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A New Rhynchocephalian from the Late Triassic of Southern Brazil Enhances Eusphenodontian Diversity

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We describe a new eusphenodontian, *Lanceirosphenodon ferigoloi* gen. et sp. nov., from the Upper Triassic (Norian) *Riograndia* Assemblage Zone (AZ) of the Candelária Sequence (Santa Maria Supersequence) of Rio Grande do Sul, Brazil. The new taxon consists of an almost complete left dentary with dentition, which exhibits a mosaic of features considered 'typical' of non-eusphenodontian rhynchocephalians, along with others reported for eusphenodontian taxa. It has the typical rhynchocephalian regionalized dentition with 19 teeth and also pleuroacrodont implantation; the additional dentition presents alternation of size and shape, with the last additional teeth resembling a spear in labial view. A well-developed chin is also present. Our phylogenetic analysis places *Lanceirosphenodon* as one of the most basal eusphenodontians and reinforces the hypothesis that Rhynchocephalia underwent an early diversification, probably in the Early Triassic, followed by an explosion in morphological disparity. Based on the ontogenetic sequence of *Sphenodon*, *Lanceirosphenodon* fitted between stages T2 and T3, representing a probable early juvenile individual. In spite of its ontogenetic stage, the set of characters present in *Lanceirosphenodon*, including two autapomorphies, supports its recognition as a new taxon. This new taxon increases our knowledge of the faunal diversity in the Triassic of Gondwana and more locally for the *Riograndia* Assemblage Zone of southern Brazil.

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Keywords: Rhynchocephalia; Eusphenodontia; *Riograndia* Assemblage Zone; South America; Triassic

Introduction

Rhynchocephalia was proposed by Günther (1867) to include the 'peculiar' *Sphenodon punctatus* (Günther 1867; Evans & Jones 2010). Later on, other taxa, such as proganosaurs, mesosaurs, rhynchosaurs and claraziids (e.g. Osborn 1903; Evans & Jones 2010), were included in this group which are now regarded as phylogenetically distant from *Sphenodon* (Evans & Jones 2010). Almost a century after Günther's work, the cladistic approach triggered by Gauthier *et al.* (1988) recognized Rhynchocephalia as a monophyletic group that includes *Gephyrosaurus* and Sphenodontia (*sensu* Benton 1985), constituting with Squamata the clade Lepidosauria (e.g. Gauthier *et al.* 1988; Reynoso & Clark 1998; Reynoso 2000; Evans 2003; Jones 2009; Apesteguía *et al.* 2012; Rauhut *et al.* 2012; Jones *et al.* 2013; Martínez *et al.* 2013). The taxonomic composition of Rhynchocephalia is currently stable (e.g. Jones 2009;

Apesteguía *et al.* 2012), but relationships within the clade remain unresolved (see Hsiou *et al.* 2015).

During the Late Triassic–Middle Jurassic, Rhynchocephalia was a highly diverse, cosmopolitan group, with around 50 extinct taxa described so far (Evans & Jones 2010; PRR, pers. obs.). Consequently, rhynchocephalians were the most abundant lepidosaurs during the first half of the Mesozoic. Today, only one species remains, *Sphenodon punctatus*, which is restricted to New Zealand (Daugherty *et al.* 1990; Evans *et al.* 2001; Jones *et al.* 2009; Evans & Jones 2010; Hay *et al.* 2010; Jones & Cree 2012; Rauhut *et al.* 2012). The chronological range of Rhynchocephalia has usually been considered to extend from the Late Triassic to Recent (e.g. Evans *et al.* 2001; Apesteguía *et al.* 2012; Rauhut *et al.* 2012). However, the 'Vellberg jaws' (cf. *Diphydontosaurus* sp.) from the Erfurt Formation of Germany, dated at 239–249 Ma, which corresponds to the end of the Middle Triassic

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(Ladinian), now represent the oldest record of the group (Jones *et al.* 2013). Based on molecular data and the fossil record, Jones *et al.* (2013) proposed that the divergence between Squamata and Rhynchocephalia may have occurred about 240.8 million years ago, corresponding to the beginning of the Ladinian. However, new studies based on molecular and morphological data have estimated the origin of Squamata at around 257 Ma (near the Permian/Triassic boundary; Simões *et al.* 2018; Hsiou *et al.* 2019), which would move the divergence between the Squamata and Rhynchocephalia back to that time.

Constitution of Rhynchocephalia

Gauthier *et al.* (1988) defined Rhynchocephalia as a monophyletic group including *Gephyrosaurus* and Sphenodontia (*sensu* Benton 1985). The latter clade is defined as *Sphenodon* and all rhynchocephalians that are closer to *Sphenodon* than to *Gephyrosaurus*. Several analyses have resulted in a well-supported, large clade within Sphenodontia, which was informally called 'crown-Sphenodontia' (e.g. Fraser & Benton 1989; Apesteguía *et al.* 2012; Apesteguía & Carballido 2014), 'derived-Sphenodontia' (e.g. Apesteguía *et al.* 2012, 2014; Jones *et al.* 2012) or 'derived rhynchocephalians' (e.g. Jones 2008, 2009). Recently, Herrera-Flores *et al.* (2018) proposed the formal name Eusphenodontia for this stable clade, which is defined as the least inclusive clade containing *Polysphenodon muelleri*, *Clevosaurus hudsoni* and *Sphenodon punctatus*.

Basal rhynchocephalians or non-eusphenodontians, such as the Late Triassic *Diphydontosaurus* and the Early Jurassic *Gephyrosaurus*, do not form a monophyletic group but do share several distinctive features: (1) apicobasally tall and very narrow slender teeth; (2) an oval and flat dental symphysis divided by a deep groove; (3) a fairly straight ventral margin of the dentary; (4) an elongated anteroposterior joint of the mandible, suggesting a low degree of propalinal movement; (5) simple, small, conical teeth with ovoid bases and without flanges, whose mesiodistal and labiolingual dimensions are similar; (6) adult individuals with at least four or five successional teeth in the anterior portion of the tooth row; (7) the absence of a broad, deep Meckelian canal; (8) an absence of secondary bone development (secondary dentine according to Fraser [1986]) below the tooth row; (9) several rows of palatine teeth; (10) a simple articulation between the premaxilla and the maxilla, involving only a small overlap; (11) relatively narrow nasals; (12) a low coronoid projection (Säilä 2005; Jones 2008, 2009; Apesteguía *et al.* 2012; Apesteguía & Carballido 2014); and (13) the presence of pleurodont tooth implantation. *Gephyrosaurus* has an almost totally pleurodont dentition, with some peculiarities in the posterior-most teeth, which have shallower roots (Jenkins *et al.* 2017). *Diphydontosaurus* and some other Triassic and Jurassic genera, such as *Planocephalosaurus*, have anterior teeth with a pleurodont tooth implantation, whereas the posterior teeth have acrodont implantation (Fraser & Shelton 1988; Säila 2005; Jenkins *et al.* 2017).

Whiteside & Duffin (2017) and Whiteside *et al.* (2017) recently described new Late Triassic rhynchocephalians that were also considered basal forms: *Gephyrosaurus evansae* and *Penegephyrosaurus curtiscoppi* from the Holwell quarry complex (Rhaetian), near Bristol (England), and *Deltadectes elvetica* from the Upper Gruhalde Member of the Klettgau Formation (Norian/Rhaetian), Hallau (Switzerland; Whiteside *et al.* 2017). However, these authors did not perform any phylogenetic analyses.

Within Eusphenodontia, five groups are frequently recovered and are relatively consistent in different phylogenetic analyses:

1. Clevosaurs (e.g. Wu 1994; Reynoso 1996, 1997; Jones 2006; Rauhut *et al.* 2012; Martínez *et al.* 2013; essentially Clevosauridae of Bonaparte & Sues 2006; Hsiou *et al.* 2015, 2019; Herrera-Flores *et al.* 2018). This is a quite unstable group in terms of its composition and internal relationships, because the inclusion of several *Clevosaurus* species in cladistic analyses has resulted in the recovery of unresolved clades (see Hsiou *et al.* 2015, 2019; Herrera-Flores *et al.* 2018). Also, this clade includes *Polysphenodon*, *Brachyrhinodon* and *Clevosaurus* spp. (with the exception of *Cl. latidens*, which was renamed *Fraserosphendon latidens*; Herrera-Flores *et al.* 2018). Moreover, Herrera-Flores *et al.* (2018) and Hsiou et al. (2019) considered *Polysphenodon* to lie outside this clade.

2. Sphenodontinae (e.g. Reynoso 1996; Apesteguía & Novas 2003; Rauhut *et al.* 2012; Martínez *et al.* 2013; Hsiou *et al.* 2015), which is composed of *Sphenodon*, *Oenosaurus*, *Cynosphenodon* and *Zapatodon* (e.g. Reynoso 1996; Apesteguía & Novas 2003; Rauhut *et al.* 2012; Martínez *et al.* 2013). However, some phylogenetic analyses have recovered Sphenodontinae as a paraphyletic group (e.g. Apesteguía *et al.* 2012, 2014; Apesteguía & Carballido 2014).

3. Opisthodontia, which includes *Opisthias*, *Priosphenodon*, *Toxolophosaurus*, *Eilenodon* and *Sphenotitan*. This is a more stable group and was defined by Apesteguía & Novas (2003) as a clade including all sphenodontians that are more closely

Table 1. Temporal and geographical distribution of Gondwanan rhynchocephalians during the Mesozoic. **Abbreviations: Fm,** Formation; **Gr,** Group; **Mb,** Member; **Seq,** Sequence; **Superseq,** Supersequence.

AGE	TAXON	AUTHOR	COUNTRY	GEOLOGIC UNIT
CRETACEOUS				
Campanian	*Kawasphenodon expectatus*	Apesteguía 2005	Argentina	Los Alamitos Fm
Campanian	Sphenodontinae indet.	Apesteguía & Jones 2012	Argentina	Allen Fm, Malargue Gr
Campanian	*Lamarquesaurus cabazai*	Apesteguía & Rougier 2007	Argentina	Allen Fm, Malargue Gr
Turonian–Santonian	Indeterminate	Hsiou *et al.* 2016	Brazil	Adamantina Fm, Bauru Gr
Cenomanian	*Priosphenodon avelasi*	Apesteguía & Novas 2003	Argentina	Candeleros Fm, Neuquén Gr
Cenomanian	*Kaikaifilusaurus calvoi*	Simon & Kellner 2003	Argentina	Candeleros Fm
Albian?	*Priosphenodon minimus*	Apesteguía & Carballido 2014	Argentina	La Paloma Mb, Cerro Barcino Fm, Chubut Gr
Barremian	*Tingitana anoualae*	Evans & Sigogneau-Russell 1997	Morocco	Ksar Metlili Fm
JURASSIC				
Callovian–Oxfordian?	*Sphenocondor gracilis*	Apesteguía *et al.* 2012	Argentina	Lower Mb, Cañadón Asfalto Fm
Toarcian	*Rebbanasaurus jaini*	Evans *et al.* 2001	India	Kota Fm
Toarcian	*Godavarisaurus lateefi*	Evans *et al.* 2001	India	Kota Fm
Early Jurassic	*Clevosaurus* sp.	Sues & Reisz 1995	South Africa	Elliot Fm or Clarens Fm
TRIASSIC				
Norian	*Sphenotitan leyesi*	Martínez *et al.* 2013	Argentina	Quebrada del Barro Fm
Norian	*Clevosaurus brasiliensis*	Bonaparte & Sues 2006	Brazil	Top of Candelária Seq, Santa Maria Superseq
Norian	*Lanceirosphenodon ferigoloi*	This study	Brazil	Top of Candelária Seq, Santa Maria Superseq
Carnian–Norian	*Clevosaurus hadroprodon*	Hsiou *et al.* 2019	Brazil	Base of Candelária Seq, Santa Maria Superseq

related to *Priosphenodon* than to *Sphenodon* (see also Rauhut *et al.* 2012; Martínez *et al.* 2013).

4. Eilenodontinae, which includes *Priosphenodon*, *Toxolophosaurus* and *Eilenodon*, and represents the sister group of *Opisthias* (e.g. Apesteguía & Novas 2003; Apesteguía *et al.* 2012, 2014; Rauhut *et al.* 2012).

5. Finally, a clade with propalinal taxa, which includes sphenodontines, eilenodontines and their relatives (*sensu* Apesteguía 2005; Apesteguía *et al.* 2012, 2014). Recently, Herrera-Flores *et al.* (2018) proposed the clade Neosphenodontia for the most inclusive clade containing *Sphenodon punctatus* but not *Clevosaurus hudsoni*. The latter definition includes the last four aforementioned clades (clades 2–5).

There are three other minor eusphenodontian groups that are consistently recovered in various phylogenetic analyses: (1) pleurosaurs, which include the aquatic *Pleurosaurus goldfussi*, *Pl. ginsburgi*, *Palaeopleurosaurus posidoniae* and *Vadasaurus herzogi* (e.g. Rauhut *et al.* 2012; Apesteguía *et al.* 2014; Pleurosauridae of Bever & Norell [2017]); (2) 'sapheosaurs', which include *Kallimodon* and *Sapheosaurus* (e.g. Apesteguía *et al.* 2012, 2014; Rauhut *et al.* 2012); and (3) a clade formed by *Theretairus* and *Sphenovipera* (e.g. Apesteguía & Novas 2003; Apesteguía *et al.* 2012, 2014; Martínez *et al.* 2013; Bever & Norell 2017).

In the Southern Hemisphere, few rhynchocephalian fossils are known from the Triassic and Jurassic periods.

In contrast, the Cretaceous fossil record of Gondwana is more taxonomically diverse with great morphological disparity, especially in Argentina (see Table 1). The oldest Gondwanan records of rhynchocephalians are: (1) *Clevosaurus hadroprodon* Hsiou *et al.*, 2019 discovered in the Late Triassic *Hyperodapedon* Assemblage Zone (AZ; late Carnian) from the base of the Candélaria Sequence (Santa Maria Supersequence), southern Brazil (Hsiou *et al.* 2019); (2) *Clevosaurus brasiliensis* Bonaparte & Sues, 2006, from the *Riograndia* AZ, at the top of the Candélaria Sequence (Bonaparte & Sues 2006; Soares *et al.* 2011; Horn *et al.* 2014); and (3) *Sphenotitan leyesi* Martínez *et al.*, 2013, from the Quebrada del Barro Formation, Marayes-El Carrizal Basin, western Argentina (Martínez *et al.* 2013). The two latter taxa are Norian in age, and each represents the most abundant component within its respective faunal association (Bonaparte *et al.* 2010; Martínez *et al.* 2013; Bolze *et al.* 2015; see Discussion, below).

