

An additional specimen of owenettid procolophonoid from the Middle Triassic of Southern Brazil

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Owenettids are small procolophonoids that survived beyond the Permo-Triassic boundary. The fossil record of owenettids range from the upper Permian to the Middle Triassic. These records come from South Africa, Madagascar, Tanzania, Germany, and Brazil. Despite its conservative anatomy, some species depict some peculiar traits, such as *Candelaria barbouri*. This owenettid comes from Middle Triassic of Brazil and is characterized by the presence of temporal openings, a highly unusual trait in procolophonoids. Here, a new specimen of *C. barbouri* is described. The specimen comes from the “Posto” site, an iconic fossiliferous locality from southern Brazil. The material is assigned to *C. barbouri* based on the presence of temporal openings. In addition, its owenettid affinities are supported by two phylogenetic analyses. The new specimen is the first parareptile from the “Posto” site, providing further data for biostratigraphic hypotheses. Finally, a morphological disparity analysis reveals no overlapped areas between the morphospace occupied by procolophonoids and owenettids, reinforcing the existence of these two distinct groups. Furthermore, the morphospace area occupied by owenettids is far reduced in comparison to that of procolophonoids, reflecting the conservative anatomy of owenettids.

Key words: Parareptilia, Procolophonia, Owenettidae, *Candelaria barbouri*, phylogeny, Ladinian, Santa Maria Formation, South America.

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Introduction

Owenettidae (Broom 1939) is a low diversity group of small procolophonoids that range from the upper Permian (Broom 1939; Piveteau 1955) to the Middle Triassic (Cisneros et al. 2004; Martinelli et al. 2016a). The oldest owenettids are quarried from upper Permian strata of South Africa and Madagascar (Broom 1939; Piveteau 1955; Reisz and Scott 2002). Immediately after the Permo-Triassic extinction event, the group is recorded from Lower Triassic strata of South Africa and Madagascar (Reisz and Scott 2002; Modesto et al. 2003; Ketchum and Barrett 2004). Finally, Middle Triassic owenettids are recorded from Tanzania, Germany, and Brazil (Price 1947; Cisneros et al. 2004; Da-Rosa et al. 2004; Tsuji et al. 2013; Martinelli et al. 2016a).

The fossil record of owenettids from Brazil is limited to some poorly preserved specimens of *Candelaria barbouri* (Price 1947; Cisneros et al. 2004), one of the youngest

and largest owenettid. The specimens were excavated from two distinct fossiliferous localities of southern Brazil (Da-Rosa et al. 2004), which are considered Ladinian to ?early Carnian in age (Martinelli et al. 2017; Schultz et al. 2020). In the present study, a putative new specimen of *C. barbouri* from the “Posto” site is described. This site is one of the most iconic fossiliferous localities of southern Brazil, yielding exceptionally preserved specimens of the giant top tier predator *Prestosuchus chiniquensis* (Roberto-da-Silva et al. 2020), as well as monotypic accumulations of several individuals in close association (França et al. 2011; Ugalde et al. 2020). Moreover, its faunal content precedes the dawn of the dinosaur era, providing evidences from one of the last Mesozoic terrestrial ecosystems not ruled by dinosaurs. The new specimen is the first parareptile from the “Posto” site, providing further data for biostratigraphic hypotheses. In addition, the new specimen reinforces some peculiar traits of *C. barbouri* (e.g., presence of temporal openings).

