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Ruhuhuaria reiszi, a new procolophonoid reptile from the Triassic Ruhuhu Basin of Tanzania



Ruhuhuaria reiszi, un nouveau reptile procolophonoïde du bassin triasique de Ruhuhu de Tanzanie

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ABSTRACT

The Middle Triassic Lifua Member of the Manda Formation (Ruhuhu Basin, southwestern Tanzania) hosts a diverse fauna dominated by therapsids and archosauromorphs. Reexamination of fossils from previous expeditions in addition to new field collections has brought many new taxa to light. Discovered in the collections of the Cambridge Museum of Zoology, *Ruhuhuaria reiszi* gen. et sp. nov. is the first procolophonoid reptile described from the Ruhuhu Basin. Although the fossil is poorly preserved, CT scanning reveals crucial diagnostic morphology, in particular the highly labio-lingually expanded tooth bases and enlarged anterior dentary teeth. A phylogenetic analysis shows *Ruhuhuaria* is nested within the owenettids, but results in an otherwise poorly resolved tree. The discovery of *Ruhuhuaria* provides further evidence of the persistence of owenettids into the Middle Triassic, and their coexistence with procolophonids well into the Triassic.

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R É S U M É

Le membre médiotriasique de Lifua de la formation de Manda (bassin de Ruhuhu, Sud-Ouest tanzanien) est l'hôte d'une faune diverse, dominée par les thérapsidés et les archosauromorphes. Le réexamen de fossiles collectés lors d'expéditions précédentes et nouvelles ont mis en lumière de nombreux taxons nouveaux. Découvert dans les collections du Muséum de zoologie de Cambridge, *Ruhuhuaria reiszi* gen. et sp. nov. est le premier reptile procolophonoïde du bassin de Ruhuhu à être décrit. Bien que le fossile soit mal préservé, une tomodynamométrie révèle des caractères diagnostiques, en particulier une base des dents très développée labio-lingualement et des dents antérieures du dentaire élargies. Une analyse phylogénétique démontre que *Ruhuhuaria* fait partie des owenettidés, mais résulte en un arbre par ailleurs mal résolu. La découverte de *Ruhuhuaria* apporte une preuve supplémentaire de la persistance des Owenettidae et donc de l'existence de deux clades séparés de procolophoniens durant le Trias moyen.

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1. Introduction

The Ruhuhu Basin of Tanzania consists of a depositional sequence that includes three terrestrial tetrapod bearing formations, spanning from the Middle Permian to the Middle Triassic (Fig. 1); Sidor et al., 2010; Wopfner, 2002. It overlaps with parts of the Karoo Basin of South Africa in temporal expanse and faunal composition; however, the Ruhuhu Basin has yielded an increasing number of endemic taxa (i.e. Butler et al., 2009; Crompton, 1955; Nesbitt et al., 2010, 2013). Although the lower Kingori sandstone is largely lacking in fossils, the Anisian Lifua member of the Manda Formation is quite fossiliferous and shows interesting faunal differences from that of the equivalent and better known *Cynognathus* Assemblage Zone of the South African Karoo (see Abdala et al., 2005).

In addition to a wide variety of therapsids (i.e. Cox and Li, 1983; Crompton, 1955; Haughton, 1932), the Lifua member of the Manda Formation is host to one of the most diverse Triassic archosauriform faunas (Butler et al., 2009; Nesbitt et al., 2010, 2013; Sidor et al., 2013). Unlike the therapsids and archosauriforms, other reptiles and temnospondyls are much rarer in the Manda, and yet are integral to understanding the faunal diversity of this formation and

its biostratigraphic correlation with other Middle Triassic assemblages. Fieldwork in the Ruhuhu Basin has resumed in the last few years, and new information gathered from these expeditions along with an increased understanding of the systematics and evolution of Triassic faunas worldwide has allowed for the reexamination and reinterpretation of fossils recovered from previous expeditions (see Nesbitt et al., 2013).

