000	00000	0
O. rubidgei	00001	10111	001?0	01010	0
Barasaurus	00?01	10101	00110	01010	0
Saurodectes	??001	10111	??1??	01??1	?
O. kitchingorum	00001	10110	00111	11111	1
Candelaria	00?0?	1?1-?	001?1	11111	1
Coletta	11?01	00???	1?2?0	00001	1
Sauropareion	??111	21200	111?0	000?1	1
Procolophonidae	11110	21201	11200	20001	1

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