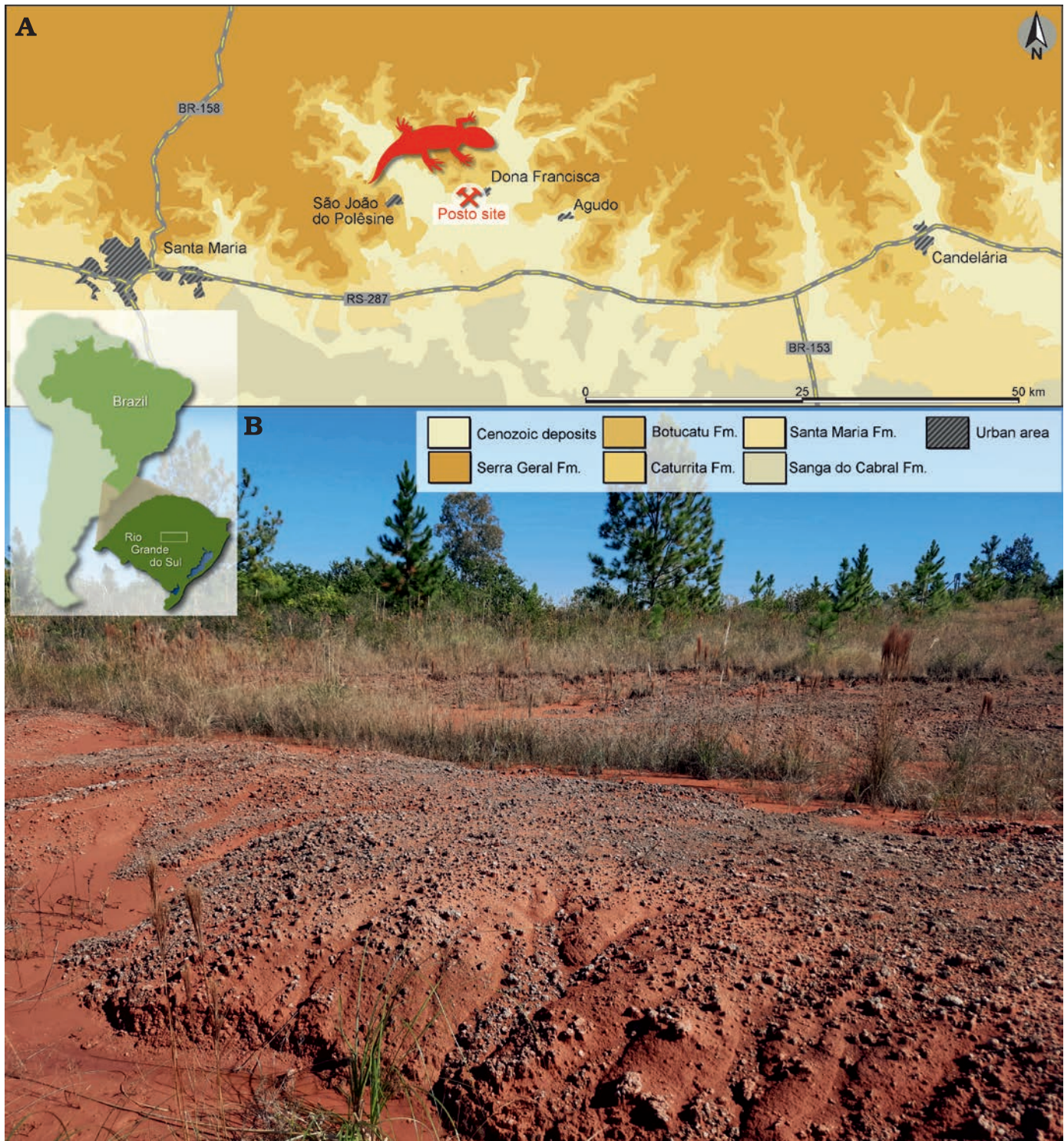


Fig. 1. A. Map of the “Posto” site and the surface distribution of the geologic units in the area (modified from Müller et al. 2020). Location of the study area within South America (inset). B. General view of the “Posto” site.

Institutional abbreviations.—BMNH, Natural History Museum, London, UK; BP, Evolutionary Studies Institute (formerly Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg, South Africa; BRSUG, University of Bristol, Geological Collection, UK; CAPP/UFMS, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia/Universidade Fede-

ral de Santa Maria, São João do Polêsine, Rio Grande do Sul, Brazil; CAMZM; Museum of Zoology, Cambridge University, Cambridge, UK; DGM, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil; IVPP, Institute for Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; NM, National Museum, Bloemfontein, South Africa; NMT, National Museum of Tanzania, Dar es Salaam,

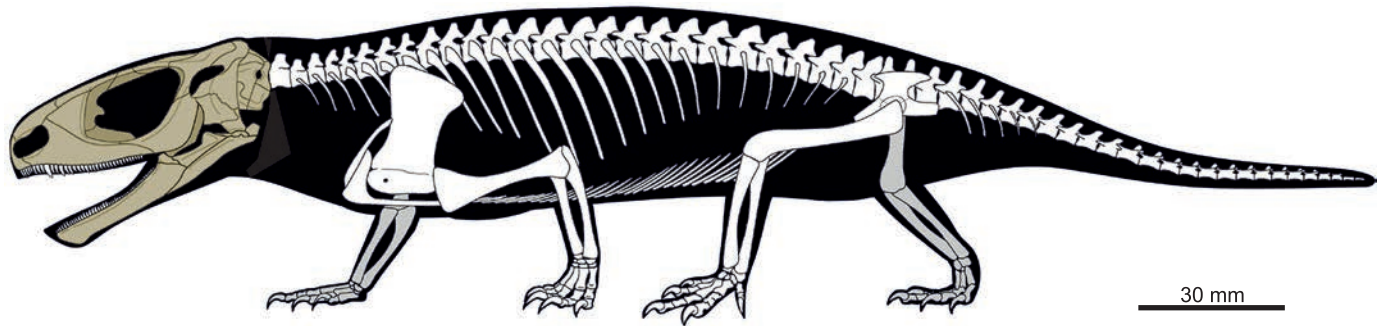


Fig. 2. Reconstructed skeleton of *Candelaria barboursi* depicting the preserved elements (in brown) of CAPP/UFMS 0225 (by Maurício S. Garcia).

Tanzania; PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; RC, Rubidge Collection, Camdeboo Municipality, Eastern Cape, South Africa; SAM, Iziko South African Museum, Cape Town, South Africa; UFMS, Laboratório de Estratigrafia e Paleobiologia, Universidade Federal de Santa Maria, Brazil; UMZC, Museum of Zoology, Cambridge University, Cambridge, UK; YPM, Yale Peabody Museum, New Haven, USA.

Other abbreviations.—MPTs, most parsimonious trees; OTU, operational taxonomic unit.

Geological setting

The new specimen comes from the “Posto” (or “Posto de Gasolina”) site. This site is located in the municipality of Dona Francisca (29°37'35.60" S; 53°22'2.86" W), Rio Grande do Sul, Brazil (Fig. 1). Site strata belong to the Pinheiros-Chiniquá Sequence (Horn et al. 2014), which is part of the Santa Maria Suspersequence of the Paraná Basin (Zerfass et al. 2003). The new specimen was excavated from the basalmost layers of the fossiliferous site, which outcrops in ravines eroded in reddish mudstone. The presence of the cynodont *Dinodontosaurus* places the site in the *Dinodontosaurus* Assemblage Zone (Ugalde et al. 2020), which is Ladinian to early Carnian in age (Marsicano et al. 2016; Ezcurra et al. 2017; Phillip et al. 2018; Schultz et al. 2020). In addition to *Dinodontosaurus*, the site yielded the cynodonts *Massetognathus ochagaviae* Barberena, 1981, and *Protheriodon estudianti* Bonaparte, Soares, and Schultz, 2006, and the archosaurs *Prestosuchus chiniquensis* Huene, 1938, and *Decuriasuchus quartacolonia* França, Ferigolo, and Langer, 2011 (Bonaparte et al. 2006; França et al. 2011; Mastrantonio et al. 2013; Pavanatto et al. 2016; Martinelli et al. 2017; Roberto-da-Silva et al. 2020). The fossiliferous content varies from isolated bones to articulated and associated skeletons (e.g., França et al. 2011; Ugalde et al. 2020). A nearby outcrop named “Bortolin” site yielded the dicynodont *Dinodontosaurus*, as well as rauisuchian archosaurs (cf. *Decuriasuchus*), cynodonts (*Chiniquodon* and *Luangwa*), and a mawsoniid coelacanth (Pavanatto et al. 2020). This outcrop area is about to 1 km distant from the “Posto” site.