Here, we describe a new rhynchocephalian taxon that represents the second genus from the *Riograndia* AZ of the Candélaria Sequence (Figs 1, 2), increasing the fossil diversity of small-sized forms in the Late Triassic of western Gondwana. The material consists of a well-preserved lower jaw with a dentition that is noticeably distinct from that of *Clevosaurus brasiliensis*. This new taxon is compared with other rhynchocephalians and its relationships are explored through phylogenetic analysis.
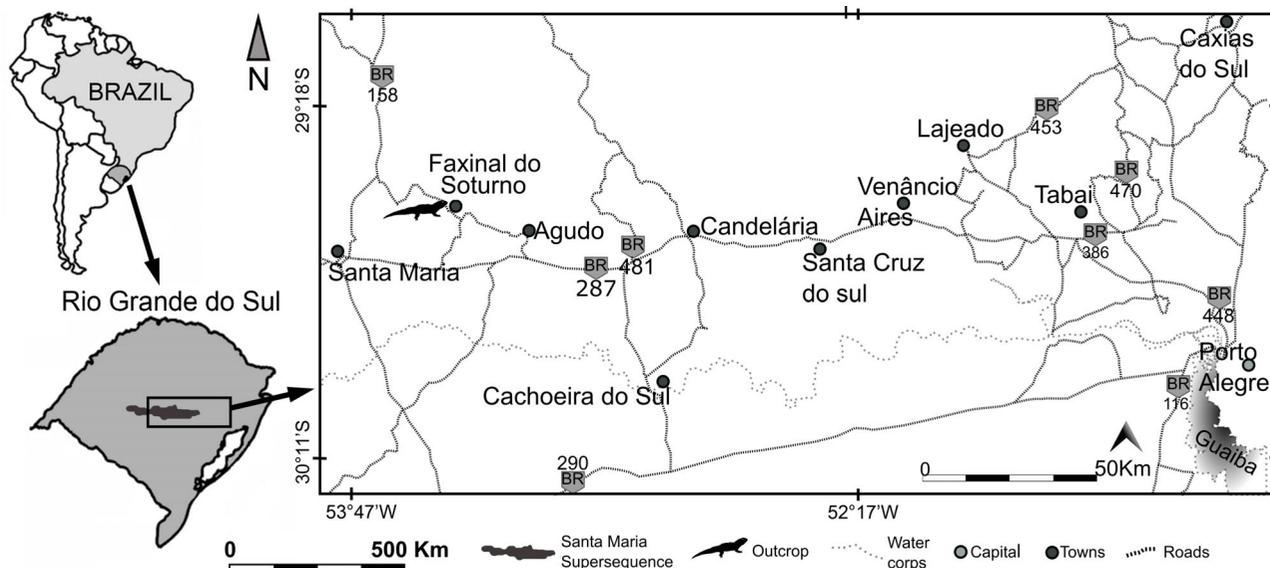
Figure 1. Map showing the geographical location of the outcrop Linha de São Luiz where the holotype of *Lanceirosphenodon ferigoloi* gen. et sp. nov. was found.

Material and methods

Institutional abbreviations

CAPPA/UFSM: Centro de Apoio à Pesquisa Paleontológica, Universidade Federal de Santa Maria, São João do Polêsine, Brazil; **IGM:** Instituto de Geologia, Universidad Nacional Autónoma de México, Ciudad Universitaria, México; **UFRGS-PV-T:** Laboratório de Paleontologia de Vertebrados, Universidade Federal do Rio Grande do Sul, Triassic Collection, Porto Alegre, Brazil.

Material

The specimen studied here, CAPPA/UFSM 0226, consists of a well-preserved left dentary, lacking only the posterior process (Fig. 2). CAPPA/UFSM 0226 was prepared at the UFRGS. Photographs were taken using an EOS Rebel T3i digital camera with a SIGMA EX DG macro lens. The images were processed with the software Inkscape v. 0.91 and GIMP v. 2.8. In addition, the specimen was scanned using the SkyScan 1173 micro-computed tomography (μCT) scanner at the Laboratório de Sedimentologia e Petrologia (LASEPE) of the Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS), Porto Alegre, Rio Grande do Sul, Brazil. The scan included 774 slices (pixel size = 9.87947 μm), obtained using a voltage of 65 kV and a current of 65 μA. The images were processed with AVIZO v. 7.1.

Phylogenetic analysis

CAPPA/UFSM 0226 was included in the data matrix of Herrera-Flores *et al.* (2018) with the addition of *Youngina*, as coded by Apesteguía *et al.* (2014). Some modifications were made to the data set of Herrera-Flores *et al.* (2018) (see Supplementary Material).

The new data matrix includes 73 characters and 49 terminal units (see Supplementary Material). The data matrix was analysed using TNT v. 1.5 (Goloboff & Catalano 2016). We performed a heuristic search, using maximum parsimony as the optimality criterion and under equal weights. All characters were non-additive (=unordered). The tree search consisted of 10,000 replicates of Wagner trees with random addition of taxa followed by tree bisection and reconnection (TBR) branch swapping, holding 10 trees per replication. The resulting most parsimonious trees (MPTs) were subjected to a final round of TBR branch swapping. In addition, decay indices (Bremer support values) were calculated and a bootstrap resampling analysis, with 10,000 pseudoreplicates, was performed. Subsequently, the Iterative Positional Congruence Reduce (IterPCR) protocol (Pol & Escapa 2006) was employed to identify unstable taxa and their possible phylogenetic positions.

Systematic palaeontology

Lepidosauria Haeckel, 1866
Rhynchocephalia Günther, 1867 (*sensu* Gauthier, Estes, & de Queiroz 1988)
Sphenodontia Williston, 1925 (*sensu* Benton 1985)
Eusphenodontia Herrera-Flores, Stubbs, Elsler, & Benton 2018
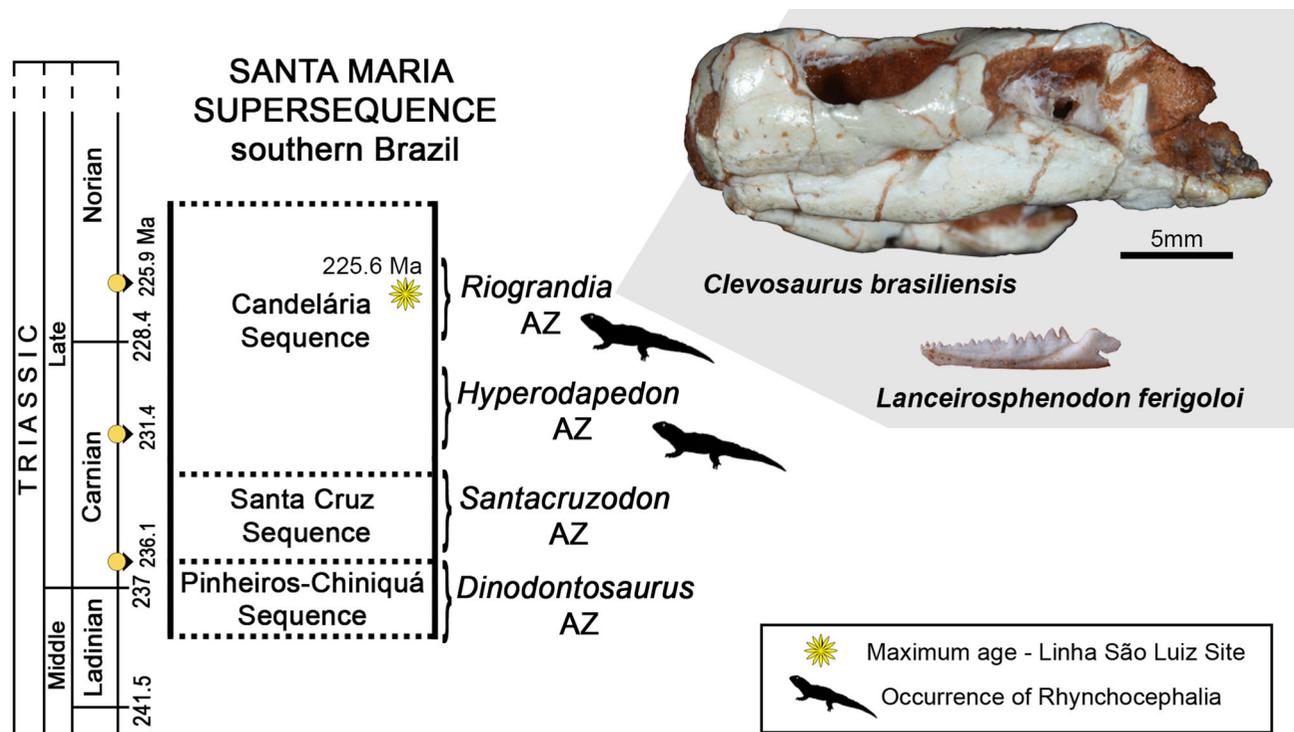***Lanceirosphenodon*** gen. nov.

Figure 2. Chrono- and biostratigraphy of Triassic units with vertebrate assemblage zones (AZ) from southern Brazil, with the skull and jaws of the holotype of Clevosaurus brasiliensis (UFRGS-PV-0748-T) and the holotype dentary of *Lanceirosphenodon ferigoloi* (CAPPA/UFSM 0226) in lateral view and at the same scale. The ages (Ma) of the column follow Gradstein et al. (2012). Chrono- and biostratigraphy were modified from Zerfass *et al.* (2003) and Horn et al. (2014). The radiometric dates of 236, 231.4 and 225.9 Ma correspond to the first half of the Chañares Formation (Marsicano *et al.* 2016; Ezcurra *et al.* 2017), the base of the Ischigualasto Formation, and the base of Los Colorados Formation (Martínez *et al.* 2013), respectively. The radiometric date of 225.6 Ma corresponds to the top of the Candelária Sequence that was obtained from rocks of the Linha São Luiz outcrop (Langer *et al.* 2018).

Type and only species. *Lanceirosphenodon ferigoloi* sp. nov.

Derivation of name. 'Lanceiros' in Portuguese means 'spear', in reference to the shape of the last additional teeth that are reminiscent of a spearhead and in recognition of the 'Lanceiros Negros' (Black Lancers), a group formed by slaves armed with long spears, who fought for freedom during the Farroupilha Revolution in Rio Grande do Sul State, Brazil (1835–1845), and whose massacre brought about the end of the war. 'Sphenodon' refers to the extant genus *Sphenodon*.

Diagnosis. As for the type and only known species.

Lanceirosphenodon ferigoloi sp. nov.
(Figs 3–6)

Derivation of name. In honour of Dr Jorge Ferigolo, a renowned Brazilian palaeontologist based at the Museu de Ciências Naturais of the Fundação Zoobotânica do Rio Grande do Sul (MCN/FZBRS, Porto Alegre, Brazil), who headed the Brazilian Pro-Guaíba Project, in which several localities and new fossils from the Triassic of the

Rio Grande do Sul State were discovered, including the first rhynchocephalian materials.

Holotype. CAPPA/UFSM 0226, left dentary missing the posterior part, with an almost complete dentition.

Locality and horizon. Linha São Luiz outcrop (29°33′45′S, 53°26′48′W), located north of Faxinal do Soturno city, Rio Grande do Sul State, Southern Brazil (Fig. 1). This outcrop belongs to the top of the Candelária Sequence, Santa Maria Supersequence, which is interpreted as a fluvial/deltaic depositional environment (Horn *et al.* 2014), and its fossil content is assigned to the *Riograndia* AZ (Soares *et al.* 2011; Fig. 2). The maximum depositional age of the outcrop, based on zircon U-Pb analyses, is 225.42 ± 0.37 Ma (Norian; Langer *et al.* 2018).

Diagnosis. Small sphenodontian rhynchocephalian differing from all other rhynchocephalians in having the following combination of features (*asterisks indicate autapomorphies): dentary with a low and slightly triangular coronoid process; alternation of size and shape of the additional teeth of the dentary (similar to
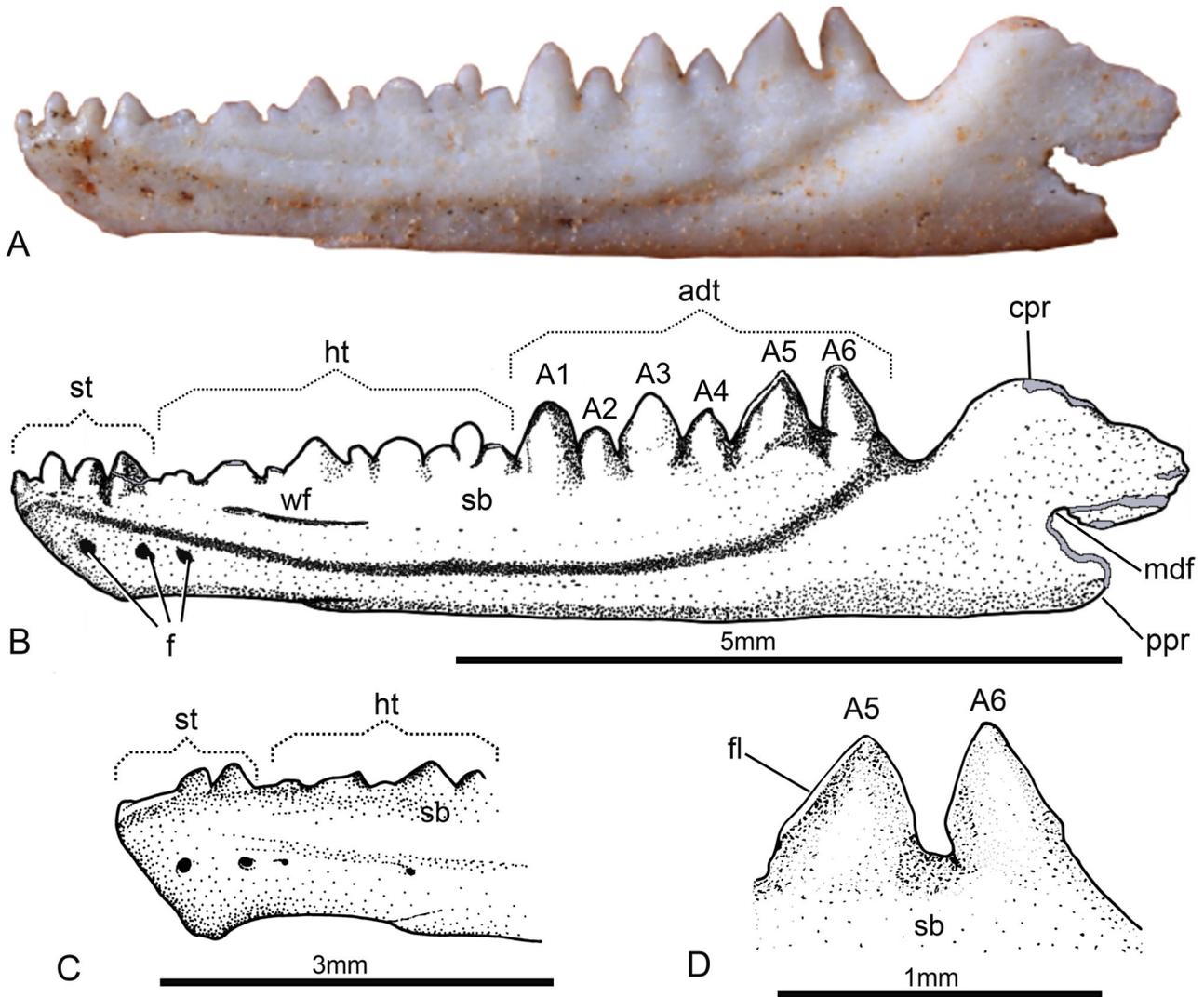
Figure 3. Dentary of *Lanceirosphenodon ferigoloi* gen. et sp. nov., CAPPA/UFSM 0226. **A,** photograph of the specimen in lateral view. **B,** drawing of the specimen in lateral view. **C,** detail of the symphyseal region (in a slightly more ventral position than in B). **D,** detail of the two last additional teeth. Abbreviations: **A(n),** additional tooth (number); **adt,** additional teeth; **cpr,** coronoid process; **f,** mentonian foramina; **fl,** flange; **ht,** hatchling teeth; **mdf,** mandibular foramen; **ppr,** dentary posterior process; **sb,** secondary bone; **st,** successional teeth; **wf,** wear facet.

that observed in the anterior additional teeth of the maxilla of *Sphenodon*), where the apicobasally tall teeth are 'D'-shaped and the apicobasally short ones are almost cylindrical; the last additional teeth (although 'D'-shaped) slightly resemble a spear in labial view; teeth without ornamentation; anterolateral flanges in the additional teeth; marginal dental implantation with a certain degree of posterior acrodonty and the successional teeth with pleurodonty*; anteriorly developed subdental shelf; symphyseal region with a conspicuous groove (similar to *Cynosphenodon* and *Sphenovipera*) that is continuous with the Meckelian groove; well-developed and pointed chin (mentonian process)*.