Interesting components of Triassic faunas were the procolophonoids, the only parareptile clade (sensu Tsuji and Müller, 2009) to have survived the end-Permian mass extinction (Ruta et al., 2011). Comprised of the procolophonids and the owenettids (sensu Lee, 1995), the procolophonoids were very diverse by the end of the Early Triassic (Tsuji and Müller, 2009), and had become quite widespread; members of the clade have been found in Triassic sediments from all seven continents (see Cisneros and Ruta, 2010). Owenettids are known almost exclusively from the Late Permian and Early Triassic of the South African Karoo (Cisneros et al., 2004; Gow, 2000; Modesto et al., 2002, 2003; Reisz and Scott, 2002). The exceptions are *Barasaurus besairei*, an owenettid from the Late Permian and Early Triassic of Madagascar (Ketchum and Barrett, 2004; Piveteau, 1955), and *Candelaria barboursi* from the Middle Triassic of Brazil (Cisneros et al., 2004). The latter is the youngest owenettid yet found, and suggests that members of this clade existed for much longer than was previously thought (Cisneros et al., 2004), with all other members of the clade going extinct by the end of the Induan (Modesto et al., 2003). Their small size and apparent rarity in Permo-Triassic faunas likely contribute to the paucity of known fossils.

This paper describes a new owenettid taxon, the first procolophonoid from the Ruhuhu Basin of Tanzania. We undertake an evaluation of its relationships to other Permo-Triassic procolophonoids, and also discuss its significance to the evolution and biogeography of the only clade of parareptiles to have survived the end-Permian mass extinction.

Institutional abbreviations – BP: Bernard Price Institute of Palaeontology, University of the Witwatersrand, Johannesburg, South Africa; CAMZM: Museum of Zoology, Cambridge University, Cambridge, UK.

2. Materials and methods

CAMZM T997, the type and only specimen, consists of an isolated skull with occluded mandible collected in 1933 and re-discovered in a specimen drawer at the Museum of Zoology, Cambridge in 2008. The partial skull and mandible was collected from the Lifua Member of the Manda Formation by Stockley in 1932–3, reportedly from the B29 locality. Records (Haughton, 1932) indicate that this site also produced fossil No. S519; a “large labyrinthodont”, and Haughton also described the distal half of a right humerus, which he assigned to the rhynchosaur *Stenaulorhynchus major*. Very little matrix remains on the specimen, and much of it is covered with a thick layer of glue. The specimen may have been prepared using acid, resulting in considerable damage. No additional preparation was attempted given the delicate state of the fossil.

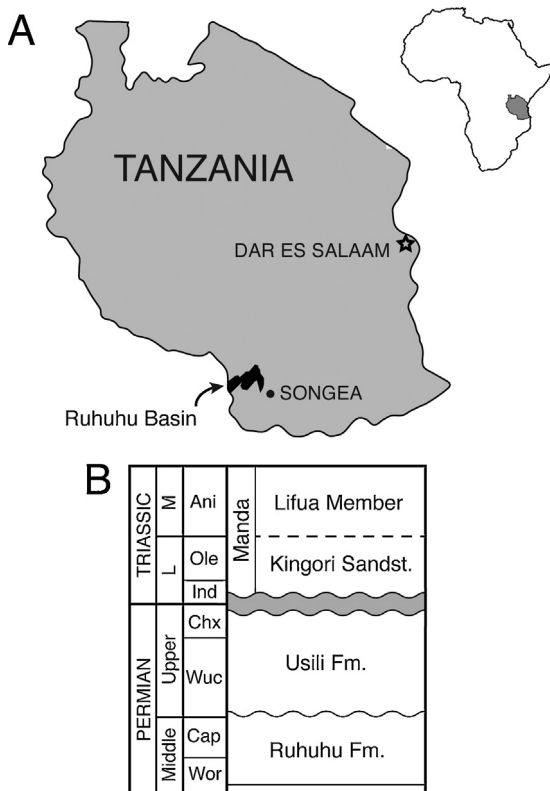


Fig. 1. Location of the Ruhuhu Basin, Tanzania (A). Redrawn from Sidor et al., 2010, with a stratigraphic column of terrestrial vertebrate bearing sediments (B).

Fig. 1. Localisation du bassin de Ruhuhu, Tanzanie (A), redessinée d'après Sidor et al., 2010, avec colonne stratigraphique des sédiments contenant des vertébrés terrestres (B) adaptée d'après Sidor et al. (2010).

Adapted from Sidor et al., 2010.