Material and methods

Material.—The specimen (Fig. 2) here described is housed at the Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia/Universidade Federal de Santa Maria (CAPP/UFMS), under the code CAPP/UFMS 0225. It was submitted to mechanical preparation with the aid of air scribe tools, scalpels, and needles. The specimen was stabilized with Paraloid B-72 (Koob 1986).

Phylogenetic analyses.—The phylogenetic affinities of CAPP/UFMS 0225 were investigated employing two distinct data matrices. In the first analysis, CAPP/UFMS 0225 was scored in the data matrix of Tsuji et al. (2013), which is a modified version of the data matrices of Modesto et al. (2003) and Cisneros et al. (2004). Following the taxonomic proposal of Hamley et al. (2020), “*Owenetta*” *kitchingorum* and *Saurodekteles rogersorum* were merged in a single operational taxonomic unit (OTU) named *Saurodekteles kitchingorum*. The final data matrix includes 21 characters and 11 OTUs. The analysis was conducted in the software TNT v. 1.1 (Goloboff et al. 2008) following the parameters of Tsuji et al. (2013): using an exhaustive search, where all characters were weighted equally and the character 21 was treated as ordered (i.e., additive).

In the second analysis, CAPP/UFMS 0225 was scored in the data matrix of Pinheiro et al. (2021), which combines owenettids in a single OTU named “Owenettidae”. The aim of this experimental approach is to test if the specimen nests with this OTU. Following Pinheiro et al. (2021), *Phaanthosaurus* was set as inactive. The final data matrix includes 59 characters and 28 active OTUs. The analysis was performed in the software TNT v. 1.1 (Goloboff et al. 2008) and employed the same parameters of Pinheiro et al. (2021), hence, the most parsimonious trees were recovered with a “Traditional search” (random addition sequence + tree bisection reconnection) with 100 replicates of Wagner trees (with random seed = 0), and using tree bisection re-connection and branch swapping (holding 100 trees save per replicate). All characters were treated as having equal weight, and the following characters were treated as ordered: 1, 8, 18, 26, 31, and 32.

Decay indices (Bremer support values) and bootstrap values (1000 replicates) were obtained with TNT v. 1.1

(Goloboff et al. 2008). The strict consensus trees were generated using all trees recovered in the analysis and all OTUs. The updated data matrix of full Tsuji et al. (2013) and the full coding to CAPP/UFMS in the second phylogenetic analysis (employing the data matrix of Pinheiro et al. 2021) are available as Supplementary Online Material.

Cluster analysis.—In order to test putative implications of the new specimen on previous biostratigraphic frameworks, the Jaccard Similarity Coefficient was used to construct a dendrogram with an updated version (incorporating the new specimen) of the dataset of Martinelli et al. (2017). The dataset of Martinelli et al. (2017) includes 11 fossiliferous localities assigned to the *Dinodontosaurus* Assemblage Zone, as well as 19 taxa. The analysis was carried using the software PAST (Hammer et al. 2001).

Morphospace occupation analysis.—The morphological disparity of owenettids was investigated employing the procedures of Wills (1998). First, a dataset of cranial characters was constructed (see SOM, Supplementary Online Material available at http://app.pan.pl/SOM/app66-Mueller_SOM.pdf). The dataset combines data from the phylogenetic matrices (i.e., Tsuji et al. 2013; Pinheiro et al. 2021) employed in the phylogenetic analyses performed here. The complete list of characters and the dataset are available as Supplementary Online Material. A Euclidean distance matrix (EDMA) was calculated from the dataset using the software MATRIX (Wills 1998). Then, a principal coordinate analysis (PCoA) was performed for the EDMA with the multivariate package GINKGO (Bouxin 2005). The centroid of all operational taxonomic units (OTUs) was taken as the origin of multivariate axes, and the Cailliez method of negative eigenvalue correction was adopted. Finally, a bivariate graph with axes 1 and 2 of the PCoA was constructed using the software PAST (Hammer et al. 2001).

Systematic palaeontology

Parareptilia Olson, 1947

Procolophonoidea Romer, 1956

Owenettidae Broom, 1939

Genus *Candelaria* Price, 1947

Type species: *Candelaria barbouri* Price, 1947; Candelária, Brazil, Ladinian–Carnian, Triassic.

Candelaria barbouri Price, 1947

Fig. 3.

Holotype: DGM 314Ra skull and mandible in occlusion (Price 1947).

Type locality: Sanga Pinheiros (29°46'19" S, 52°44'54" W), municipality of Candelária, Rio Grande do Sul, Brazil.

Type horizon: Santa Maria Supersequence, Pinheiros-Chiniquá Sequence, Paraná Basin. These strata are Ladinian to early Carnian in age (Marsicano et al. 2016; Ezcurra et al. 2017; Phillip et al. 2018; Schultz et al. 2020).

Material.—UFMS 11076 and UFMS 11131, two complete skulls with mandibles in occlusion and associated postcrania (Cisneros et al. 2004). The specimens were excavated from “Cortado” site (29°44'55"S, 53°00'06"W), municipality of Novo Cabrais, Rio Grande do Sul, Brazil (Da-Rosa et al. 2004). The outcrops pertain to the same horizon as those from which the holotype was recovered (Cisneros et al. 2004). CAPP/UFMS 0225, an almost complete skull with mandibles in occlusion. Despite its completeness degree, the bone surface is poorly preserved. The specimen was excavated from from “Posto” site (29°37'35.60"S, 53°22'2.86"W), municipality of Dona Francisca, Rio Grande do Sul, Brazil. This site is Ladinian to early Carnian in age.