Anatomical description and comparisons

CAPPA/UFSM 0226 consists of a well-preserved, incomplete left dentary with its dentition exposed only in lateral view. The lingual surface of the dentary is obscured by matrix. Features of the lingual surface and internal structures were accessed using the μCT images. Measurements and ratios are given in Tables 2 and 3, respectively. Post-dentary bones are not preserved.

Dentary

The dentary is dorsoventrally shallow and anteroposteriorly long and slender. It is very small in overall size in
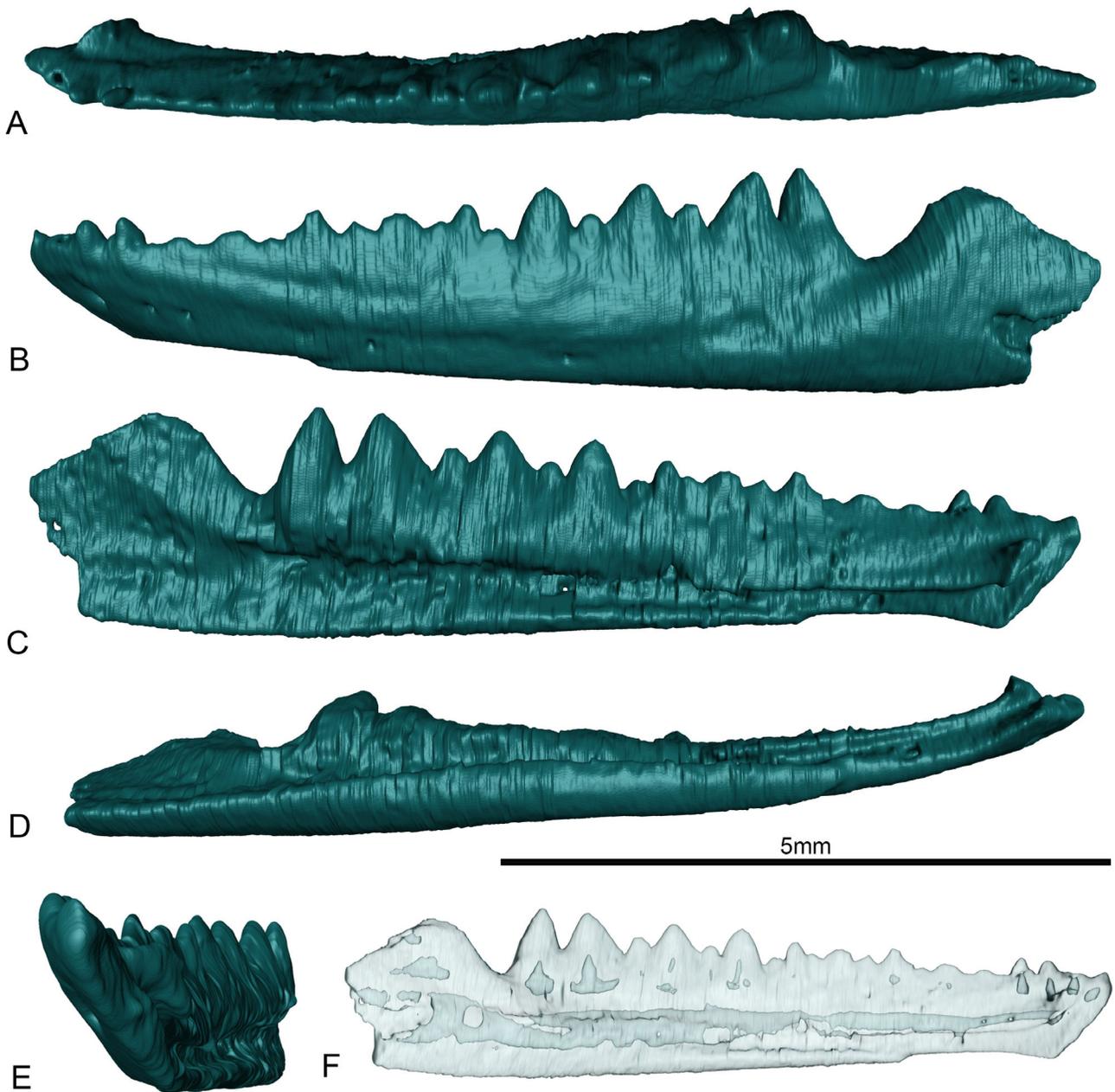
Figure 4. Three-dimensional rendering of the dentary of *Lanceirosphenodon ferigoloi* gen. et sp. nov., CAPPA/UFSM 0226 in **A,** dorsal, **B,** lateral, **C,** medial, **D,** ventral and **E,** anteromedial views. **F,** transparency showing empty spaces (in dark grey).

comparison to the early ontogenetic stages of other fossil rhynchocephalians, where available (see Robinson 1976; Reynoso 1997, 2003; Reynoso & Clark 1998; Apesteguía *et al.* 2012). Its preserved portion is 9.1 mm in length. The height of the dentary decreases anteriorly, being 1 mm in depth in the pre-coronoid region. The length (l) from the tip of the symphysis to the anterior edge of the coronoid process is 7.1 mm, and the maximum height (h) of the jaw pre-coronoid process is 1.2 mm, resulting in an h/l ratio of 0.17. As commonly

observed in juvenile individuals, the dentary shows little development of secondary bone, which is completely absent from its anterior-most region. Secondary bone is a feature commonly observed in rhynchocephalians, but is absent in basal taxa, such as *Gephyrosaurus* and *Diphydontosaurus* (Fraser 1988; Apesteguía *et al.* 2012). The limited growth of secondary bone (Fig. 3A–C) in this juvenile specimen is mainly restricted to the anterior region of the dentary, similar to the pattern observed in specimens of *Cynosphenodon* (IGM 6659: probably
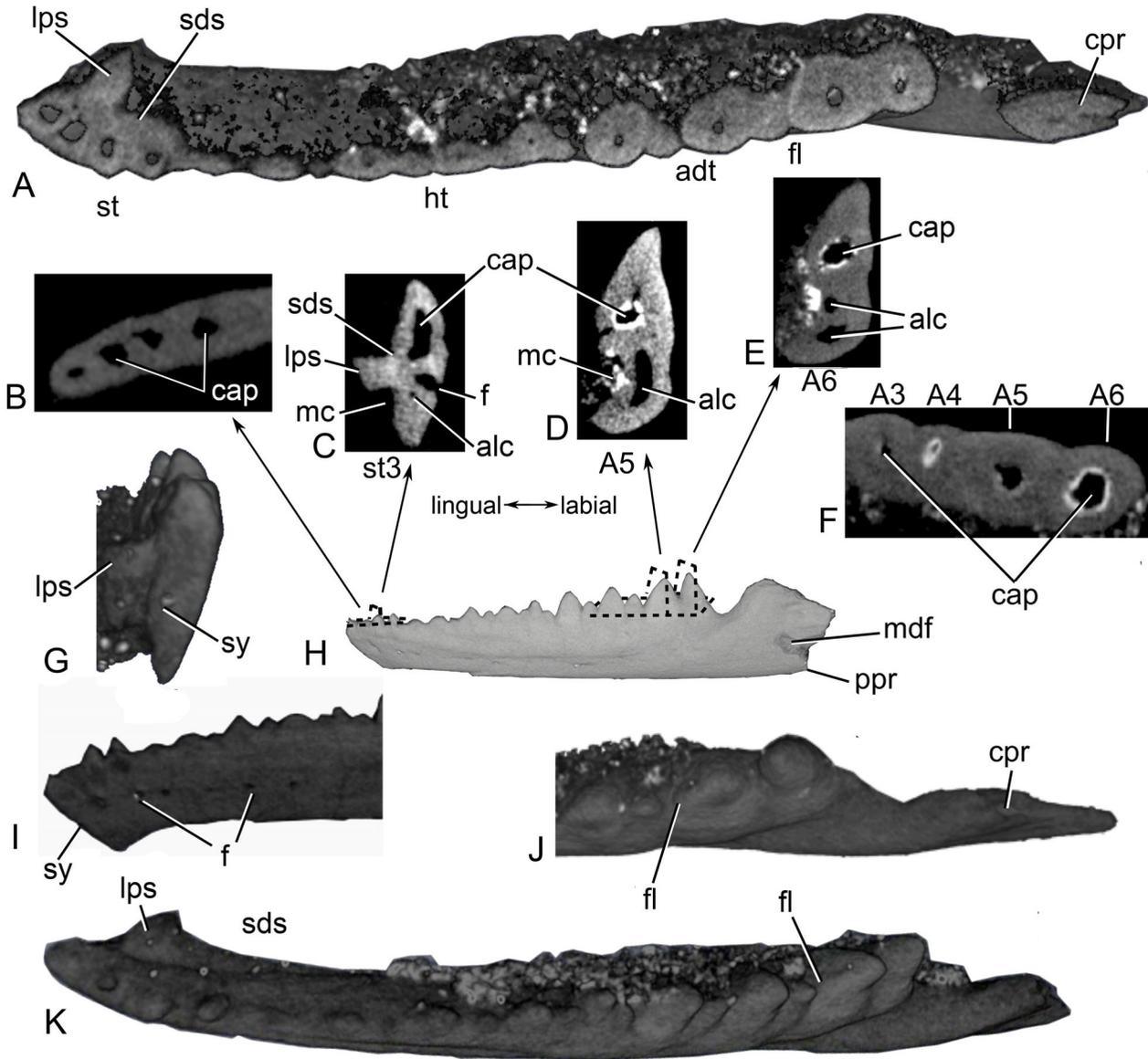
Figure 5. μCt images of dentary of *Lanceirosphenodon ferigoloi* gen. et. sp. nov., CAPPA/UFSM 0226. A, axial section in dorsal view of dentary. **B,** axial section of anterior region of dentary in occlusal view. **C,** coronal section of the third successional tooth. **D,** coronal section of the fifth additional tooth. **E,** coronal section of the sixth additional tooth. **F,** axial section of the posterior region of the dentary in occlusal view. **G,** detail of the symphyseal region in anterior view. **H,** dentary in lateral view. **I,** detail of the anterior region in dorsal view. **J,** detail of the posterior region in dorsal view. **K,** dentary in dorsal view. **Abbreviations: A(n),** additional tooth (number); **adt,** additional teeth; **alc,** alveolar canal; **cap,** pulp cavity; **cpr,** coronoid process; **f,** mentonian foramina; **fl,** flange; **ht,** hatchling teeth; **lps,** post-symphyseal lamina; **mc,** Meckelian canal; **mdf,** mandibular foramen; **ppr,** dentary posterior process; **sds,** subdental shelf; **st,** successional teeth; **st3,** third successional tooth; **sy,** symphysis.

'ontogenetic stage S' of Harrison [1901a, b]; see Reynoso 2003, fig. 1A) and especially IGM 6658 ('ontogenetic stage T3–T4' of Robinson [1976]; see Reynoso 2003, fig. 1B) (Figs 3C, 4C, 5I).

In lateral view (Figs 3, 4B, 5H, I), seven mental foramina are irregularly spaced along the dentary. The anterior-most foramen is the largest and the posterior-most is the second largest. The ventral margin of the dentary is nearly straight and its symphyseal region projects mediodorsally. A straight ventral margin is a feature seen in basal forms, but it is also present in *Sphenocondor* and in some eusphenodontians, such as *Cynosphenodon* (Reynoso 1996, 2003; Apesteguía *et al.* 2012). The dorsal margin of the dentary is slightly bowed in occlusal view, with a concave lingual outline (Figs 4A, 5K). The mentonian process of the symphysis
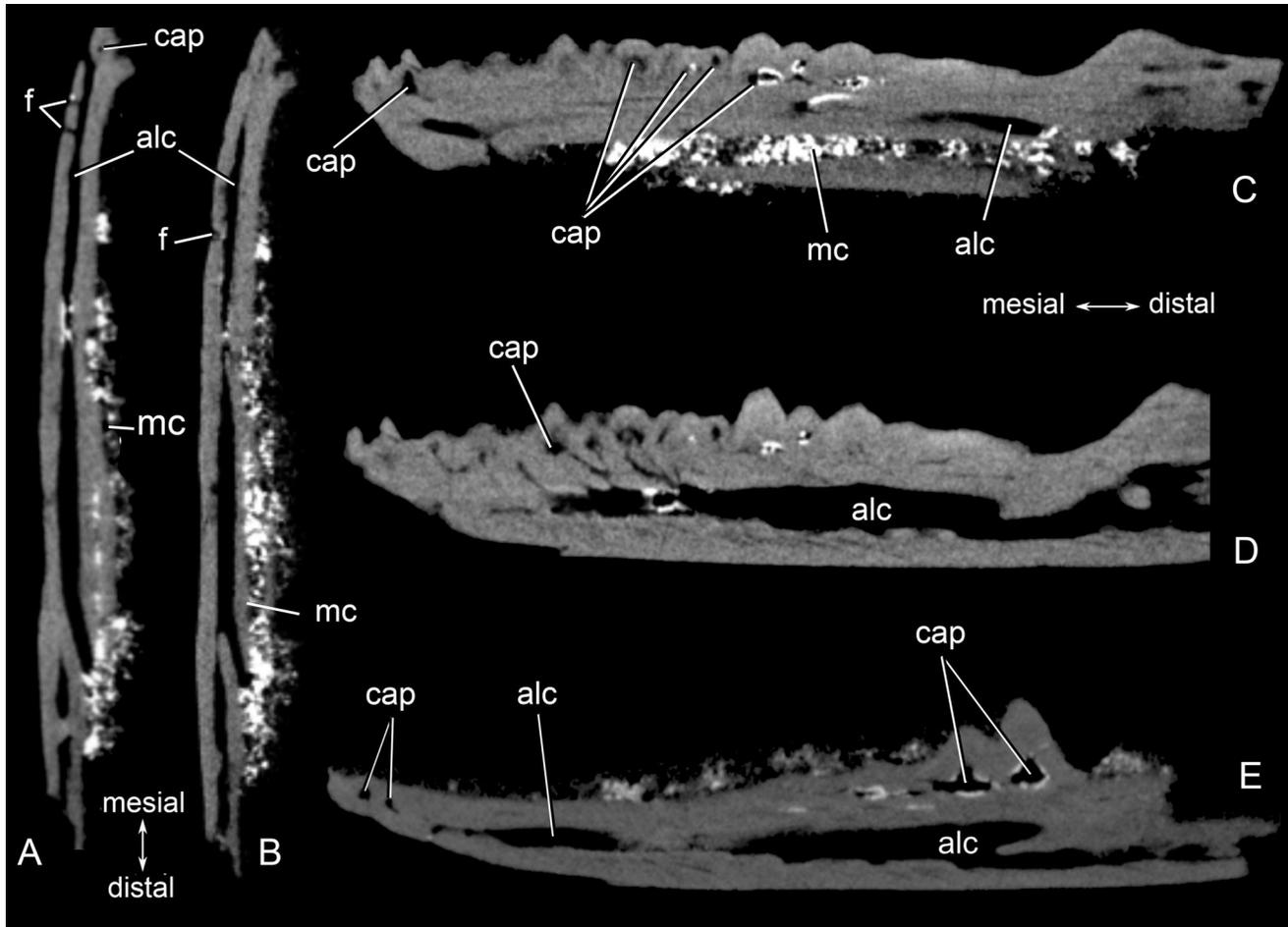
Figure 6. µCT images of dentary of *Lanceirosphenodon ferigoloi* gen. et sp. nov., CAPPA/UFSM 0226. **A, B,** coronal sections in different levels of the dentary. **C, D, E,** sagittal sections in different levels of the dentary. **Abbreviations: alc,** alveolar canal; **cap,** pulp cavity; **f,** mentonian foramina; **fl,** flange; **mc,** Meckelian canal.