Due to the unfavourable condition and large amount of glue on the fossil, very little morphological information could be discerned with unaided observation. Therefore, X-ray micro-computed tomography (CT) was used, whereby the difference between yellowed glue, consolidated matrix, and bone could be easily seen. Much more detailed anatomy is visible with the CT scan than can be observed with the naked eye. CT scanning of the material was performed at the Museum für Naturkunde Berlin using a Phoenix|x-ray Nanotom (GE Sensing and Inspection Technologies GmbH, Wunstorf, Germany). Scans were made with 90 kV, 70 μ A, 500 ms, voxel size of 33.39 μ m, and comprised 1440 images in total. A tungsten target and a Cu filter 0.1 mm thick were used in modus 0, averaging 3, and skip 2. Slices were then reconstructed with the datos|x-reconstruction software version 1.5.0.22 (GE Sensing and Inspection Technologies GmbH, Phoenix|x-ray) and the volume was segmented and analyzed in VG Studio Max 2.1 (Volume Graphics, Heidelberg, Germany).

3. Systematic palaeontology

Reptilia [Laurenti, 1768](#)

Parareptilia [Olson, 1947](#)

Procolophonina [Seeley, 1888](#)

RUHUHUARIA REISZI, gen. et sp. nov.

(Figs. 2–3)

Diagnosis—Small procolophonoid reptile that differs from all other procolophonoids by a unique combination of traits. A minimum of 24 alveoli on the dentary, the presence of an orbitotemporal crest, overall labio-lingual expansion of the tooth bases, and an acute ventral temporal emargination. Differs from all other known taxa by a single autapomorphy, the presence of significantly enlarged anterior dentary teeth with labio-lingually expanded bases.

Holotype—CAMZM T997, a partial skull and occluded mandible.

Locality and Horizon—B29 of [Stockley \(1932\)](#), approximately 15 km southwest of Usili Mountain along the Ruhuhu River. Lifua Member of the Manda beds in the Ruhuhu Basin of Tanzania. Early Middle Triassic (Anisian).

Etymology—Genus from *Ruhuhu*, the basin in southwestern Tanzanian in which the fossil was found. The specific epithet honours Robert R. Reisz, in recognition of his vast contributions to knowledge of Late Palaeozoic and Early Mesozoic tetrapods, including parareptiles.

4. Description

4.1. General features

The skull is not very well preserved, and is missing most of the region anterior to the frontal, much of the skull roof posterior to the frontal, the left cheek area, and most of the palate. Most of the mandible is preserved, though it is occluded to the skull.

The skull is sub-triangular in outline, and this is best indicated by the mostly intact mandible. The skull is approximately 2.5 cm in length. This is considerably