Emended diagnosis.—According to Cisneros et al. (2004), *Candelaria barbouri* differs from all other owenettids by its relatively large size (at least 30% larger than all other known owenettid specimens, but see Bradley and Nesbitt 2017) and by a suite of characters related to the presence of a temporal fenestra.

Description.—Whereas the skull and mandibles are almost completely preserved, bone contacts are poorly discernable (Fig. 3). Furthermore, CAPP/UFMS 0225 lacks the right portion of the snout. The skull is 43 mm in length. The largest known specimen of *Candelaria barbouri* is 49 mm in length (UFMS 11076; Cisneros et al. 2004). Conversely, other owenettids are smaller in size, for instance, the length of the holotypic skull of *Ruhuhuaría reishi* Tsuji, Sobral, and Müller, 2013 (CAMZM M T997) is 25 mm (Tsuji et al. 2013). However, an additional specimen (UMZC T1162) suggests that *R. reishi* could have reached 40 to 50 mm in length (Bradley and Nesbitt 2017), resembling the size of *Candelaria barbouri*. The maximum width of the posterior half of the skull is approximately 30 mm. Therefore, the ratio between length and width of the skull is 1.43. In some procolophonids, such as *Procolophon trigoniceps* Owen, 1876, and *Kapes bentoni* Spencer and Storrs, 2002 (Carroll and Lindsay 1985; Zaher et al. 2019), it is less than 1. The height of the skull with mandibles in occlusion is about the same along its length (anterior half approximately 20.5 mm and posterior half approximately 20 mm). Nevertheless, the specimen shows some degree of dorsoventral sedimentary compression. Whereas the orbits are approximately 15 mm in length, the shape and dimensions of the external nares are uncertain.

Distinct from several parareptiles (e.g., *Macroleter poezicus* Tverdochlebova and Ivachnenko, 1984, PIN 4543/3; *Nyctiphruetus acudens* Efremov, 1938, PIN 4659/1; Tsuji 2006; Säilä 2010), the specimen lacks ornamentation (i.e., grooves and tubercles) on the dorsal surface of the skull. As typical of procolophonoids, the snout tapers anteriorly and the skull is sub-triangular in dorsal view (Fig. 3A₁, A₂). The anterior portion of the skull is poorly preserved. Therefore, the number of premaxillary and maxillary teeth, as well as details of the morphology of premaxilla and maxilla are uncertain. The prefrontal forms the anterior and the ventral

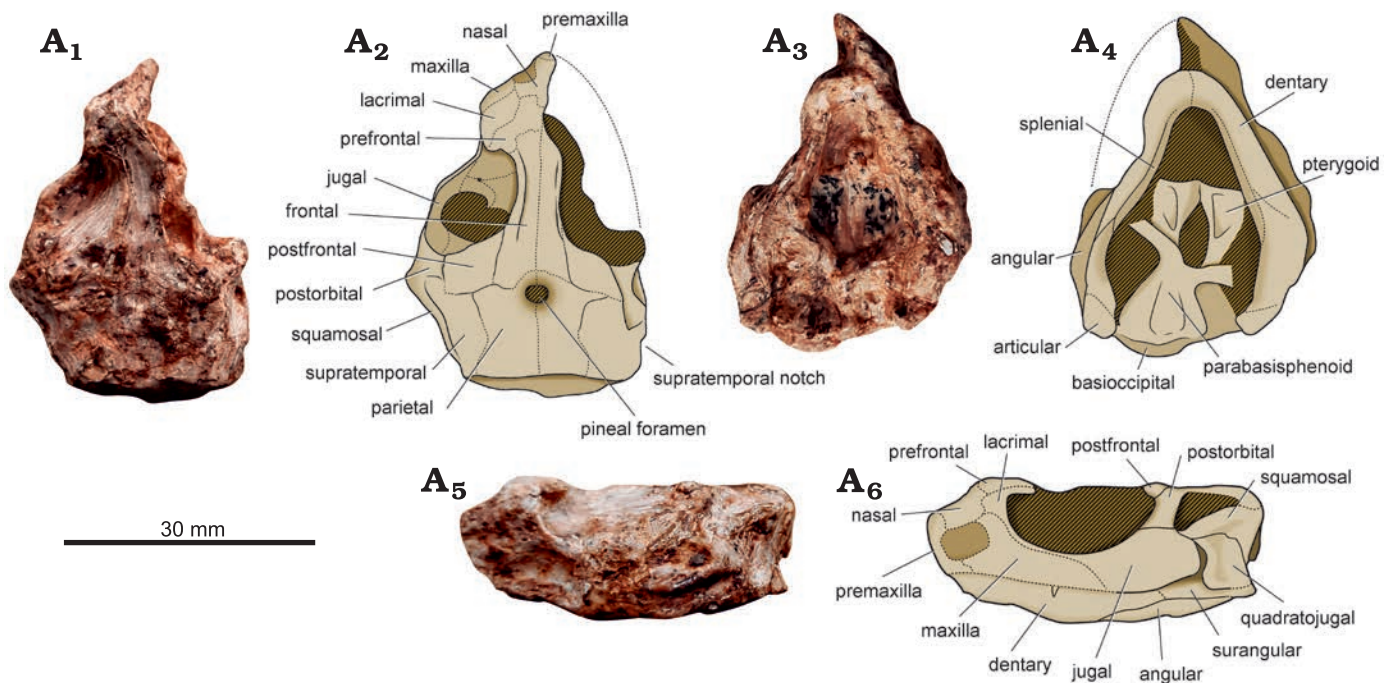


Fig. 3. Owenettid procolophonoid *Candelaria barbouri* (CAPPA/UFSM 0225) from the “Posto” site, Dona Francisca, Rio Grande do Sul, Brazil; Ladinian, Middle Triassic. Skull and mandible in dorsal (A₁, A₂), ventral (A₃, A₄), and left lateral (A₅, A₆) views. Photographs (A₁, A₃, A₅) and explanatory drawings (A₂, A₄, A₆).