Table 2. Measurement values of CAPPA/UFSM 0226.

Measurement	Value (mm)
Maximum length of dentary	9.16
Length of dentary at coronoid process (anteriorly)	7.12
Minimum height of jaw (anteriorly)	1.00
Minimum height of jaw (anteriorly, with tooth)	1.08
Maximum height of jaw at pre-coronoid region	1.22
Height of jaw at coronoid process	1.81
Length of coronoid process at base	1.69
Length of coronoid process at top	0.48
Height of coronoid process	0.52
Height of last successional tooth (labial)	0.24
Length of last successional tooth (labial)	0.31
Height of last successional tooth (lingual)	0.27
Length of last successional tooth (lingual)	0.30
Maximum transverse width of last successional tooth	0.19
Maximum mesiodistal length of last successional tooth	0.26
Height of A6 tooth (labial)	0.85

is well-developed and its tip is slightly rounded in lateroventral view (Figs 3B, C, 4B, E, 5I). Regarding the shape of the ventral margin and the symphysis,

CAPPA/UFSM 0226 is very similar to juvenile specimens of *Cynosphenodon* ([IGM 668 [T3–T4] and IGM 6659 [S1]), *Theretairus* and *Planocephalosaurus*,

Table 3. Proportion values. **Abbreviations: A,** additional tooth; **d,** distal; **h,** height; **l,** length; **LST,** last successional tooth; **m,** mesial; **w,** maximum transverse width.

Ratio	Value
Maximum pre-coronoid/pre-coronoid length	0.170
LST lingual h/l	0.900
LST labial h/l	0.770
LST occlusal m-d/w	1.060
LST lingual h/labial h	1.125
A6 lingual h/l	1.490
A6 labial h/l	1.440
A6 occlusal m-d/w	1.060
A6 lingual h/labial h	1.030
A5 lingual h/l	1.190
A5 labial h/l	1.330
A5 occlusal m-d/w	1.580
A5 lingual h/labial h	0.820

although the ventral margin is more rounded in the latter two taxa (Reynoso 2003).

Based on the µCT images, the dentary of CAPPA/UFSM 0226 has a subdental shelf that is anteriorly conspicuous in medial view, but becomes narrower under the anterior hatchling teeth, until it disappears below the level of the last hatchling tooth (Fig. 5A, K). In the anterior region, dorsal to the subdental shelf, the dentary has a pronounced post-symphyseal lamina. The Meckelian canal is apparently open and its anterior end is angled downwards, curving medially both in the symphyseal and posterior regions. Anteriorly, the Meckelian canal reaches the symphysis and is continuous with a small groove over the symphyseal facet (Figs 4C, D, F, 5A, C–E, G, K, 6 A–C). This combination of features is particularly similar to the conditions seen in *Cynosphenodon* and *Sphenovipera* (Reynoso 2003, 2005), and also to those in *Gephyrosaurus* and *Diphydontosaurus* (Evans 1980; Whiteside 1986; Whiteside & Duffin 2017).

In anterior view, the symphysis has a narrow, oval shape and its ventral tip has a stake-like process (Figs 4C–E, 5G). There is a poorly developed spur on the anterodorsal portion of the dentary, similar to that of *Sphenodon* (Jones *et al.* 2012, fig. 5) and very similar to that of juvenile specimens of *Cynosphenodon* (Reynoso 2003), but not to adult specimens of the latter taxon, in which a more developed spur is clearly seen.

The coronoid process is not complete, but its broken portion seems to be small and, consequently, this process remains low and slightly triangular in shape. The mandibular foramen is dorsoventrally tall. In medial view, the adductor fossa is wide and starts almost at the same level as the top of the coronoid process (Fig. 4C, F). However, this portion of the jaw is partially covered, probably by calcite, which is denser than the bone, and hampers observation of some features in the µCT images.

Dentition

The regionalized dentition is well preserved, with 19 teeth. Several dental generations are represented and arranged in an anteroposterior sequence, including four successional teeth, nine hatchling teeth and six additional teeth. The teeth in the anterior portion of the dentary are positioned in a more ventral plane than those of the posterior region (Figs 4A, 5A, K).

The successional teeth are the most columnar ones. The anterior-most tooth is the smallest of the successional series and the posterior-most one is the least columnar, with an almost triangular shape (Fig. 3). No 'caniniform' tooth is present. The cross section of the successional teeth is circular and wear facets are not present; secondary bone is also absent (Figs 3, 5B). All successional teeth show weakly pleurodont implantation (Fig. 5C): the labial region near the base of the teeth slightly overlies the lateral surface of dentary (Fig. 5A, C, K). In addition, the lingual part of the base of each tooth is fused to the subdental shelf; consequently, they were not acrodont in implantation (*sensu* Augé 1997). To be considered acrodont, the tooth base should not be fused to the subdental shelf or the subdental shelf should be absent (Jenkins *et al.* 2017). The overall arrangement of the successional teeth of CAPPA/UFSM 0226 is similar to that observed in juvenile specimens of *Cynosphenodon* (IGM 668 [T3–T4] and IGM 6659 [S1]; see Reynoso 2003, fig. 1A, B).

The hatchling series begins after the fourth successional tooth. Nine hatchling teeth of acrodont implantation are preserved in alternating size, as seen in most rhynchocephalians (e.g. Robinson 1976; Reynoso 2003). The shape varies from triangular to cylindrical. The four posterior hatchling teeth display on their labial face a slightly ventrally projecting curvature (Fig. 5K). The first anterior hatchling tooth is fully worn, and in general the anterior teeth have the highest degree of wear, with conspicuous labial wear facets. The degree of wear decreases posteriorly (Fig. 3). The change in crown shape, from triangular to cylindrical, may also be an artefact of wear. The cross section of the hatchling teeth is ovoid and labiolingually compressed, which may be also an effect of lateral wear. Based on the µCT images, the pulp cavity appears to have the same shape.

There are six additional teeth. They are acrodont and the largest teeth in the dentary. A peculiarity of CAPPA/UFSM 0226 is the alternating sizes of the additional teeth (Figs 3, 4), similar to the pattern seen in the maxilla of *Sphenodon* (Robinson 1976, fig. 3; Jones *et al.* 2012, fig. 4d). In this taxon, the first additional teeth appear to alternate in size, and are observed during stage T2 (see Ontogenetic considerations, below). In subsequent stages (after T2), the new additional teeth do

not alternate in size (Robinson 1976, figs 2, 3). The apex of the additional teeth of *Lanceirosphenodon*, as well as the posterior hatchling teeth, display on their labial face a slight ventrally projecting curvature (Fig. 5J, K). The pulp cavity of the additional teeth tends to be circular.

The additional teeth A1, A3 and A5 are 'D'-shaped in labial view, with an anterolateral flange, these characteristics being more marked in A5 (Fig. 3). This difference could be the result of more intense wear in A1 and A3 than in A5. The teeth A3 and A4 are triangular and A6 is conical in labial view. All additional teeth have a smooth crown. The base of the crown exhibits a thickening. We suggest that this thickening may be some kind of ankylosis because the μCT images do not show any difference in density between this thickening and the tooth itself (Figs 3A, B, 5D, E, K). In cross section, the bases of A1, A3 and A5 are nearly circular, and the flanges have the appearance of a protuberance (Fig. 5A, F). In A2 and A4 this protuberance is absent or almost imperceptible and the cross section at the base is circular, as also observed in A6 (Fig. 5F). The gap between A6 and the coronoid process is very short, and possibly due to the more medial position of this tooth; it could represent a newly erupted tooth. In the last four hatchling teeth and in the additional teeth we can observe the enamel, which is thicker in the additional teeth (Fig. 3A, D).

The alveolar canal runs medially through the dentary below the tooth row, and dorsolaterally to the Meckelian canal. This alveolar canal bifurcates dorsomedially in the posterior region (Fig. 6). It is possible that the 'cavity' noted in immature specimens of *Rebbanasaurus jaini* by Evans *et al.* (2001) represents bifurcation of the alveolar canal. This suggestion is supported by the morphology of the cross section of the dentary CAPPA/UFSM 0226, at the level of A6 (Fig. 5E), which exhibits two 'canals' or 'cavities', as also shown by Evans *et al.* (2001), but at the level of A5 these two 'cavities' merge (Fig. 5D). In the transverse and sagittal sections, this bifurcation is more evident (Fig. 6). As Evans *et al.* (2001) observed, this 'cavity' of the alveolar canal could be filled in mature animals. Laterally, the alveolar canal has branches that connect to each dentary foramen. Also, there is a foramen with a connection to the Meckelian canal. In addition, there are other very small 'canals' connected with the pulp cavity of the hatchling teeth, and between the pulp cavity of the remaining teeth (Fig. 6).

The combination of pleurodont implantation anteriorly (successional teeth) and acrodont implantation posteriorly (hatchling and additional teeth) seen in CAPPA/UFSM 0226 (Fig. 4A, C, D, K) (*sensu* Edmund 1969; revised in Jenkins *et al.* 2017, fig. 1) is common in some Triassic rhynchocephalians (e.g. *Diphydontosaurus*, the 'Vellberg Jaws' [cf. *Diphydontosaurus*], *Whitakersaurus* and possibly *Planocephalosaurus*; Fraser & Shelton 1988; Heckert *et al.* 2008; Jenkins *et al.* 2017). This pattern also resembles the agamid mode of pleurodonty (see discussions in Jenkins *et al.* [2017] and Haridy [2018]).

Although CAPPA/UFSM 0226 shares some characteristics with non-eusphenodontians (i.e. *Gephyrosaurus* and *Diphydontosaurus*), such as a slender dentary with a straight ventral margin, and the presence of the two types of dental implantation, it differs from these taxa in possessing a regionalized dentition (successional, hatchling and additional teeth), the growth of secondary bone (although poorly developed) and the presence of flanges on teeth crowns.

CAPPA/UFSM 0226 differs from *Planocephalosaurus* in the shape of the teeth in lateral view. The successional teeth of *Lanceirosphenodon* are rather columnar and the other teeth have an isosceles triangle shape, while they tend to show an equilateral triangular (more pyramidal) shape in *Planocephalosaurus*, but not as marked as in *Clevosaurus*. With respect to the coronoid process, it is higher in *Planocephalosaurus* than in CAPPA/UFSM 0226. The latter also differs from juvenile specimens of *Clevosaurus hudsoni* (see Fraser 1988), because its hatchling teeth do not have anterior and posterior flanges that form a 'sharp razor-like structure' (Fraser 1988, p. 114). We observed that the additional teeth of CAPPA/UFSM 0226 tend to have an isosceles triangle shape in lateral view, whereas in juveniles of *Clevosaurus brasilensis* (e.g. UFRGS-PV-0613-T; UFRGS-PV-0972-T) they tend to have an equilateral triangle (more pyramidal) shape. Otherwise, CAPPA/UFSM 0226 has conspicuous anterolateral flanges, which are poorly developed and/or absent in *Cl. brasiliensis*.

CAPPA/UFSM 0226 differs from Gondwanan non-sphenodontians in lacking a diastema between its successional and hatchling teeth and in lacking ornamentation on the tooth crowns. With respect to the Indian taxa *Rebbanasaurus* and *Godavarisaurus*, CAPPA/UFSM 0226 is different because it lacks the notch that divides the symphysis and the tooth series in anterior view (Evans *et al.* 2001). It is important to note that the absence of caniniform teeth in CAPPA/UFSM 0226 could be related to its ontogenetic state, as it is in *Cynosphenodon*, in which juveniles do not have caniniform teeth, but adults do (Reynoso 2003).

Phylogenetic analysis

The maximum parsimony analysis produced 136 MPTs that are 273 steps in length (consistency index = 0.385;

retention index = 0.695). The topology of the strict consensus tree is partially congruent with that obtained by Herrera-Flores *et al.* (2018) and differs mainly in that the clade Neosphenodontia was not recovered; consequently, a polytomy of eusphenodontians was formed. However, other clades were resolved, as in Herrera-Flores *et al.* (2018) and other contributions (e.g. Apesteguía *et al.* 2014; Hsiou *et al.* 2015). Another difference is the position of *Rebbanasaurus*, which is placed as the sister group of the 'Gondwanan clade' (*sensu* Apesteguía *et al.* 2012), which includes *Godavarisaurus* and *Sphenocondor*, whereas Herrera-Flores *et al.* (2018) recovered *Rebbanasaurus* in a polytomy with *Pelecymala*, the 'Gondwanan clade' and Eusphenodontia.

In all MPTs, *Lanceirosphenodon ferigoloi* is nested within Eusphenodontia, forming a trichotomy with the genus *Polysphenodon* and the clade 'Clevosauridae' + Neosphenodontia. *Pelecymala* is a rogue taxon, because in some trees it is recovered as the sister taxon of Eusphenodontia (a position also recovered in the analysis of Herrera-Flores *et al.* [2018]), whereas in others it is nested in the pleurosaurid clade.

In the strict consensus tree, a polytomy was generated among the main clades of Eusphenodontia (*sensu* Herrera-Flores *et al.* 2018) and *Lanceirosphenodon*. The internal relationships of the clevosaurid clade and among the sphenodontines *Derasmosaurus*, *Oenosaurus*, *Zapatadon* and *Ankylosphenodon* are not resolved (see Supplementary Material Fig. S1).

The clade Eusphenodontia is supported by two synapomorphies: shape of the posterior end of the maxilla, dorsoventrally broad (character 8: 0→1); and absence of striations in successional dentary teeth (character 65: 0→1). *Lanceirosphenodon* bears two autapomorphies: a well-developed, pointed mentonian process (character 33: 1→2); and a marginal dental implantation with a certain degree of posterior acrodonty (character 42: 2→1).

The IterPCR protocol identified *Deramosaurus* and *Pelecymala* as unstable taxa. When pruning *Deramosaurus*, one additional node is formed, and when *Pelecymala* is pruned, seven additional nodes are formed (Figs 7, Supplementary Material Fig. S3). After pruning these taxa, the new analysis produced 34 MPTs of 268 steps (consistency index = 0.396; retention index = 0.708). The topology of the strict consensus tree is congruent with that obtained by Herrera-Flores *et al.* (2018), but differs slightly in a few details: *Rebbanasaurus* is again placed as the sister taxon of the 'Gondwanan clade' (*sensu* Apesteguía *et al.* 2012), and the relationships among *Oenosaurus*, *Zapatadon* and *Ankylosphenodon* are resolved when *Deramosaurus* is removed.