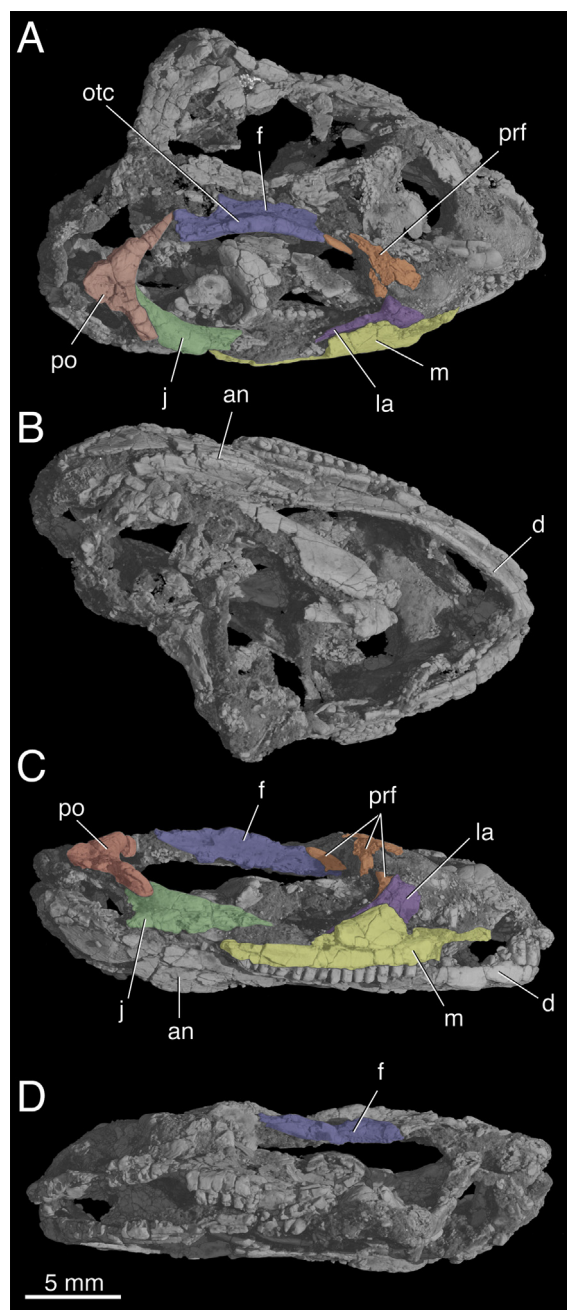
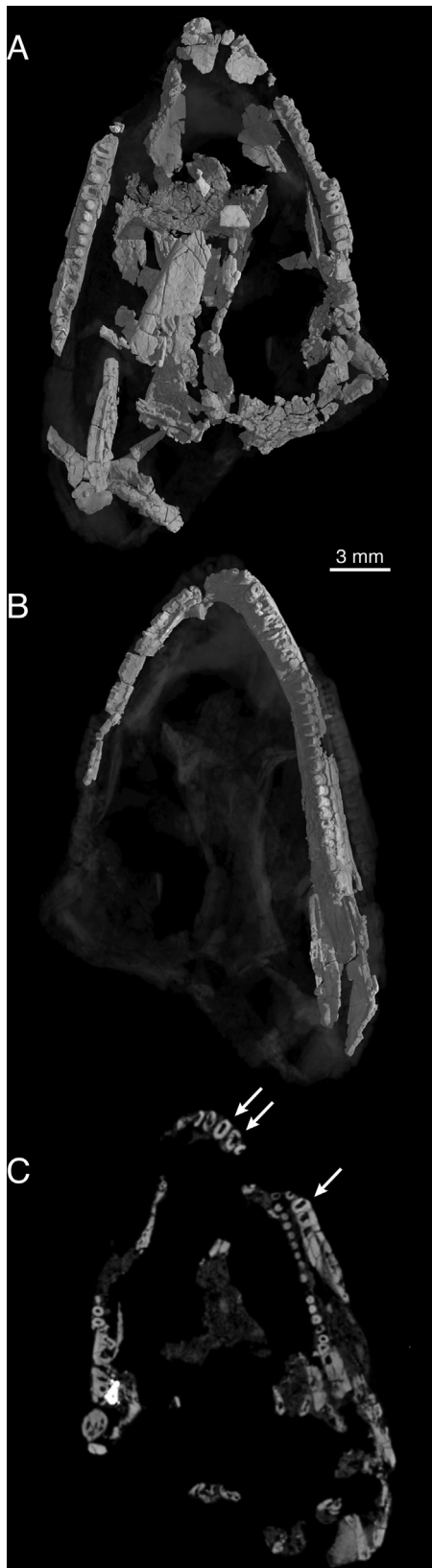


Fig. 2. CT image of CAMZM T997 in dorsal (A), ventral (B), right lateral (C), and left lateral view (D). Abbreviations: an: angular; d: dentary; f: frontal; j: jugal; la: lacrimal; m: maxilla; otc: orbitotemporal crest; po: postorbital; prf: prefrontal. Color available online.

Fig. 2. Image CT de CAMZM T997, en vues dorsale (A), ventrale (B), latérale droite (C) et latérale gauche (D). Abréviations: an: angulaire; d: dentaire; f: frontal; j: jugal; la: lacrimal; m: maxillaire; otc: crête orbito-temporale; po: postorbitale; prf: préfrontal. En couleur sur Internet.

smaller than the largest owenettid, *Candelaria barbouri* ([Cisneros et al., 2004](#); [Price, 1947](#)), though this smaller size is more in line with the rest of the owenettids. The orbits are large, primarily due to the posterior extension, and extend



over half of the skull length. The interorbital portion of the skull roof is thin.

4.2. Skull and mandible

Only isolated portions of the premaxillae are preserved, and only the bases of some of the premaxillary teeth (Fig. 3A). The premaxillary teeth are much larger than the cheek (maxillary) teeth in cross section, and retain the labio-lingually expanded bases (Fig. 3C).