half of the orbital margin. There is an orbital flange projecting from the anteromedial margin of the orbit (Fig. 3A₁, A₂), such as in other specimens of *C. barbouri* (e.g., UFSM 11076, UFSM 11131), where it is formed across the contact between the lacrimal and the prefrontal (Cisneros et al. 2004). In *Owenetta rubidgei* Broom, 1939 (RC 50) and *Saurodekte kitchingorum* Reisz and Scott, 2002 (BP/1/4195a; Reisz and Scott 2002) it is less developed. The orbit of CAPPA/UFSM 0225 is roofed anteriorly by the prefrontal and frontal, and posteriorly by postfrontal. The latter is large, resembling other owenettids, whereas in procolophonids it is comparatively reduced. Medially, the orbit is rimmed by a longitudinal orbitotemporal crest (Fig. 3A₁, A₂). This crest is usually present and well-developed in owenettids (Cisneros et al. 2004; Tsuji et al. 2013). However, a similar crest occurs in some procolophonids (*Kapes bentoni*, BRSUG 29950-13; *Procolophon trigoniceps*, CAPPA/UFSM 0189). The frontals are narrow, resulting in a very narrow interorbital breadth, which resembles the condition of *Ruhuhuaria reishi* (CAMZM T997; Tsuji et al. 2013).

The orbit of CAPPA/UFSM 0225 lacks the posterior enlargement typical of procolophonids. On the other hand, the specimen bears a putative temporal opening, such as *Candelaria barbouri* (Cisneros et al. 2004). The fenestra is located at the dorsal half of the posterior portion of the skull (Fig. 3A₅, A₆). It is longer (8 mm) than tall (2 mm). The temporal opening is separated from the orbit by the postorbital, which forms the anterior rim of the opening. The postorbital also contributes to the anterior dorsal half of the fenestra, whereas the dorsoventrally short squamosal forms the ventral margin. The lateral margin of the supratemporal bears a

notch (Fig. 3A₁, A₂), which occurs in *Saurodekte kitchingorum* (BP/1/4195a; BP/1/6025; Reisz and Scott 2002; Modesto et al. 2003) and *Owenetta rubidgei* (SAM PK K 7582; Reisz and Scott 2002). This notch is considered absent in the other specimens of *C. barbouri* (Cisneros et al. 2004).

The ventral margin of the posterior portion of the jugal directs dorsally, forming an acute temporal emargination between the contact with the quadratojugal (Fig. 3A₅, A₆). This contact is reduced and restricted to the posterodorsal corner of the jugal, a typical trait of owenettids (Reisz and Scott 2002; Modesto et al. 2003). The posterior half of the jugal is dorsoventrally expanded, whereas in *Saurodekte kitchingorum* (BP/1/4195a) it is slender. The anteroventral corner of the quadratojugal projects anteriorly, forming a sigmoid anterior margin. The quadratojugal lacks any horn-like projection, which is usually present in procolophonines (e.g., *Procolophon trigoniceps*, NM QR3201; *Teratophon spinigenis* Gow, 1977, SAM PK-K10174; Cisneros 2008) and leptopleuronines (e.g., *Hypsognathus fenneri* Gilmore, 1928, YPM 55831; Sues et al. 2000).

The pineal foramen is small (2 mm in length) and circular in outline. It is located within a depressed surface (Fig. 3A₁, A₂). Moreover, it rests posterior to posterior margin of the orbit, such as in other owenettids (Cisneros et al. 2004). In contrast, the posterior margin of the orbitotemporal fenestra of procolophonids is anterior to or at the level of the pineal foramen (Cisneros 2008). The posterior margin of the skull is straight to concave. It differs the specimen from procolophonids like *Pentaedrusaurus ordosianus* Li, 1989 (IVPP V873) and *Mandaphon nadra* Tsuji, 2017 (NMT RB16; Tsuji 2017), which bear a posteriorly projected margin. The pos-

terolateral corner of the skull is rounded and featureless, whereas in *Procolophon trigoniceps* (BMNH R1949; Carroll and Lindsay 1985) the corner forms an acute angle with a prominent spine.

The palate and ventral portion of the braincase are partially visible (Fig. 3A₃, A₄). The suture between the parasphenoid and basioccipital is obscured. There is a shallow depression on the ventral surface of these bones. The interpterygoid vacuity is long and narrow. The cultriform process is not preserved. The pterygoid is long and wide. On the ventral surface, there is a longitudinal fossa medially bounded by a longitudinal ridge and laterally bounded by an oblique ridge. It resembles the morphology of *Sauropareion kitchingorum* (BP/1/4195a), which bears rudimentary teeth in each ridge. The presence of these teeth in CAPP/UFMS 0225 is uncertain. The transverse process of the pterygoid is anterolaterally projected. The additional palatal bones are not visible.

The mandible is triangular in ventral view (Fig. 3A₃, A₄), such as the skull. The posterior portion is far wider than the anterior end. The anterior portion of the mandible shows a gently transverse constriction in ventral view, resulting in a narrow symphyseal region. Conversely, *Ruhuhuarua reiszi* (CAMZM T997) lacks this constriction, showing a parabolic-shaped symphyseal region in ventral view. In lateral view, the dorsoventral height of each mandibular ramus is about the same along its length. Hence, the dorsal and ventral margins of the dentary run parallel. The ventral margin of the anterior end of the dentary is slightly ventrally expanded. The splenial forms the medial surface of the anterior half of the lower jaw. However, its contacts are poorly preserved. The posterior tip of the lower jaw deflects ventrally, whereas in *Owenetta rubidgei* (SAM PK K 7582) it is straight. Such as in other owenettids, the craniomandibular articulation occurs approximately at the same dorsoventral level of the dentary tooth line.