Eusphenodontia is now supported by five synapomorphies: shape of posterior end of maxilla, dorsoventrally broad (character 8: 0→1); marginal teeth with lateral and/or wear facet (character 46: 0→1); general organization of premaxillary teeth in adults, merged into a chisel-like structure (character 49: 0→1); a single row plus one isolated tooth in palatine (character 52: 0→1); and absence of striations in successional dentary teeth (character 65: 0→1).

As already recovered in other phylogenetic analyses, the strict consensus tree shows *Gephyrosaurus*, *Diphydontosaurus*, *Planocepalosaurus* and *Rebbanasaurus*, with *Godavarisaurus* and *Sphenocondor*, the Gondwanan clade (*sensu* Apesteguía *et al.* 2012), as successively closer sister groups to Eusphenodontia. Also, several previously recognized groups of Rhynchocephalia were consistently recovered, including Sphenodontia (*sensu* Benton 1985), Eusphenodontia, clevosaurs (or Clevosauridae), Neosphenodontia, homoeosaurids, pleurosaurids, sapheosaurids, Opisthodontia, Eliendontinae and Sphenodontinae (with the same composition obtained by Herrera-Flores *et al.* 2018).

In general, the Bremer support values are low, between 1 and 2, with the exception of Sphenodontia (4). However, similar Bremer support values have been recovered in many different analyses of Rhynchocephalia (e.g. Apesteguía *et al.* 2012, 2014; Bever & Norell 2017; Herrera-Flores *et al.* 2018). Nevertheless, certain nodes are maintained in the different analyses carried out so far. The low support values may be related to the large amount of missing data, as already observed by Ezcurra *et al.* (2014, p. 2), who mentioned "that taxa with high amounts of missing data may reduce node support values not as a result of a real low robustness of the node, but because of ambiguous optimizations generated by unknown character states".

The data set analysed here has 16 taxa (32.65%) with 0–25% missing data, eight taxa (16.33%) with 26–50% missing data, 22 taxa (44.90%) with 51–75% missing data, and three taxa (6.12%) with > 75% missing data, from a total of 49 taxa. In relation to the 73 characters used in the data set, 11 characters (15%) have 0–25% missing data, 39 characters (53%) have 26–50% missing data, 22 characters (30%) have 51–75% missing data, and one character (1.37%) has > 75% missing data. In addition to the amount of the missing data, the total number of characters in the data set can also affect the bootstrap value (Soltis & Soltis 2003). Indeed, the bootstrap value decreases with the addition of characters that are compatible with but not informative for that node, characters that are autapomorphies, invariant characters, and characters that do not contradict the characters that support the clade (Soltis & Soltis 2003). Finally, it is
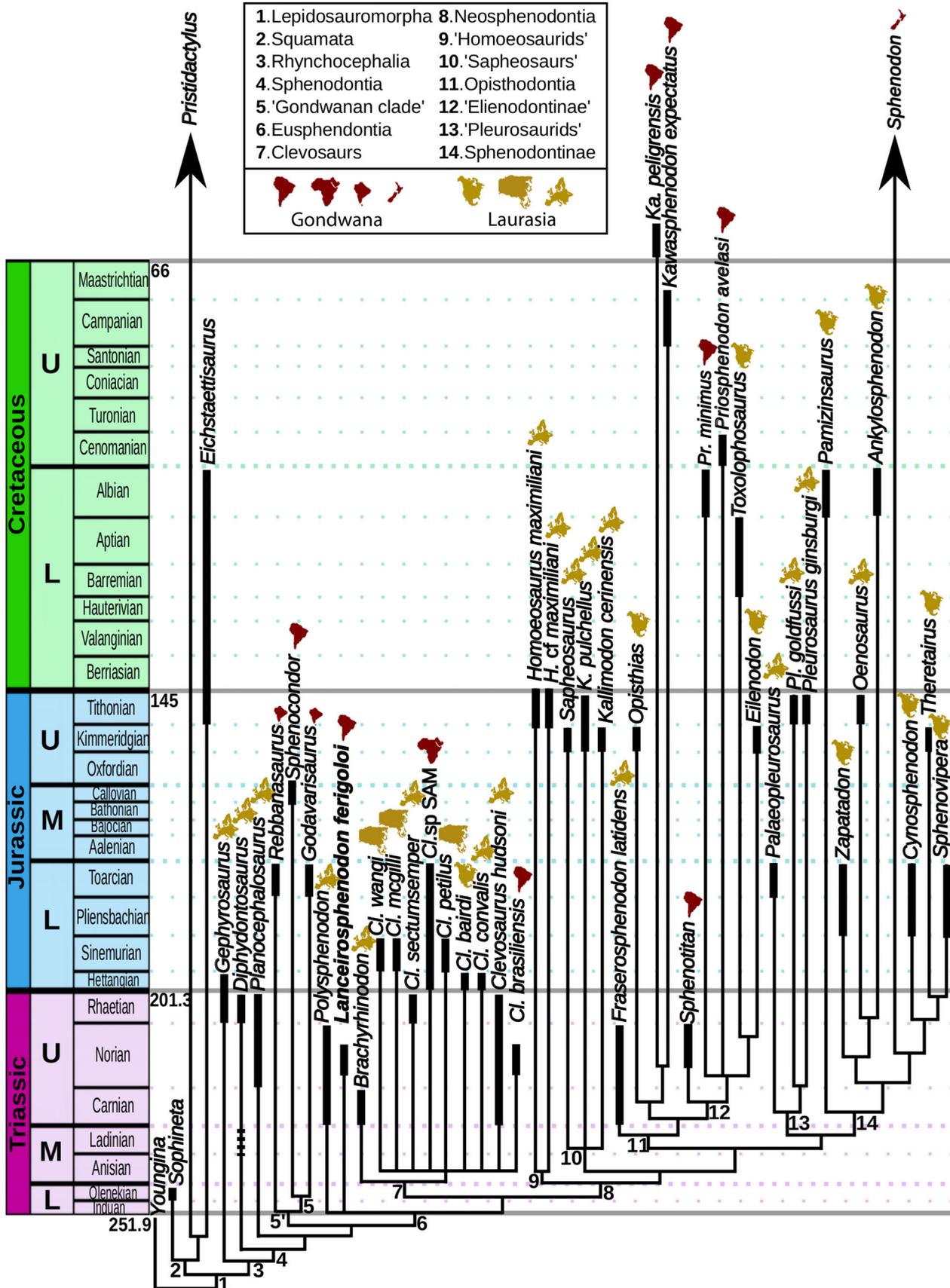
Figure 7. Time-scaled strict consensus topology exhibiting rhynchocephalian relationships (derived after iterPCR protocol; see text).

important to note that *Lanceirosphenodon* was recovered in Eusphenodontia in both topologies, independently of the low Bremer support values.

Discussion

Taxonomic and phylogenetic considerations

The new taxon presented here, *Lanceirosphenodon ferigoloi*, exhibits a mosaic of features considered 'typical' of non-eusphenodontian rhynchocephalians, along with others reported in Eusphenodontia. Common features shared with non-eusphenodontian rhynchocephalians include a slender dentary with a straight ventral margin and the presence of two types of dental implantation (pleurodont anteriorly and acrodont posteriorly). Also, the presence of a pronounced post-symphyseal lamina is shared with *Gephyrosaurus* and *Diphydontosaurus*. Additionally, the anterior end of the Meckelian canal angles downwards, running over the anterior surface of the post-symphyseal lamina, and it is continuous with a small groove over the symphyseal facet. However, these latter features are also seen in *Cynosphenodon* and *Sphenovipera*, members of Neosphenodontia (Reynoso 2003, 2005).

Lanceirosphenodon shares the following features with eusphenodontians: regionalization of the dentition with successional, hatchling and additional teeth; flanges on the teeth; growth of secondary bone; marginal teeth with lateral wear facets. However, some of these features are randomly distributed among a few non-eusphenodontian sphenodontians. The autapomorphies of *Lanceirosphenodon* are as follows: (1) Mentonian process well-developed and pointed. A similar condition is present in *Cynosphenodon*, *Theretairus* and *Sphenovipera*, which are distantly placed within Neosphenodontia. Therefore, this is a homoplastic trait that appeared at least twice in Sphenodontia. (2) The presence of marginal dental implantation with a certain degree of posterior acrodonty. A similar trait was reported for the non-eusphenodontians *Diphydontosaurus* and *Planocephalosaurus*, indicating a homoplastic condition, but unique for *Lanceirosphenodon* considering its phylogenetic placement.

The mixture of plesiomorphic and apomorphic features in *Lanceroisphenodon*, and the lack of information for this taxon given that it is based solely on a lower jaw, justifies its placement at the base of Eusphenodontia (Fig. 7), within a trichotomy (*Lanceirosphenodon*, *Polysphenodon* + [clevosaurs + Neosphenodontia]). Consequently, finding additional specimens of this taxon will be necessary to improve its phylogenetic placement.

The relationships of *Lanceirosphenodon* and *Polysphenodon* are unresolved in our analysis, but the combination of features present in the former taxon is unique. In the data matrix the same 23 characters are scored with '?' in *Polysphenodon* and *Lanceirosphenodon*, only four characters are scored the same (characters 43, 44, 46, 47), and one character is scored differently (character 42: marginal dental implantation, type). The other 45 characters are missing data for *Lanceirosphenodon* and scored for *Polysphenodon*. Although its placement is unresolved (Fig. 7), *Lanceirosphenodon* has marginal dental implantation with a certain degree of posterior acrodonty, which is absent in *Polysphenodon*. Also, the last additional teeth of the jaw of *Polysphenodon* are more elongated antero-posteriorly, with a posterolingual flange, whereas in *Lanceirosphenodon* the teeth have an anterolateral flange.

Ontogenetic considerations

The majority of the rhynchocephalian fossil record consists of complete or fragmentary lower jaws, with a few preserved skulls (e.g. Reynoso 2003), mostly belonging to adult individuals. Moreover, only some taxa are based on both juvenile and sub-adult specimens: *Clevosaurus hudsoni* (Fraser 1988), *Paminzisaurus tlayuaensis* (Reynoso 1997), *Cynosphenodon huizachalensis* (Reynoso 2003), *Zapatodon ejidoensis* (Reynoso 2005) and *Cl. brasiliensis* (Bonaparte & Sues 2006; Arantes *et al.* 2009; Romo de Vivar & Soares 2015). However, besides some brief contributions (e.g. Fraser 1986, 1988; Reynoso 1996; Jones 2008), only two papers focus on ontogenetic development in fossil rhynchocephalians, based especially on the dentary of *Cy. huizachalensis* (Reynoso 2003) and *Cl. brasiliensis* (Romo de Vivar & Soares 2015). Conversely, ontogenetic development in *Sphenodon* is well documented (e.g. Dendy 1899; Harrison 1901a, b; Robinson 1976; Fraser 1986; Rieppel 1992; Jones 2008; Howes & Swinnerton 2010).

Changes have been observed in the type of dental implantation present during ontogeny for some members of Rhynchocephalia, for example *Diphydontosaurus* (Whiteside 1986). In this taxon, the dentition changes during ontogeny from pleuroacrodont implantation to a predominantly acrodont implantation. This implantation transition occurs in the first ontogenetic stages after birth, and strongly suggests that acrodont teeth are derived from a pleurodont emplacement. This suggests that acrodonty was derived phylogenetically from a pleurodont condition in rhynchocephalians (e.g. Whiteside 1986; Whiteside *et al.* 2017). With the currently available data, this hypothesis seems correct because only early diverging taxa have a dentition with a pleurodont – or anteriorly pleurodont and posteriorly

acrodont – implantation, whereas later branching taxa have only acrodont implantation. Based on these observations, it is currently unknown whether the dentition in *Lanceirosphenodon* (CAPPA/UFSM 0226) is due to its ontogenetic stage. Only the discovery of new specimens can clarify this topic.

Dental implantation that is weakly pleurodont anteriorly and acrodont posteriorly is only observable using µCT imaging. Without this method, the condition of *Lanceirosphenodon* could not have been described. This demonstrates that a revaluation of rhynchocephalian implantation types is important and necessary, as suggested by Jenkins (2017), because some taxa currently considered acrodont may have another type of dental implantation, such as pleurodont, or pleurodont and acrodont, in the same jaw (Jenkins *et al*. 2017). Also, as observed by other authors (e.g. Whiteside & Duffin 2017; Whiteside *et al*. 2017), there are variations in the types of dental implantation considered pleurodont, acrodont or a mixture of the two in Rhynchocephalia. For example, in some pleurodont implantation types, pits can be absent or present; and in some cases they are placed on the lingual surface of the labial side of the dentary (or maxilla) while in others this condition is weakly developed. The same occurs for some acrodont conditions, in which there are different degrees of ankylosis. Dentitions that resemble a dental battery, as in *Ankylosphenodon* or *Onorenosaurus*, cannot be comparable to the acrodont implantation present in clevosaurs (e.g. Jenkins *et al*. 2017; Whiteside & Duffin 2017). Considering that the evolution of dental implantation types in Rhynchocephalia is an important feature with direct implications for understanding their diversity, new imaging techniques should furnish new information about the implantation patterns of already described taxa (and new ones). Such modifications should produce substantial changes in the configurations of data matrices, and consequently in the phylogenetic hypotheses obtained.

It is not trivial to assign an ontogenetic stage to fossil material of rhynchocephalians, and in general this is done based on comparisons with the ontogeny of *Sphenodon* (e.g. Harrison 1901a, b; Robinson 1976), in which the initial embryonic stages are denominated with the letters C–S, and advanced embryonic stages with the letters Q, R and S. Neonates and juveniles are represented with the letter T, having four stages: T1 (a few weeks), T2 and T3 (a few months) and T4 (juveniles). After T come subadults, adults and mature adults (Dendy 1899; Robinson 1976; Reynoso 2003; Howes & Swinnerton 2010). The comparisons between ontogenetic stages of *Sphenodon* should be treated with caution, however, as already pointed out by Apesteguía *et al*.