Neither of the maxillae is completely preserved, but a portion of the right can be seen in lateral view. The ventral-most portion of the dorsal process of the maxilla is visible in left lateral view (Fig. 2C), but not enough is preserved to determine whether the animal possessed the anterolateral maxillary foramen present in most parareptiles (Laurin and Reisz, 1995). As in 'Owenetta' *kitchingorum* and *Candelaria*, the suborbital ramus of the maxilla is short, only extending halfway under the orbit. It has been suggested that a shorter maxilla is a feature of Triassic owenettids, whereas Permian forms have a longer suborbital ramus that consequently contains a larger number of teeth (Cisneros et al., 2004). In CAMZM T997, the right maxilla has a minimum of 18 alveoli with space for at least four more (Fig. 3A). Some owenettids that branch off closer to the root of Owenettidae such as *Owenetta rubidgei* have as many as 30 maxillary teeth (Reisz and Scott, 2002) and the number decreases in taxa that branch off closer to the crown, with all known owenettids having more than 18 (Cisneros, 2008b). Amongst procolophonids, *Coletta seca* and *Kitchingnathus untabeni* have a maximum of 15–16 (Cisneros, 2008a; Gow, 2000), with more crownward taxa having as few as 6 (Cisneros, 2008b). See below for a more complete description of the dentition.

The lacrimal is visible on the right side (Fig. 2C). In lateral view it is tall and plate-like; however, the anterior and posterior process are not preserved, so its relationship to the naris anteriorly and the contact with the jugal posteriorly cannot be described.

Though the pre- and post-frontals are not completely preserved, it is evident that a lateral process of the frontal forms a large portion of the dorsal orbital margin (Fig. 2A, C). Portions of the right prefrontal can be seen, particularly in lateral view (Fig. 2A, C). The ventral process of the prefrontal can be seen in the anterior portion of the orbit, extending interior and slightly posterior to the posterior edge of the lacrimal. Although a portion of the prefrontal can be seen on the dorsal skull roof, it is not preserved well enough to determine the medial extent of the element. Though not completely preserved, there appears

Fig. 3. CT image of CAMZM T997 in which the mandible has been segmented from the skull, making the tooth rows visible in occlusal view. Skull in ventral view (A), mandible in dorsal (occlusal) view (B), and transverse section at level of dentary tooth bases (C). Arrows showing enlarged, labio-lingually expanded tooth bases on the anterior dentary (above) and maxilla (below).

Fig. 3. Image CT de CAMZM T997, dans laquelle la mâchoire a été séparée du crâne, rendant les rangées de dents visibles en vue occlusale. Crâne en vue ventrale (A), mâchoire en vue dorsale (occlusale) (B) et section transversale au niveau des bases de dents (C). Les flèches indiquent des bases de dents élargies, développées labio-lingualement sur la partie antérieure du dentaire (en haut) et du maxillaire (en bas).

to be an orbitotemporal crest (sensu Cisneros et al., 2004) that is formed by the lateral margins of the prefrontal, frontal, and postfrontal (Fig. 2A). This feature is present in other owenettids and *Nyctiphruretus acudens* (Saila, 2010), as well as some procolophonids (Cisneros, 2008b). The existence of this feature was asserted for ‘nycteroleters’; however, in specimens of *Macroleter poezicus* this region is periodically upraised by a series of bosses rather than consisting of consistent, smooth crest (Tsuji, 2006).

The temporal region is not preserved in its entirety, and the glue binding the fragments of matrix could easily be mistaken for bone. It is easy to see why the fossil was provisionally called a diapsid given the state of the temporal region. The CT data is particularly helpful in this area (Figs. 2–3). The right postorbital is preserved almost in its entirety, and the posteroventral edge is emarginated (Fig. 2A), but it is not clear whether this emargination is for the reception of the jugal, in which case the postorbital would have been displaced significantly posteriorly, or whether it represents the anterior and dorsal margin of a potential upper temporal fenestra. The lack of skull elements posterior to this feature, both in the left and right sides makes it impossible to ascertain whether there was temporal fenestra in *Ruhuhuaría* based solely on CAMZM T997. Temporal fenestration is variable in procolophonoids, but in addition to a ventral temporal emargination, a large fenestra is present in *Candelaria* (Cisneros et al., 2004) and temporal fenestration is highly variable in parareptiles in general (Cisneros et al., 2004; Tsuji, 2006). A portion of the jugal is present and visible in right lateral view (Figs. 2A, C). Although the jugal is somewhat obscured by the ventral process of the postorbital that has shifted downwards, it is possible to make out what looks like a finished posterior edge of the jugal, indicating that there was a ventral emargination of the postorbital region. The angle of the posterior edge of the jugal also indicates that the emargination would have been acute rather than broad as it is in procolophonids such as *Procolophon trigoniceps* (Carroll and Lindsay, 1985).