Phylogenetic analysis

The first phylogenetic analysis (i.e., employing the data matrix of Tsuji et al. 2013) recovered 13 most parsimonious trees (MPTs) of 33 steps each (consistency index = 0.758; retention index = 0.814). CAPP/UFMS 0225 nests within Owenettidae in all MPTs (Fig. 4A). The node is supported by four synapomorphies: (i) presence of a notch on the lateral margin of the supratemporal [9 (0→1)]; (ii) humerus without an entepicondylar foramen [14 (0→1)]; (iii) presence of orbitotemporal crests [18 (0→1)]; and (iv) the presence of broad posteriorly expanded nostrils [20 (0→1)]. The characters 14 and 20 are encoded as uncertain (“?”) for CAPP/UFMS 0225. The inner affinities of Owenettidae are unsolved. The clade is the sister taxa of Procolophonidae, which present the same topology recovered by Cisneros et al. (2004) and Tsuji et al. (2013).

The second phylogenetic analysis (i.e., employing the data matrix of Pinheiro et al. 2021) recovered three MPTs

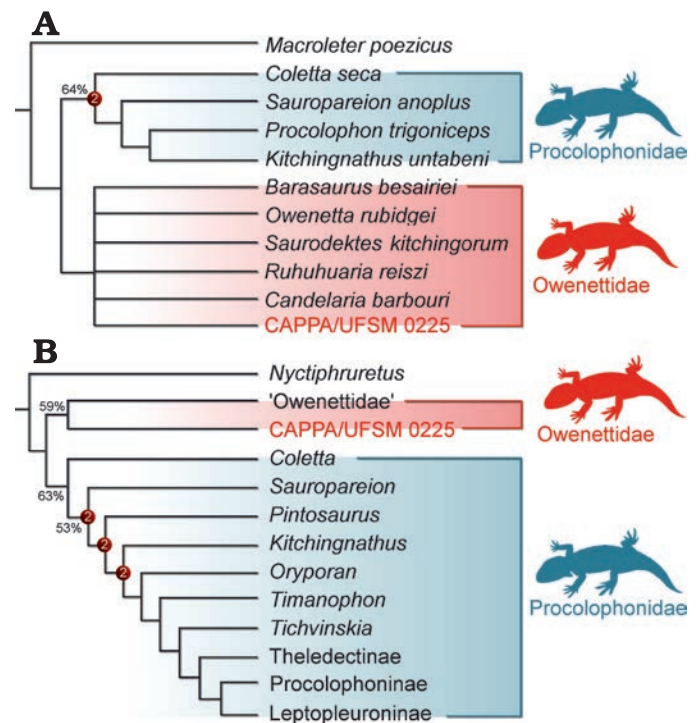


Fig. 4. Results of the phylogenetic analyses. **A**. Strict consensus tree of the first analysis depicting the phylogenetic position of CAPP/UFMS 0225. **B**. Abbreviated strict consensus tree of the second analysis depicting the phylogenetic position of CAPP/UFMS 0225. Numbers on nodes represent Bremer support values higher than one and Bootstrap values higher than 50%.

of 134 steps each (consistency index = 0.612; retention index = 0.787). The specimen is positioned as the sister taxon of “Owenettidae” (note: according to Cisneros 2008, characters for the “Owenettidae” have been coded on the basis of *Barasaurus besairiei* and *Owenetta rubidgei*) in all MPTs (Fig. 4B), which is supported by the postfrontal contacting frontal, parietal, postorbital and supratemporal [11 (0→1)]. The remaining topology of the strict consensus tree is equivalent to that of Pinheiro et al. (2021).

Discussion

Taxonomic assignment.—The inner phylogenetic affinities of parareptiles have been intensively disputed (e.g., Laurin and Piñeiro 2017; MacDougall et al. 2018; Ford and Benson 2020; Cisneros et al. 2021). Nevertheless, CAPP/UFMS 0225 is here regarded as an owenettid procolophonoid based on the following suite of traits: (i) absence of ornamentation on the external surface of the skull, which distinguishes the specimen from non-procolophonoid procolophonians; (ii) very narrow interorbital breadth, which distinguishes the specimen from several procolophonids; (iii) presence of orbitotemporal crests, which occurs in owenettids and *Nyctiphruetus* (Cisneros et al. 2004); (iv) deep temporal emargination between jugal and quadratojugal, a typical trait of owenettids (Reisz and Scott 2002); (v) enlarged