(2012). We consider that *Lanceirosphenodon* CAPPA/ UFSM 0226 could represent an individual between ontogenetic stages T2 and T3 as proposed for *Sphenodon* (Robinson 1976), because it possesses the following features: (1) the relative sizes of the last two posterior successional teeth seem more developed than those observed in *Sphenodon* in stage T3–T4 (Robinson 1976), and in *Cynosphenodon* (IGM 669; stage S) and mainly IGM 668 (stage T3–T4). (2) The large number of hatchling teeth, with lateral wear and little occlusal wear, is compatible with that shown for stages T2–T3 illustrated by Robinson (1976). (3) The presence of a considerable number of additional teeth but no greater than the number of hatchling teeth is a condition similar to stage T3 of Robinson (1976), although *Lanceirosphenodon* possesses more additional teeth than *Sphenocondor*, which is considered to be between T3 and T4. The hatchling teeth of *Sphenocondor* have a higher degree of wear than *Lanceirosphenodon*, and the lower wear in the latter could suggest the presence of more additional teeth than in *Sphenocondor*. If dental development in the *Lanceirosphenodon* dentary occurred in the same mode as in the *Sphenodon* maxilla, the presence of four additional teeth (of six in total), with alternating sizes, may indicate that *Lanceirosphenodon* was in at least stage T2 at the time of its death. However, two adjacent teeth do not show such alternation of size, meaning that the specimen could be a little older, equivalent to stage T3 of Robinson (1976). (4) Finally, the poor growth of secondary bone in the anterior region is very similar to the pattern observed in *Cynosphenodon* (IGM 668; T3–T4). We reject the possibility that the holotype of *Lanceirosphenodon* could correspond to stage T1, due to the presence of additional teeth, and we also discount stage T4 due to the presence of hatchling teeth in considerable number and with little occlusal wear, although the holotype of *Lanceirosphenodon* is smaller in size than the specimen (T2?) of *Paminzisaurus* and the specimens IGM 668 (T3–T4) and IGM 669 (S) of *Cynosphenodon*. It should be noted that we consider the first four anterior teeth to be successional teeth and not anterior hatchling teeth, mainly because they possess a larger base, they are taller in lateral view, they tend to have a more cylindrical shape and they show no evidence of strong wear. However, in the case of *Cynosphenodon* (IGM 668) it has been considered that there are two anterior hatchling teeth posteriorly followed by two successional teeth, the most posterior one being considered as a caniniform. By contrast, in the dentary of *Sphenodon* in stage T3, the anterior hatchling teeth begin to be replaced by the successional teeth, and in stage T4 the caniniform tooth is already developed. Nonetheless, in *Sphenocondor*,

which has been estimated at stages T2–T3, the first three (probably four) anterior teeth are considered successional teeth, but in *Sphenodon* it is during stage T2 that the maxillary anterior hatchling teeth begin to be replaced by the successional teeth. In contrast, based on the characteristics mentioned above as well as on comparisons with other fossil taxa and the different ontogenetic stages of *Sphenodon*, we opted to describe the four anterior teeth as successional teeth. As an alternative hypothesis, the two anterior teeth could be anterior hatchling teeth and the next two would be the first successional teeth.

Other characteristics indicating that *Lanceirosphenodon* (CAPPA/UFSM 0226) is an early juvenile (T2–T3) are related to the alveolar canal. One of these features is observed in the posterior region, where the alveolar canal appears to bifurcate, while in cross section it is observed to have two channels or cavities: (1) the alveolar canal and (2) the 'cavity' (*sensu* Evans *et al.* 2001). The 'cavity' in mature organisms is filled and not observable (Evans *et al.* 2001). Reinforcing this idea, Dosedělová *et al.* (2016) reported that the alveolar canal ('dental cavity') is filled during ontogeny in chameleons. In the case of CAPPA/UFSM 0226, this cavity is empty and clearly observable in the posterior region (Fig. 5), a feature typical of neonates or juvenile organisms. However, it is necessary to revaluate other rhynchocephalian dentaries to test whether the alveolar canal and the cavity are effectively the same structure, the 'cavity' being a bifurcation of the alveolar canal, or whether they are different structures, and to establish their changes during ontogeny.

Another feature that indicates CAPPA/UFSM 0226 is a neonate or a juvenile is the presence of channels that connect the pulp cavities of each tooth (Fig. 6). This trait has been reported in juvenile *Chameleon*, which also possesses an acrodont dentition (Dosedělová *et al.* 2016), and in *Sphenodon* (Kieser *et al.* 2009).

It is important to mention that even if CAPPA/UFSM 0226 is in ontogenetic stages T2–T3, the degree of development of the mentonian process is comparable to T3–T4 of *Cynosphenodon* (IGM 6658), a taxon in which adults have a well-developed mentonian process. Moreover, the well-developed mentonian process with a protruding tip in *Lanceirosphenodon* is similar in development and form to that of *Theretairus* (Reynoso 2003), which is an adult specimen. Consequently, this feature apparently developed early in the ontogeny of *Lanceirosphenodon*.

Finally, as already discussed, the changing type of dental implantation during ontogeny, the presence of the three dental series in adult organisms and the number of teeth in each series are traits relevant for phylogenetic analysis. Consequently, the phylogenetic analyses we performed (plus all other analyses already done) include a mixture of taxa based on individuals of different ontogenetic stages (e.g. *Lanceirosphenodon*, *Sphenocondor* and *Paminzisaurus* are based only on immature specimens). Although this mixture is not recommended in phylogenetic analyses, it is so far the only way to analyse this group, considering that several taxa are based on singleton specimens. Nevertheless, *Lanceirosphenodon* exhibits a set of diagnostic features that distinguish it from all other known rhynchocephalians.

Diversity and abundance of rhynchocephalians in the *Riograndia* AZ

The *Riograndia* AZ (top of the Candelária Sequence, Santa Maria Supersequence; Zerfass *et al.* 2003; Soares *et al.* 2011; Horn *et al.* 2014) is particularly distinct from other Brazilian Triassic AZs in its high diversity of small-sized animals, including a basal lepidosauromorph (*Cargninia enigmatica*; Bonaparte *et al.* 2010), a procolophonian (*Soturnia caliodon*; Cisneros & Schultz 2003), a sphenodontian (*Clevosaurus brasiliensis*; Bonaparte & Sues 2006), an archosaur of uncertain affinity (*Faxinalipterus minima*; Bonaparte *et al.* 2010; Soares *et al.* 2013) and several probainognathian cynodonts (e.g. *Brasilodon quadrangularis*, *Brasilitherium riograndensis*, *Minicynodon maieri*, *Riograndia guaibensis*, *Irajatherium hernandezi*; Bonaparte *et al.* 2001, 2003, 2005, 2012; Martinelli *et al.* 2005; Soares *et al.* 2011; Oliveira *et al.* 2011). This assemblage of small-sized species is mainly restricted to two sites – Linha São Luiz in Faxinal do Soturno County and Sesmaria do Pinhal in Candelária County (Rio Grande do Sul State) – which are approximately 85 km from each other. Other medium- to large-sized faunal components are known from the *Riograndia* AZ, in either the previously mentioned sites (e.g. the dinosaur *Guaibasaurus candelariensis*; Bonaparte *et al.* 1999) or closely located ones (e.g. Cerro Botucaraí, Candelária), including the dicynodont *Jachaleria candelariensis*, dinosaurs and phytosaurs (e.g. Araújo & Gonzaga 1980; Kischlat & Lucas 2003; Bittencourt *et al.* 2012; Pinheiro 2016), as well as in other regions (e.g. Agudo and São Martinho da Serra; Leal *et al.* 2004; Ferigolo & Langer 2007; Müller *et al.* 2015). The discovery of the rhynchocephalian *Lanceirosphenodon ferigoloi* from the Linha São Luiz outcrop increases the diversity of small-sized animals in the *Riograndia* AZ. However, it is based only on its holotype specimen. Conspicuously, *Clevosaurus brasiliensis* is the most abundant taxon in both sites with small-sized animals. After the discovery of these sites, most of the resulting publications have dealt with cynodonts (e.g. Bonaparte *et al.* 2001, 2003, 2005, 2010, 2012; Martinelli *et al.* 2005; Martinelli & Bonaparte
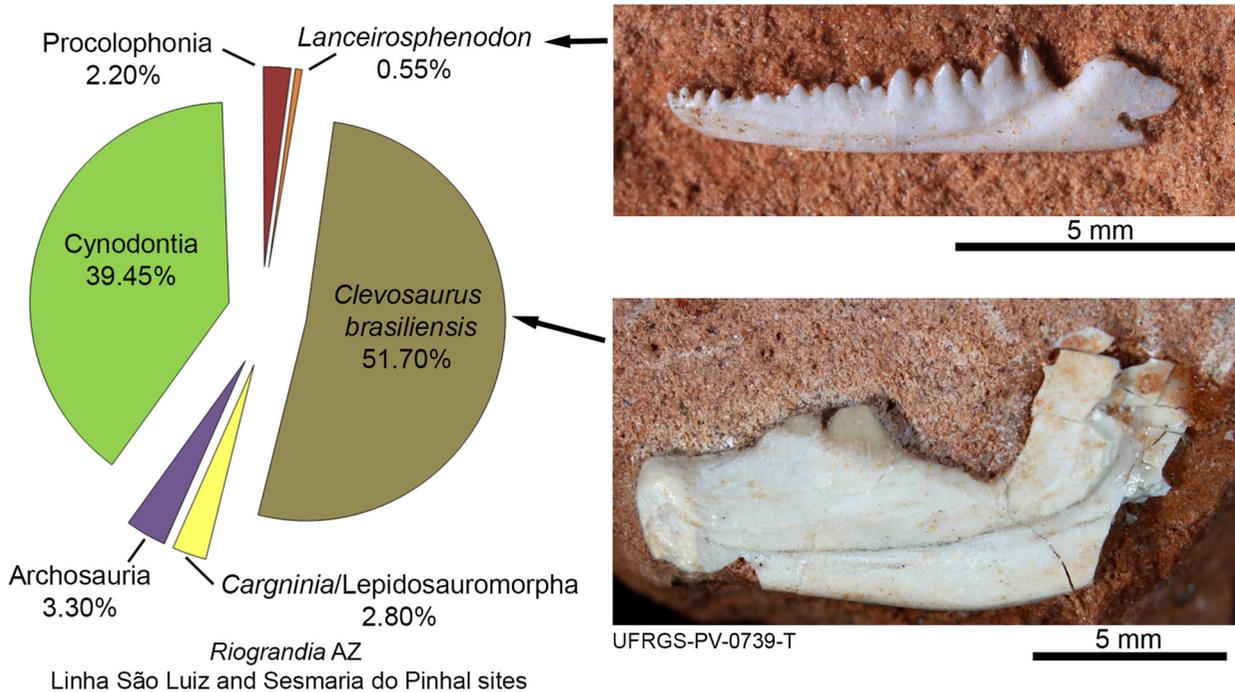
Figure 8. Relative abundance of vertebrate taxa recovered in two sites (Linha São Luiz and Sesmaria do Pinhal outcrops) with rhynchocephalians from the *Riograndia* Assemblage Zone (AZ) (see text for explanation).

2011; Oliveira *et al.* 2011; Soares *et al.* 2011), giving the impression that this was the most abundant (and diverse) group. Because of this, Martínez *et al.* (2015) concluded that cynodonts were predominant (~70%) over other faunal components in the Linha São Luiz site. Consequently, the authors mentioned that the Brazilian site differed conspicuously from the Late Triassic faunal association of the Quebrada del Barro Formation (San Juan Province, Argentina), in which sphenodontian specimens are the predominant elements.

To address this issue, we analysed the main collection of small-sized animals from the Linha São Luiz and Sesmaria do Pinhal outcrops, housed at the UFRGS. These specimens have been collected and prepared since 2000 and represent a significant sample of the faunal composition of both sites. From a total of 180 specimens (179 from the UFRGS collection plus the holotype of *Lanceirosphenodon* from CAPPA-UFSM; not including still unprepared specimens) the percentage of specimens from each taxon is as follows: 51.70% *Clevosaurus brasiliensis*; 0.55% *Lanceirosphenodon*; 39.45% cynodonts (17.2% *Riograndia*; 16.70% *Brasilodon-Brasilitherium-Minicynodon*; 5.55% *Irajatherium*); 3.30% archosaurs (*Faxinalipterus*, *Guaibasaurus* and Archosauria indet.); 2.80% lepidosauromorphs (*Cargninia* and Lepidosauromorpha indet.); and 2.20% procolophonians (*Soturnia*) (Fig. 8). This results in a predominance of sphenodontians over cynodonts and other faunal

components. The predominance of sphenodontians is a trait shared with the faunal association of the Quebrada del Barro Formation in Argentina. This analysis reveals that *Clevosaurus brasiliensis* is the most abundant taxon in both sites from the *Riograndia* AZ and that sphenodontians (*Cl. brasiliensis* and *Lanceirosphenodon*) are not as diverse as the probainognathian cynodonts, which are represented by five taxa (possibly three taxa if *Brasilodon*, *Brasilitherium* and *Minicynodon* are merged into a single taxon; Liu & Olsen 2010; Martinelli & Bonaparte 2011; Martinelli 2017).

Lanceirosphenodon ferigoloi and the early diversity of rhynchocephalians

Until now, *Clevosaurus hadropodon* (Brazil), *Cl. brasiliensis* (Brazil) and *Sphenotitan layesi* (Argentina) were the only Triassic taxa of rhynchocephalians from Gondwana. The two latter species are characterized by their robust skull (although *Cl. brasiliensis* is a small-sized animal) and are the most abundant components of their respective faunal associations. The three non-eusphenodontian forms known to date from Gondwana are all from the Jurassic: the Indian genera *Godavarisaurus* and *Rebbaanasaurus* (Kota Formation, Toarcian; Evans *et al*. 2001) and the Argentinean genus *Sphenocondor* (Asfalto Formation, Callovian–Oxfordian; Apesteguía *et al.* 2012) (Figs 7, 9; Table 1).
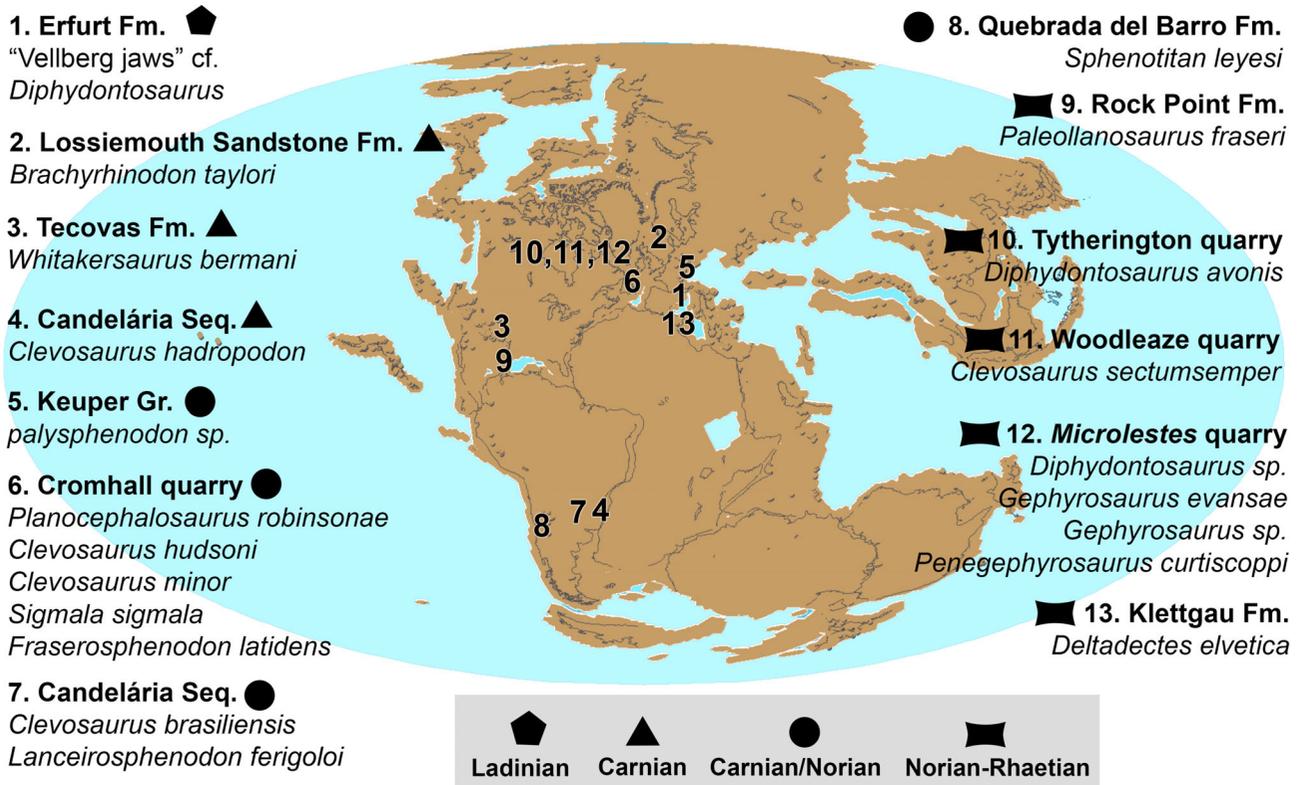
1. **Erfurt Fm.** ⬠
"Vellberg jaws" cf.
Diphydontosaurus

2. **Lossiemouth Sandstone Fm.** ▲
Brachyrhinodon taylori

3. **Tecovas Fm.** ▲
Whitakersaurus bermani

4. **Candelária Seq.** ▲
Clevosaurus hadropodon

5. **Keuper Gr.** ●
palysphenodon sp.