The mandible is partially preserved with the complete tooth row of the right dentary visible when segmented from the skull (Fig. 3B). The dentary contains a minimum of 24 tooth positions, which, like the maxillary teeth, have labio-lingually expanded bases (Figs. 2B, 3B, C). Portions of the splenial can be seen but the nature of the symphysis cannot be determined. A small fragment of the angular is also visible along with parts of the surangular and what is likely a portion of the prearticular (Fig. 2B).

4.3. Dentition

Tooth morphology is one of the more distinctive features of procolophonid anatomy. The tooth row of CAMZM T997 is flush with the maxillary surface (Fig. 2C), as it is in procolophonids that branch off closer to the root of Procolophonidae (such as *Coletta*, *Pintosaurus magnidentis*, and *Sauropareion anoplus* (Cisneros, 2008b)). As stated above, only 18 teeth and/or alveoli are preserved on the right maxilla; however, it is clear from the CT scan that the bases of these teeth are labio-lingually expanded, as much as two times as wide labio-lingually as mesio-distally (Figs. 3A, C).

The largest and anteriormost teeth, both in the dentary and mandible, show this morphology most clearly, whereas the more posterior teeth have less expanded bases. The transverse expansion of the base of the maxillary teeth is a recognized synapomorphy of Procolophonidae (Cisneros, 2008b). The presence of this trait in *Ruhuhuaría* is therefore unexpected given its owenettid-like appearance. The dentary teeth are likewise expanded and seem to increase in size anteriorly (Fig. 3C), a feature that has not been observed in other taxa and is therefore an autapomorphy of *Ruhuhuaría*. No complete crowns are preserved; however, the teeth appear to bear single cusps, and they are simple, conical, and not recurved (Fig. 2). There is also no evidence of any infolding of the dentine (Fig. 3C).

There is little evidence in owenettids of lateral expansion of the cheek teeth, but rarely are the skulls preserved in a way that the base of the teeth is visible, often with the mandible occluded to the skull (i.e. BP/1/4105, Reisz and Scott, 2002); thus, it must be noted that the shape of the tooth bases are not known for all owenettid taxa. Indeed, it is only the CT scan that permitted us to recognize the lateral expansion of the base of the teeth in *Ruhuhuaría*.

5. Discussion

5.1. Taxonomic discussion and rationale

At first glance this fossil is ambiguous in appearance. CAMZM T997 was tentatively identified as a diapsid reptile on the specimen label in the collection, and indeed, it is obvious that this small skull likely belongs to a small reptile. An assignment to a known taxon is difficult, but close examination has revealed four aspects of the morphology that can be identified as characters of a known clade, and through this an assignment can be made:

- lateral expansion of the base of the teeth. As shown by the CT scan, all of the teeth, particularly those more anterior, are labio-lingually expanded at their base while remaining peg-like and sub circular in cross section for the remainder of their length with the anteriormost teeth the most expanded;
- sub-triangular skull;
- very narrow interorbital breadth, with large, posteriorly-expanded orbits;
- orbitotemporal crests, present in the parareptile *Nyctiphruretus* (Saila, 2010) and owenettids. Amongst known Permo-Triassic fossils, only procolophonoids have this combination of characters.

5.2. Phylogenetic analysis

Based on the above determination as a procolophonoid, a phylogenetic analysis of this clade was conducted in order to determine the relationships of the new taxon. The matrix was modified from Cisneros et al. (2004), which was in turn based on that of Modesto et al. (2003). These are the only matrices that scored every known owenettid species separately. Other taxa were added to the matrix: the procolophonoid *Kitchingnathus* was included, and *Procolophon* was considered monospecific, as per Cisneros (2008c). In

total, 10 ingroup taxa were included, with *Macroleter poezicus* as the outgroup (Character List, Appendix A; Character Matrix, Appendix B). All characters were weighted equally. One character, #21, maxillary tooth count, was ordered as it was in Cisneros (2008b), and Character #16 of Cisneros et al. (2004) was split into two separate characters in this analysis. Due to the incompleteness of the fossil, only six out of 21 characters could be scored for *Ruhuhuaria*. The phylogenetic analysis was completed using TNT Version 1.1, downloaded January 2013 (Goloboff et al., 2008), using an exhaustive search, which examines all possible combinations. Tree collapsing was set to max. length=0. In addition, a bootstrap resampling analysis of 5000 replicates was run and the decay indices were calculated, all using TNT.