prefrontal that contacts the supratemporal, a synapomorphy of Owenettidae (Cisneros et al. 2004); (vi) pineal foramen set posterior to the posterior margin of the orbit, a condition shared with owenettids and non-procolophonoid procolophonians; and (vii) absence of spine-like structures or bosses on the jugal, quadratojugal and supratemporal, which distinguishes the specimen from several procolophonids. The phylogenetic analyses further support the assignment of CAPP/UFMS 0225 to Owenettidae. Moreover, the presence of a pair of temporal fenestrae in CAPP/UFMS 0225 reinforces the owenettid affinity. The owenettid *Candelaria barbouri* is the only taxon which shares with CAPP/UFMS 0225 the aforementioned combination of traits plus a pair of temporal fenestrae. In addition, the size of the new specimen resembles that of *C. barbouri* and no significant differences are observable between CAPP/UFMS 0225 and the specimens of *C. barbouri*. One putative difference is the presence of a notch on the lateral margin of the supratemporal in CAPP/UFMS 0225, which seems absent in *C. barbouri* (Cisneros et al. 2004). This notch occurs in other owenettids (Reisz and Scott 2002; Modesto et al. 2003). Nevertheless, this portion is poorly preserved in all the specimens (including CAPP/UFMS 0225), hence, the presence of the notch in CAPP/UFMS 0225 and/or the absence of the notch in the other specimens is ambiguous. The assignment of CAPP/UFMS 0225 to *C. barbouri* receives further support from geological data. The specimens of *C. barbouri* are recorded from the same geological unit (Pinheiros-Chiniquá Sequence) and Assemblage Zone (*Dinodontosaurus* Assemblage Zone) which yielded the new specimen. Alternatively, if CAPP/UFMS 0225 belongs to another procolophonoid species instead of *C. barbouri*, this implies in a scenario where the group is more diverse than previously thought. In this scenario, the presence of a pair of temporal openings is a putative synapomorphy of CAPP/UFMS 0225 and *C. barbouri* instead of an autapomorphy of the latter. This scenario is less plausible and in the present study the first hypothesis is advocated. Therefore, CAPP/UFMS 0225 is regarded as a new specimen of *C. barbouri* according the following points: (i) presence of temporal openings, which is interpreted as a local autapomorphy (Cisneros et al. 2004); (ii) shared anatomy and size; (iii) and geological data.

Biostratigraphic significance.—The new specimen improves our knowledge on the faunal composition of the “Posto” site, which is dominated by large tetrapods, such as dicynodonts and archosaurs (França et al. 2011; Ugalde et al. 2020). Actually, small species are represented solely by probainognathian cynodonts (Bonaparte et al. 2006; Martinelli et al. 2016b). Moreover, CAPP/UFMS 0225 is the first parareptile excavated from the “Posto” site, improving the taxonomic diversity of this locality. The occurrence of *C. barbouri* in the “Posto” site provides new information regarding the biostratigraphic framework proposed by Martinelli et al. (2017). The authors recognize the puta-

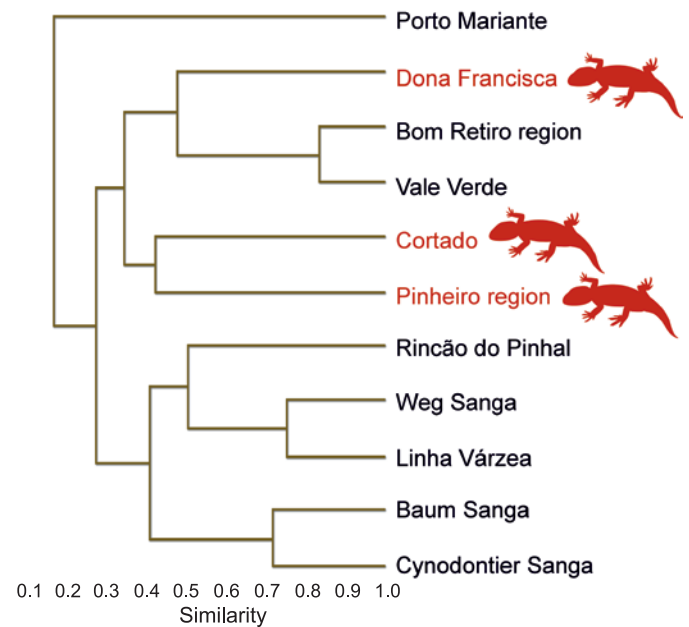


Fig. 5. Dendrogram from the updated dataset of Martinelli et al. (2017) of main localities of the state of Rio Grande do Sul yielding fossil tetrapods of the *Dinodontosaurus* Assemblage Zone. The silhouette represents the presence of *Candelaria barbouri*.

tive presence of two subzones within the *Dinodontosaurus* Assemblage Zone, where the older subzone can be characterized by the presence of the cynodonts *Aleodon cromptoni* Martinelli, Kammerer, Melo, Paes Neto, Ribeiro, Da-Rosa, Schultz, and Soares, 2017, and *Luangwa sudamericana* Abdala and Sá-Teixeira 2004, and the rhynchosaur *Brasinorhynchus mariantensis* Schultz, Langer, and Montefeltro, 2016. Whereas the “Posto” site and the nearby “Bortolin” site lack records of *A. cromptoni* and *B. mariantensis*, the traversodontid *L. sudamericana* is recorded from the “Bortolin” site (Martinelli et al. 2017; Pavanatto et al. 2020). On the other hand, the “Cortado” and the “Pinheiro” region record *A. cromptoni* and lack records of *L. sudamericana* (Martinelli et al. 2017). These latter fossiliferous localities yielded *C. barbouri*. Therefore, the presence of *C. barbouri* in the “Posto” site reinforces the faunal similarity of these outcrops. The cluster analysis based on an updated version (incorporating the new record of *C. barbouri* for the “Posto” site) of the dataset constructed by Martinelli et al. (2017) recovered a dendrogram (Fig. 5) similar to that recovered in the former study. The cophenetic correlation coefficient of the updated version is slightly higher (0.8539) than that of the former analysis (0.8474). The arrangement of the groups follows the results of Martinelli et al. (2017), where the Dona Francisca outcrops (“Posto” plus “Bortolin”) are clustered together with the sites that yielded *A. cromptoni*. Martinelli et al. (2017) and Pavanatto et al. (2020) point that several records from the *Dinodontosaurus* Assemblage Zone lack stratigraphic control, which hampers the more accurate biostratigraphic correlations. The new specimen (CAPP/UFMS 0225) was excavated by the author of the