6. **Cromhall quarry** ●
Planocephalosaurus robinsonae
Clevosaurus hudsoni
Clevosaurus minor
Sigmala sigmala
Fraserosphenodon latidens

7. **Candelária Seq.** ●
Clevosaurus brasiliensis
Lanceirosphenodon ferigoloi

● 8. **Quebrada del Barro Fm.**
Sphenotitan leyesi

⬣ 9. **Rock Point Fm.**
Paleollanosaurus fraseri

⬣ 10. **Tytherington quarry**
Diphydontosaurus avonis

⬣ 11. **Woodleaze quarry**
Clevosaurus sectumsemper

⬣ 12. *Microlestes* **quarry**
Diphydontosaurus sp.
Gephyrosaurus evansae
Gephyrosaurus sp.
Penegephyrosaurus curtiscoppi

⬣ 13. **Klettgau Fm.**
Deltadectes elvetica

⬠	▲	●	⬣
Ladinian	**Carnian**	**Carnian/Norian**	**Norian-Rhaetian**

Figure 9. Palaeogeographical reconstruction for 225.6 Ma with the distribution of Triassic rhynchocephalian taxa. The map was produced with Paleographic Map Generator (Alroy 2015).

In general for the South American Triassic, the ratio of relative abundance of *Clevosaurus brasiliensis* and *Sphenotitan layesi* is higher when compared to that of non-eusphenodotian taxa and/or more slender forms, which are less frequent (e.g. *L. ferigoloi*). This also happens in some localities in the Northern Hemisphere, such as in the United Kingdom, where the genus *Clevosaurus* is more abundant and relatively more diverse than non-eusphenodontian slender forms, like *Diphydontosaurus* and *Gephyrosaurus* (Figs 7, 9). Although there are some localities in the UK where the opposite happens (Klein *et al.* 2015; Keeble *et al.* 2018), the relative abundance of *Clevosaurus* is still greater when all localities are considered. The scarcity of non-eusphenodontians and slender forms during the Triassic in Gondwana, and elsewhere, may be related to the fact that non-eusphenodontian forms tend to be small in size and more slender. Consequently, the relative abundance in each faunistic association of each outcrop does not necessarily reflect the abundance of the biocenosis but could be more closely related to taphonomic processes.

The presence of the three eusphenodontian taxa in the Triassic of Gondwana, *Clevosaurus hadroprodon*, *Cl.* *brasiliensis* and *Sphenotitan layesi* (whose taxonomic groups – clevosaurs and Opisthodontia – are also found in Laurasia), together with the new basal eusphenodontian *Lanceirosphenodon ferigoloi*, indicates that: (1) Rhynchocephalia had an early diversification with an explosion of morphological disparity, with a series that split among non-eusphenodontian forms and *Lanceirosphenodon*, *Polysphenodon* and clevosaurs (as already been observed by Apesteguía *et al.* [2012] for the latter clade). (2) This diversification was quickly followed by a second split within Eusphenodontia, which led to the divergence between the sphenodontines and the ophisthines into Neosphenodontia, by the Norian (Martínez *et al.* 2013). Taking into account that the 'Vellberg Jaw' (cf. *Diphydontosaurus*) is Ladinian in age, we agree with the hypothesis that a radiation of non-eusphenodontian forms took place between the end of the Early and the Middle Triassic. A radiation of non-eusphenodontian forms during the Early Triassic is compatible with the hypothesis of the origin of Rhynchocephalia before the Permo–Triassic extinction. This hypothesis is reinforced by Simões *et al.* (2018), who indicated the origin of Squamata by this time interval (see also Hsiou *et al.* 2019).

Table 4. Teeth in juvenile and immature specimens. **Abbreviations: ADT,** additional teeth; **CAN,** caniniform tooth; **HT A,** anterior hatchling teeth; **HT P,** posterior hatchling teeth; **ST,** successional teeth; *, present. Main data were taken from Fraser (1988), Renesto (1995), Reynoso & Clark (1998), Evans *et al.* (2001), Reynoso (2003), Apesteguía *et al.* (2012) and Romo de Vivar & Soares (2015).

TAXON (specimen)	STAGE	ST	CAN	HT A	HT P	ADT
Pamizaurus (IGM 6854)	T2?	0			9	2
Sphenocondor (MPEF-PV 2358)	T2–T3	3–4	?		15–16	3
Cynosphenodon (IGM 6659)	S	0		2	>9	?
Cynosphenodon (IGM 6658)	T3–T4	4	*	2	>7	?
Clevosaurus hudsoni immature (AUP 11373)	T3?	3			8?	3
Clevosaurus hudsoni juvenile [early stage]		5			12	
Clevosaurus brasiliensis (UFRGS-PV-0613-T)	Juvenile	?		?	>6	2
Clevosaurus brasiliensis (UFRGS-PV-848-T)	Juvenile	?		?	>9	2
Clevosaurus brasiliensis (UFRGS-PV-0972-T)	Juvenile	?		?	?	2
*Rebbanasaurus (*VPL/JU/KR2)	Immature	5	?		>4	?
Rebbanasaurus (VPL/JU/KR1)	Juvenile	4?			>4	?
Godavarisaurus (VPL/JU/KR39)	Juvenile	?			>6	>1
*Godavarisaurus (*VPL/JU/KR38)	Juvenile	3?			?	?
Zapatodon (IGM 3497)	T–T2					
Sphenodon series						
Sphenodon T	Hatching			3	13	
Sphenodon T2	Few weeks			3	13	3
Sphenodon T3	Few weeks			2–3	13	5
Sphenodon T4	Several months	2?	*		6	8
Lanceirosphenodon (CAPPA/UFSM 0226)	T2–T3	4	?		9	6
Diphydontosaurus (MCSNB 4862)	Juvenile			9 – 10 pleurodont anterior teeth		

Figure 10. Life reconstruction of *Lanceirosphenodon ferigoloi* (made by Jorge Blanco).

Rhynchocephalia was formerly very diverse, as evidenced by its variety of body shapes, sizes, habits and diets (e.g. Jones 2008, 2009; Evans & Jones 2010). After taking ontogeny into account, *Lanceirosphenodon* was small in size when compared to specimens of other genera of similar ontogenetic stages, and was even smaller than *Paminzisaurus* (Reynoso 1997; see Table 4). Regardless of the appearance of being a small rhynchocephalian, with a dentary measuring less than 30 mm in length, the occurrence and phylogenetic position of *Lanceirosphenodon* fits with the trends of size evolution previously proposed for the clade (Apesteguía & Carballido 2014, fig. 7). Moreover, the dentition of *Lanceirosphenodon* suggests an insectivorous diet, similar to those of other basal taxa or the ontogenetically immature individuals of more derived taxa. Some taxa, such as *Sphenodon* and *Clevosaurus*, become omnivorous as adults (Fraser 1988; Jones 2008; Meloro & Jones

2012; Romo de Vivar & Soares 2015). The diet of *Lanceirosphenodon* is inferred from the shape of the teeth, which varies from columnar to triangular, as well as tooth dimensions (mesiodistal length *versus* labiolingual width), which correspond to the 'pierce' morphotype (*sensu* Jones 2009) which is indicative of an insectivorous diet. As shown in Supplementary Material Fig. S3, the teeth of *Lanceirosphenodon* are positioned very close to the teeth of *Gephyrosaurus*, *Diphydontosaurus*, and *Planocephalosaurus* when included in the database provided by Jones (2009) (Supplementary Material Fig. S3), suggesting similar feeding habits for these taxa.

Conclusions

In this contribution, we describe a new genus and species of rhynchocephalian, *Lanceirosphenodon ferigoloi* (Fig. 10), based on a well-preserved lower jaw with dentition. This new taxon represents a basal eusphenodontian, with a mosaic of plesiomorphic and apomorphic features. Ontogenetically, the holotype specimen CAPPA/UFSM 0226 is considered to fall in stage T2–T3 of the ontogenetic series proposed by Robinson (1976) for *Sphenodon*, which should correspond to an individual that was a few months old. We infer an insectivorous diet for *Lanceirosphenodon* based on its dental shape. The presence of this new sphenodontian increases the known faunal diversity of the *Riograndia* AZ in the Brazilian Triassic. Both this taxon and the Linha São Luiz site as a whole are important in our understanding of the early evolution of Rhynchocephalia in western Gondwana. Based on our results, the early diversification of Rhynchocephalia occurred around the Early Triassic, giving rise to the main lineages of the group.

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Supplementary material

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Supplementary Information for:

A new rhynchocephalian from the Late Triassic of southern Brazil enhances eusphenodontian diversity

Paulo R. Romo de Vivar, Agustín G. Martinelli, Annie Schmaltz Hsiou and Marina Bento Soares

We include here additional cladograms discussed in the main text (1), final character list used for the phylogenetic analyses (2), and the modified data matrix (3).

1. Additional cladograms

Figure S1. Strict Consensus Tree of 136 most parsimonious trees (273 steps each) (CI = 0.385; RI = 0.695). Bremmer support and Standard Bootstrap are indicated above the nodes (Bremmer support / Standard Bootstrap).

Figure S2. Topology obtained by iterPCR protocol. Strict Consensus Tree of 34 most parsimonious trees (268 steps each) (CI = 0.396; RI = 0.708). Bremmer support and Standard Bootstrap are indicated above the nodes (Bremmer support / Standard Bootstrap). The two reduced cladograms in the down left part of the figure show the new nodes when the taxa with "??" were pruned.

2. Character list

Description of 73 characters used in the phylogenetic analyses, 72 of which are the same used by Herrera-Flores *et al.* (2018), Hsiou *et al.* (2015) and Apesteguía *et al.* (2014). Some modifications were made to the dataset of Herrera-Flores *et al.* (2018), as follows:

Character 39 (Coronoid process, height relative to that of the jaw at the level of the anterior end of the coronoid process). We used it as was proposed by Bever & Norell (2017). We scored *Clevosaurus convalis*, *Cl. bairdi*, *Cl. petilus*, *Cl. sectumsemper*, *Cl. mcgilli* and *Cl. wangi* based on bibliographic revision, and *Cl. brasiliensis* by direct observation (UFRGS-PV-606-T, UFRGS-PV-748-T, UFRGS-PV-754-T, UFRGS-PV-758-T).

Character 42 (Marginal dental implantation, type). We scored *Planocephalosaurus* with '1' (degree of posterior acrodonty), following the score by Reynoso (1996). Also, we considered

this genus as having the anterior dentition weakly pleurodont and the posterior one acrodont, following Jenkins *et al.* (2017) and Fraser & Shelton (1988).

Character 44 (Dentary regionalization with small juvenile teeth in the anterior region of maxilla and dentary). We simplified it as in Reynoso (1996), because the character states are redundant with those of Character 42.

Character 73 (Anterior caniniform teeth in maxillae and dentary). We added this character that was taken from Bever & Norell (2017; see character 80 of their list of characters, and 78 in the matrix).

Characters 62 and 63. These were removed, because in the original data set of Apesteguía et al. (2014), and subsequent works (Hsiou *et al.* 2015; Herrera-Flores *et al.* 2018), all taxa were coded as missing data (?). Consequently, our dataset has 73 characters and not 75 (which would be expected when adding one character to the data set of 74 original characters).

The modified characters are denoted with an asterisk. The original source of each character is indicated between brackets.

Abbreviations

A&14, Apesteguía *et al.* (2014);
AGR12, Apesteguía *et al.* (2012);
AN03, Apesteguía & Novas (2003);
B85, Benton (1985);
BN17, Bever & Norell (2017);
E88, Evans (1988);
FB89, Fraser & Benton (1989);
G88, Gauthier *et al.* (1988);
H&15, Hsiou *et al.* (2015)
HF18, Herrera-Flores *et al.* (2018);
R96, Reynoso (1996);
R97, Reynoso (1997);
RC98, Reynoso & Clark (1998);
S94, Sues *et al.* (1994);
W94, Wu (1994).

1. Antorbital region, length relative to skull length: one-third or more (0); between one-fourth and one-third (1); one fourth or less (2).
(HF18, H&15, A&14, AN03, R96, S94, W94)

2. Orbit, length relative to skull length: one third or greater (0); less than one third (1). (HF18, AH&15, A&14, AN03, RC98)

3. Supratemporal fenestra, length relative to orbit length: less than 75% (0); 75% or greater (1).
(HF18, AH&15, A&14, AN03, S94)

4. Supratemporal fenestra, length relative to skull length: one-fourth or less (0); more than one-fourth (1).
(HF18, AH&15, A&14, AN03, R96, W94)

5. Lower temporal fenestra, length relative to skull length: one-fourth or less (0); more than one-fourth (1).
(HF18, AH&15, A&14, AN03, R96, W94)

6. Maxilla, premaxillary process: elongate (0); reduced (1).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

7. Maxilla, participation in margin of external naris: entering into margin (0); excluded from margin by posterodorsal process of premaxilla (1).
(HF18, AH&15, A&14, AN03, R9, S94)

8. Maxilla, shape of posterior end: tapering posteriorly or very narrow (0); dorsoventrally broad (1).
(HF18, AH&15, A&14, AN03, R96, W94)

9. Lacrimal: present (0); absent (1).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

10. Jugal, shape of dorsal process: broad and short (0); narrow and elongate (1).
(HF18, AH&15, A&14, AN03, R96, W94)

11. Prefrontal and postfrontal, profuse sculpture on bone surface: absent (0); present (1).
(HF18, AH&15, A&14, AN03)

12. Prefrontal-jugal contact: absent (0); present (1).
(HF18, AH&15, A&14, AN03, R97, S94)

13. Postorbital, marked dorsal ridge and deep ventrolateral concavity: absent (0); present (1).
(HF18, AH&15, A&14, AN03)

14. Frontals, relation: separated (0); fused (1).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

15. Parietals, relation: separated (0); fused (1).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

16. Parietal, width between supratemporal passages relative to interorbital width: broader (0); narrower (1).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

17. Parietal crest: absent (0); present (1).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

18. Parietal, shape of posterior edge: greatly incurved inward (0); slightly incurved inward (1); convex (2).
(HF18, AH&15, A&14, AN03, R96, W94)

19. Parietal foramen, position relative to anterior border of supratemporal fenestra: posterior (0); at the same level or anterior (1).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

20. Lower temporal bar, position: aligned with the maxillary tooth (0); bowed away beyond the limit of the abductor chamber (1).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

21. Lower temporal bar, posteroventral process of jugal: absent (0); poorly- to moderately-developed, less than half the length of the lower temporal fenestra (1); well-developed, half the length of the lower temporal fenestra or more (2).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

22. Palatine, shape of posterior end: tapers posteriorly (0); widens posteriorly (1).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