Five most parsimonious trees were recovered, consisting of 34 steps (strict consensus; Fig. 4). The strict consensus tree has a Consistency Index (CI) of 0.7353, and a Retention Index (RI) of 0.7955. Owenettidae continues to be monophyletic but the clade is not supported by more than 50% of the bootstrap replicates, and the relationships within the clade are not well resolved. As in previous analyses (Cisneros et al., 2004; Modesto et al., 2003), the two *Owenetta* species are not monophyletic, with *O. rubidgei* the sister taxon to *Barasaurus* and 'O.' *kitchingorum* forming a sister group relationship with *Candelaria*. Thus, 'O.' *kitchingorum* continues to be only provisionally assigned to the genus. The remaining

members of the Owenettidae including *Ruhuhuaria* and *Saurodekte*s fall within an unresolved polytomy (Fig. 4). The analysis did not support the clade of *Saurodekte*s + (*O. kitchingorum* + *Candelaria*) of Cisneros et al. (2004), with *Saurodekte*s instead falling within an unresolved polytomy with (*O. kitchingorum* + *Candelaria*), *Ruhuhuaria*, and (*O. rubidgei* + *Barasaurus*). Procolophonidae is monophyletic and well supported (75% of bootstrap replicates and decay index of 2).

The retention of a monophyletic Owenettidae is somewhat surprising given that *Ruhuhuaria* possesses a suite of characters that appears to be transitional between owenettids and procolophonids such as the expanded bases of the maxillary teeth (generally a procolophonid character), and a relatively high tooth count (an owenettid character). Owenettidae is supported by 4 unambiguous synapomorphies: #9, supratemporal lateral margin straight (0=>1); #14, entepicondylar foramen present (0=>1); #18, presence of orbitotemporal crests (0=>1); and #20, posteriorly-expanded naris (0=>1). Of these, *Ruhuhuaria* can only be scored for character #18.

5.3. Taxonomic and biogeographic implications

The identification of this taxon as a procolophonoid has interesting implications for the evolution of procolophonians (pareiasauromorphs + procolophonoids). Owenettidae contains six species—*Barasaurus besairei*, *Candelaria barbouri*, '*Owenetta*' *kitchingorum*, *Owenetta rubidgei*, and *Saurodekte*s *rogersorum* (Cisneros et al., 2004; Modesto et al., 2003, 2004), and now *Ruhuhuaria reisi*. *O. rubidgei* is exclusively Late Permian, present in the *Cistecephalus* and *Dicynodon* Assemblage Zones of the South African Karoo Basin (Broom, 1939; Cisneros et al., 2004; Modesto and Damiani, 2007). *Barasaurus besairei* is found in the Sakamena Group of Madagascar, and fossils have been found in both Permian and Triassic Formations within this Group, indicating that the species survived the end-Permian mass extinction event (Ketchum and Barrett, 2004). Apart from *Ruhuhuaria*, there is only one other Middle Triassic owenettid: *Candelaria barbouri*, from the Ladinian of Brazil (Cisneros et al., 2004; Price, 1947). The discovery of *Ruhuhuaria* provides additional evidence of the existence of Middle Triassic owenettids as predicted by Cisneros and colleagues (2004), and that consequently, two separate clades of procolophonians (owenettids and procolophonids) co-existed well into the Triassic.

Ruhuhuaria is the first Triassic parareptile described from Tanzania, but its presence here is not unexpected given the distribution and stratigraphic occurrence of its relatives. Procolophonoids are fairly speciose, found in similarly aged faunas of South Africa, and are also found in the Triassic of Europe, North and South America, Antarctica, Australia (Bartholomai, 1979), and China (Cisneros, 2008b). Recent fieldwork in Tanzania has also produced what is a yet-to-be-described procolophonid from the Manda Formation (C. Sidor, pers. comm.), indicating that in addition to a remarkable diversity of archosauriforms, the Lifua Member of the Manda Formation may yet reveal a number of additional parareptile taxa.