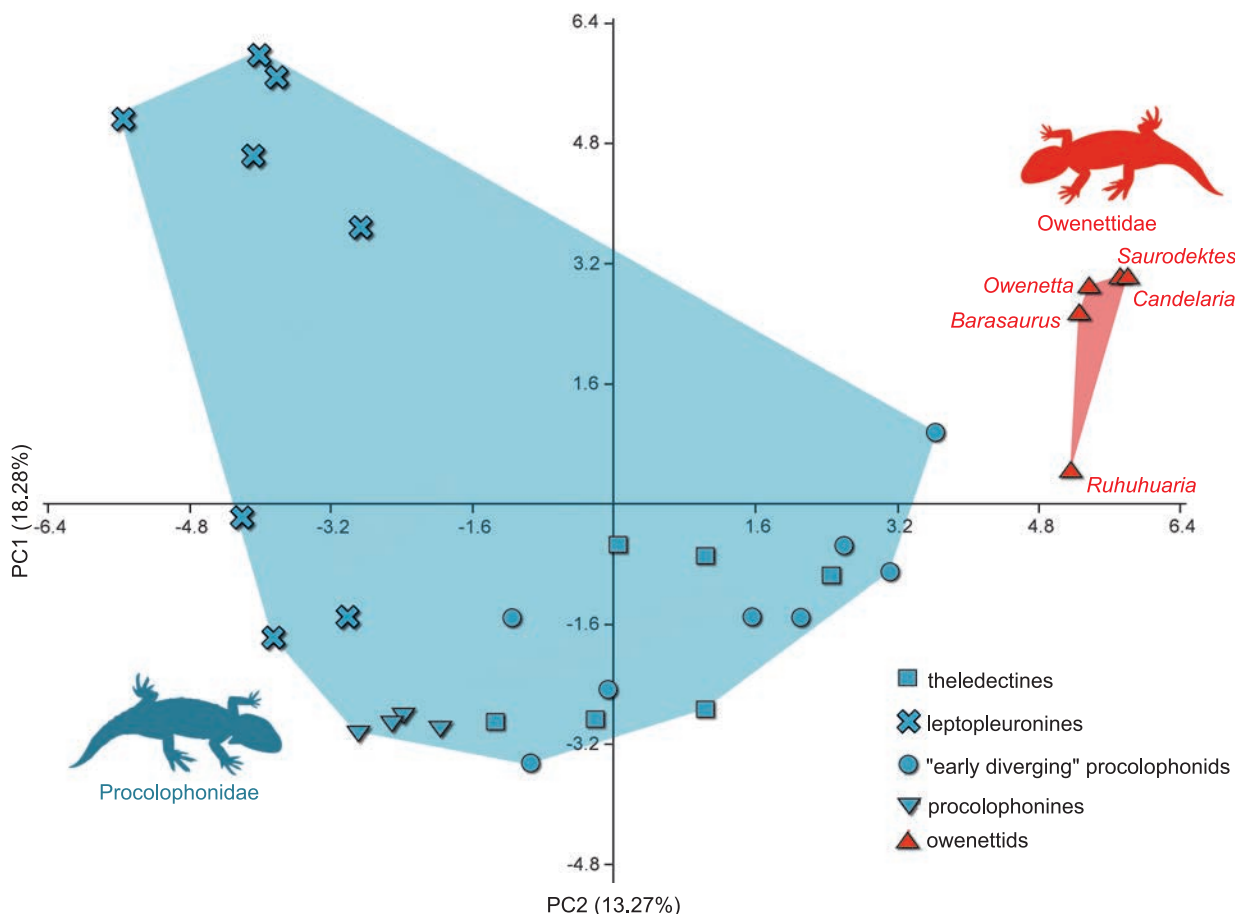


Fig. 6. Bivariate plot showing the results of the morphospace occupation analysis. Red convex hull corresponds to morphospace of owenettids and blue convex hull corresponds to morphospace of procolophonids.

present study (RTM); hence, it is safely part of the fossiliferous content of the “Posto” site and stratigraphic controlled.

Morphological disparity.—Owenettids are far less taxonomic diverse than procolophonids, their sister group (Cisneros 2008; Tsuji et al. 2013; Hamley et al. 2020). Actually, the clade was represented by six species, which were reduced to five according the taxonomic review of Hamley et al. (2020). Conversely, there are dozens of valid species of procolophonids, which present certain morphological disparity, especially regarding dental and horns anatomy (Cisneros and Ruta 2010). As expected, the morphological disparity analysis performed here reveals a morphospace area occupied by owenettids that is far more reduced in comparison to that of procolophonids (Fig. 6). This is not a surprise given the conservative cranial anatomy of the group. Nevertheless, there are some inner specializations, such as the presence of temporal openings in *Candelaria barbouri*, which is an unusual trait within procolophonoids (Cisneros et al. 2004). The presence of this trait in *C. barbouri* is corroborated by CAPP/UFMS 0225. Moreover, *Ruhuhuaria reysi* bears peculiar enlarged anterior dentary teeth with labio-lingually expanded bases (Tsuji et al. 2013), suggesting some dietary differentiation within the clade. Despite its conservative anatomy, owenettids

survive beyond the Permo-Triassic boundary (Modesto et al. 2003) and shared the terrestrial ecosystems with giant archosaurs (Roberto-da-Silva et al. 2020) and mammalian forerunners (Martinelli et al. 2016; 2017) until the Middle Triassic, when the group was extinct (Cisneros et al. 2004; Martinelli et al. 2016a).

Conclusions

CAPP/UFMS 0225 is the first owenettid from “Posto” site. This assignation is supported by two phylogenetic analyses. In addition, the unusual presence of temporal openings allows the assignation of CAPP/UFMS 0225 to *Candelaria barbouri*. The presence of *C. barbouri* in the “Posto” site provides further support for biostratigraphic correlation with two other Triassic localities from southern Brazil, reinforcing the framework proposed by Martinelli et al. (2017). Finally, a morphological disparity analysis reveals no overlapped areas between the morphospace occupied by procolophonids and owenettids, reinforcing the existence of these two distinct groups. Furthermore, the morphospace area occupied by owenettids is far reduced in comparison to that of procolophonids, which is not a surprise given the conservative cranial anatomy of the group.

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