23. Pterygoids, anterior contact between bones*: absent (0); small (1); broad (2)
(HF18, AH&15, A&14, AN03, R97)

24. Pterygoids, posterior opening of the interpterygoid vacuity between posteromedial processes: widely open (0); moderately open, as wide as the vacuity (1); almost closed by the posteromedial processes (2).
(HF18, AH&15, A&14, AN03, R97)

25. Pterygoid, central region between three rami: short (0); elongate (1).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

26. Pterygoid, participation in margin of suborbital fenestra: form part of the margin (0); excluded from margin (1).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

27. Quadrate-quadratojugal foramen, relative size: small (0); large (1).
(HF18, AH&15, A&14, AN03, RC98)

28. Quadrate-quadratojugal foramen, location: between the quadrate and the quadratojugal (0); entirely within the quadrate (1).
(HF18, AH&15, A&14, AN03, RC98)

29. Quadrate-quadratojugal emargination, shape: pronounced (0); reduced (1).
(HF18, AH&15, A&14, AN03, RC98, S94, W94, E88)

30. Supratemporal, as a discrete bone: present (0); absent (1).
(HF18, AH&15, A&14, AN03, R97, S94)

31. Inferred jaw motion: orthal (0); propalinal (1).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

32. Degree of propaliny, measured either as palatal tooth row extension or length in which palatines keep parallel to the maxillae: small palatal row, parallel line restricted to the anterior region (0); enlarged, palatines accompanying maxilla half its own length (1); palatines accompanying maxilla by its complete length (europaliny?) (2).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

33. Mandibular symphysis, mentonian process*: absent (0); reduced (1); well developed and pointed (2); well developed and rounded (3).
(HF18, AH&15, A&14, AN03)

34. Mandibular symphysis, shape: almost circular, high/length relation near one (0); oval, high/length clearly greater than one (1).
(HF18, AH&15, A&14, AN03, R96, B85)

35. Mandibular symphysis, angle between anterior margin and longitudinal axis of the mandible in lateral view: <120º, symphysis nearly vertical, typically devoid of ventral projections (0); ≥120º, symphysis anterodorsally projected (1).
(HF18, AH&15, A&14, AN03)

36. Mandibular symphysis, symphyseal spur: absent (0); well-developed, anterodorsally projected (1); moderately developed (2).
(HF18, AH&15, A&14, AN03)

37. Mandibular foramen, relative size: small (0); large (1).
(HF18, AH&15, A&14, AN03, R96, B85)

38. Glenoid cavity, shape: smooth surface, lacking an anteroposterior central ridge (0); elongate and asymmetrical surface, with a strong anteroposterior central ridge (1); symmetrical facet with a strong anteroposterior central ridge (2).
(HF18, AH&15, A&14, AN03)

39. Coronoid process, height relative to that of the jaw at the level of the anterior end of the coronoid process: (0) low, weak, less than 1/2 jaw; (1) moderately high, around 1/2 jaw height; (2) very high, nearly as high as jaw.
*This modified character takes of BN17. (BN17, A&14, AN03, R96, S94, W94)

40. Retroarticular process, shape: pronounced (0); reduced, caudally projected (1); reduced, dorsally curved (2).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

41. Dentary, posterior process, relative length: short, not reaching glenoid level (0); elongate, reaching glenoid level (1); elongate, reaching the end of glenoid level (2).
(HF18, AH&15, A&14, AN03, R97, S94)

42. Marginal dental implantation, type: pleurodont (0); degree of posterior acrodonty (1); fully acrodont (2).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

43. Tooth replacement, type: alternate (0); addition at back of jaw (1).
(HF18, AH&15, A&14, AN03, R96, B85)

44. Dentary regionalization with small juvenile teeth in the anterior region of maxilla and dentary: absent (0); present (1)
*This modified character takes of R96. (R96)

45. Dentary, posterior successionals, number in mature individuals: zero (0); one (1); two or more (2).
(HF18, AH&15, A&14, AN03, R96, G88)

46. Marginal teeth, lateral wear facets on dentary and/or medial wear facets on maxilla: absent or smooth (0); present, conspicuous (1).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

47. Marginal teeth, shape of cross section of posterior teeth: nearly circular (0); squared (1); rectangular, wider than long (2).
(HF18, AH&15, A&14, AN03, R96, FB89)

48. Premaxillary teeth, number in mature individuals: more than seven (0); seven to four (1); three or less (2).

(HF18, AH&15, A&14, AN03, R96, S94, W94)

49. Premaxillary teeth, general organization in adults: present as discrete teeth (0); merged into a chisel-like structure (1).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

50. Maxillary teeth, posteromedial flanges on posterior teeth: absent or inconspicuous (0); present as small flanges on at least one tooth (1); present as extensive flanges on most teeth (2).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

51. Maxillary teeth, anterolateral flange on posterior teeth: absent (0); present (1).
(HF18, AH&15, A&14)

52. Palatine teeth, number of tooth rows: two or more (0); a single row plus one isolated tooth (1); a single lateral row (2).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

53. Palatine teeth, flanges: completely absent (0); present at least on a few teeth (1).
(HF18, AH&15, A&14, AN03, R96, FB89)

54. Palatine teeth, hypertrophied tooth on anterior region of the palatine bone (stabbing palatine): absent (0); present (1).
(HF18, AH&15, A&14, AN03)

55. Pterygoid teeth, number of tooth rows: three or more (0); two (1); one or none (2); radial crests (3).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

56. Mandibular teeth, anterolateral flanges: absent (0); present, at least in one tooth (1).
(HF18, AH&15, A&14, AN03, R96, S94, W94)

57. Mandibular teeth, anteromedial flanges: absent (0); present (1).
(HF18, AH&15, A&14, AN03)

58. Mandibular teeth, additionals, enamel ornamentation in adults: absent (0); present, with numerous fine striae (1); present, with a combination of a few striae and wide grooves (2).
(HF18, AH&15, A&14, AN03)

59. Second sacral vertebra, posterior process: absent (0); present, small (1); present, prominent (2).
(HF18, AH&15, A&14, AN03, R96, G88)

60. Ischium, process on posterior border: absent (0); present as small tubercle (1); present as prominent process (2).
(HF18, AH&15, A&014, AN03, R96, FB89, E88)

61. Humerus, length relative to length of presacral column: <0.12 (0); between 0.12 and 0.21 (1); > 0.21.
 (HF18, AH&15, A&14, AN03, R96, FB89)

62. Dentary, proportions (pre-coronoid length/ maximum pre-coronoid height ratio, L/H): gracile, long and low, L/H < 0.18 (0); average, L/H between 0.18?0.28 (1),robust, short and high, L/H > 0.28 (2).
*Character 64 of A&14 (HF18, AH&15, A&14, AGR12)

63. Dentary, successional teeth, maximum concurrent number during ontogeny: six or more (0); three to five (1); two or less (2)
* Character 65 of A&14 (HF18, AH&15, A&14, AGR12)

64. Dentary, anterior successional teeth (not "caniniform"), number in the adult: two or more clearly discrete teeth (0); one or two poorly distinct (1); none or indistinct(2).
* Character 66 of A&14 (HF18, AH&15, A&14, AGR12)

65. Dentary, successional teeth, striation: present (0); absent (1).
* Character 67 of A&14 (HF18, AH&15, A&14, AGR12)

66. Dentary, posterior successional teeth, lingual groove: absent (0); present (1).
* Character of 68 A&14 (HF18, AH&15, A&14, AGR12)

67. Dentary, hatchling teeth, striation: absent (0); present (1)
*Old ch 69 A&14 (HF18, AH&15, A&14, AGR12)

68. Dentary, successional "caniniform" teeth, shape of basal cross section: nearly circular (0); clearly oval, labio-lingually compressed (1).
* Character of A&14 (HF18, AH&15, A&14, AGR12)

69. Mandibular teeth, additionals, grooves or fossae on labial or lingual sides: absent (0); present (1).
* Character 71 of A&14 (HF18, AH&15, A&14)

70. Mandibular teeth, additionals, posterior groove: absent (0); wide and poorly defined (1); relatively deep and well-defined (2).
* Character 72 of A&14 (HF18, AH&15, A&14)

71. Maxilla, facial process, shape of anterior margin relative to main axis of maxilla: low slope, straight or concave (0); high slope, in straight angle (1); high slope, continuous and concave (2); high slope, continuous and convex (3).
* Character 73 of A&14 (HF18, AH&15, A&14)

72. Maxilla, facial process, maximum high (FH) with respect to length of maxilla
* Character 74 of A&14 (HF18, AH&15, A&14)

73. Anterior caniniform teeth in maxillae and dentaries (Dupret 2004, 31): (0) absent; (1) present.
* (BN 2017, character 80 in the list of characters but in the matrix of BN it is character 78)

3. Modified data matrix

Youngina
00000000100000000000200000000?0000?0?00000002000000000000?10?00010??00000

Ankylosphenodon
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Clevosaurus_brasiliensis
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Eichstaettisaurus
10110000010?011000000??000???00?0?????????????????????????????????000?0

Sophineta
00010000?0??00000?0?0??00??????00?0?????00????????????????????????00000

Brachyrhinodon
211111011100?000000120120????0011101?10121101121101001?????11?????????21?

Clevosaurus_hudsoni
2111111110100010001202101000000111011101211011212010011012111?2?0?00210

Cynosphenodon
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Diphydontosaurus
100000001000010000120100000010100010001111200100000000121?000001?00000

Eilenodon
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Gephyrosaurus
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Godavarisaurus_ ??????1???????????????????????0110[0 2]?????211200[1 2]01021??100???[0 1]10010100??1

Homoeosaurus_cf_maximiliani
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Homoeosaurus_maximiliani
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Kallimodon_cerinensis
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Kallimodon_pulchellus
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Kawasphenodon_expectatus
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Kawasphenodon_peligrensis
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Oenosaurus
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Opisthias_rarus
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Palaeopleurosaurus
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Pamizinsaurus
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Planocephalosaurus
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Pleurosaurus_ginsburgi
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Pleurosaurus_goldfussi
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Priosphenodon_avelasi
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Pristidactylus
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Rebbanasaurus
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Sapheosaurus_thiollerei
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2?????????

Sphenocondor
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10100??1

Sphenodon_punctatus
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2100000111

Sphenovipera
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1??10??1

Theretairus
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Toxolophosaurus
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?01??0

Zapatadon
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???????00

CAPPA/UFSM_0226
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00?00???

Sphenotitan
211101111??11?11111121220?10011231102001210012212111001?????122100
???0?0

Pelecymala
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???0??

Polysphenodon
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???1??

Fraserosphenodon_latidens
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?0????

Clevosaurus_convalis
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?00??0

Clevosaurus_bairdi
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Clevosaurus_petilus
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Clevosaurus_sp_SAM
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Priosphenodon_minimus
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Derasmosaurus
2011??00??0?0011111?????????????????????21???1?????????????2?0??????????0

Clevosaurus_sectumsemper
?????11??????????????0??0?????0?21?01?00?21101120201?01100?????2??0?00??0

Clevosaurus_mcgilli
20111111110100?00001212101010001?1?01?001211?10212?11011?0?????????002?0

Clevosaurus_wangi
1?111111110?00?00001202111??0001????011?1211?10??201?001?0?????????002?0

4. Additional plot of teeth

We include the teeth of *Lanceirosphenodon ferigoloi* in the data plotted by Jones (2009) for testing tooth shape. The data for *L. ferigoloi* includes the last posterior successional tooth (Lst), and the two last additional teeth (A5 and A6).
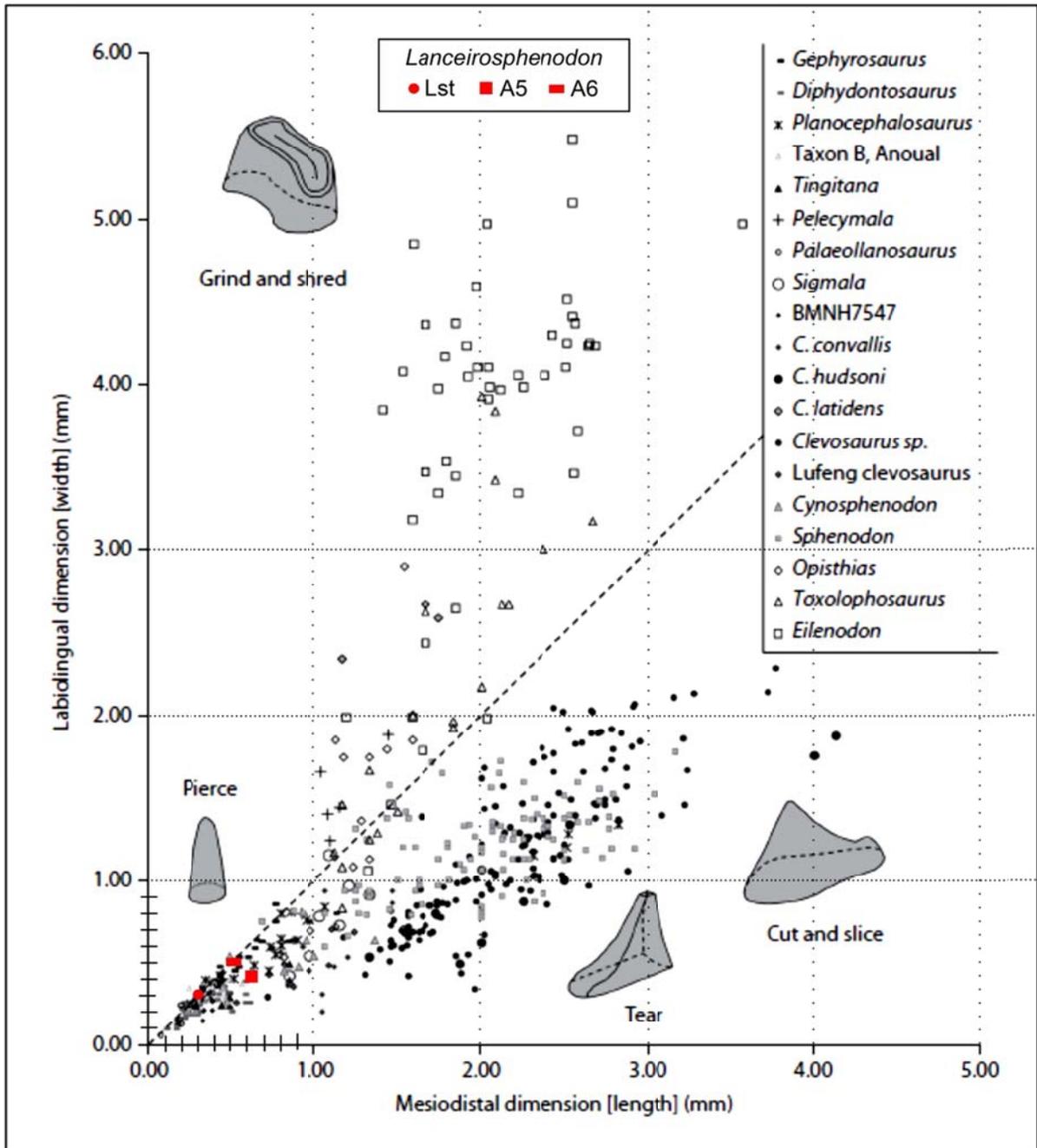
Figure S3. Dimensions of the dentary tooth base in Rhynchocephalia. Dashed line represents values of equal width and length. Diagrammatic representations of right dentary teeth in distolabial view are positioned near their respective data points. Taken and modified from Jones (2009).

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