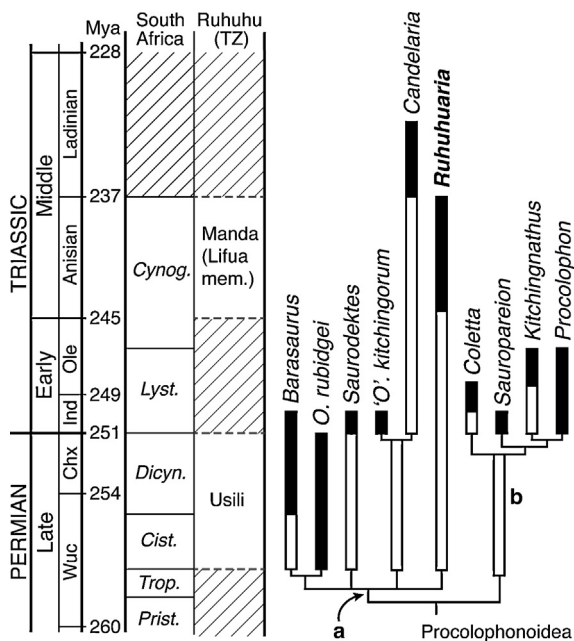


Fig. 4. Stratocladogram to scale showing the relationships determined in the phylogenetic analysis in this paper. Ghost lineages are represented by white boxes. Taxic ranges from Cisneros et al., 2004, Fig. 2. Abbreviations: a: Owenettidae; b: Procolophonidae. See text for support values.

Fig. 4. Stratocladogramme à l'échelle montrant les relations déterminées dans l'analyse phylogénétique de cet article. Les lignes fantômes sont représentées par des cases blanches. Les étendues stratigraphiques des taxons sont issues de Cisneros et al., Fig. 2. Abréviations : a : Owenettidae ; b : Procolophonidae. Voir texte.

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Appendix A. Character list.

(All following from Modesto et al., 2003).

1. Premaxillary tooth number: five or more (0); fewer than five (1). (Modified as per Cisneros et al., 2004).
2. Maxillary fossa: absent (0); present (1).
3. Lacrimal-ectopterygoid contact: absent (0); present (1).
4. Orbit posterior margin: anterior to or level with anterior margin of pineal foramen (0); posterior to it (1). (Modified as per Cisneros et al., 2004).
5. Pineal foramen: flush with skull roof (0); in a shallow fossa (1).
6. Postfrontal shape: large and contacts postorbital (0); large and contacts supratemporal (1); splint-like (2). (Modified in this analysis.)
7. Squamosal ventral point: ends dorsal to ventral margin of quadratojugal (0); extends as far ventrally as quadratojugal (1).
8. Supratemporal: broader than long (0); approximately as long as broad (1); longer than broad (2). (Modified as per Cisneros et al., 2004).
9. Supratemporal lateral margin: straight (0); with lateral notch (1).
10. Postparietal: present (0); absent (1).
11. Vomerine dentition: present as small denticles (0); present as larger teeth (1).
12. Pterygo-palatine dentition: 'continuous' (0); stops in the middle of the palatine (1). (Modified as per Cisneros et al., 2004).
13. Temporal ventral margin: roughly straight (0); forms an acute angle (1); broadly excavated (2). (Modified as per Cisneros et al., 2004).
14. Entepicondylar foramen: present (0); absent (1). (Modified from Cisneros et al., 2004).
15. Prominent anterior maxillary tooth (caniniform): absent (0); present (1).
16. Maxillary dentition formed by: straight conical teeth (0); posteriorly recurved teeth (1). (Modified in this analysis).
17. Shape of base of maxillary teeth: cross section circular (0); cross section labio-lingually expanded (1). (Modified in this analysis).
18. Orbitotemporal crests: absent (0); present (1).
19. Prefrontals: midline contact absent (0); midline contact present (1).
20. Naris shape: subcircular, unexpanded posteriorly (0); broadly expanded posteriorly (1).
21. Maxillary tooth count: 35-24 (0); 24-15 (1); 14 or fewer (2). (Modified in this analysis).

Appendix B. Character matrix.

	1	2
	123456789012345678901	
<i>Macroleter poezicus</i>	000000000000001100001	
<i>Owenetta rubidgei</i>	0000110111001?0001010	
' <i>Owenetta</i> ' <i>kitchingorum</i>	000011011000111101111	
<i>Barasaurus besairiei</i>	00?0110100110001010	
<i>Coletta seca</i>	11?1120??1?1?0000002	
<i>Sauropareion anoplus</i>	1111121200111?0010002	
<i>Saurodekte rogersorum</i>	??00110111??1?001??2	
<i>Candelaria barbouri</i>	00?011?1-?001?1101111	
<i>Kitchingnathus untabeni</i>	11?112?001??2?001??01	
<i>Procolophon trigoniceps</i>	111102120111200010002	
<i>Ruhuhuarua reisi</i>	0??????????1?011??1	

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