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A new rhynchosaur maxillary tooth plate morphotype expands the disparity of the group in the Ischigualasto Formation (Late Triassic) of Northwestern Argentina

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ABSTRACT

Rhynchosaurs are a clade of quadruped, herbivorous stem-archosaur diapsids restricted to the Triassic Period. The group became globally distributed and the numerically dominant tetrapods of several terrestrial ecosystems before their extinction. Derived rhynchosaurs are characterized by a specialized masticatory apparatus, composed of a blade-and-groove occlusion with multiple longitudinal maxillary tooth rows. The morphology of the maxillary tooth plate has shown to be taxonomically and phylogenetically informative. So far, two rhynchosaur maxillary tooth plate morphotypes are known in Argentina, one belonging to an unnamed stenaulorhynchine from the Chañares Formation and the other to the hyperodapedontine *Hyperodapedon sanjuanensis*, the single rhynchosaur species currently name for the Ischigualasto Formation. Here we describe a new rhynchosaur maxillary tooth plate morphotype based on an indeterminate hyperodapedontine specimen from the Ischigualasto Formation. This maxillary tooth plate (PVL 2728) possesses a single longitudinal groove that divides symmetric lateral and medial tooth-bearing areas with relatively large tooth crowns, which is an uncommon combination of features among hyperodapedontines. These qualitative observations in addition to quantitative analyses show that the morphology of PVL 2728 differs from that of, at least, other sampled South American rhynchosaurs. Therefore, this specimen expands the morphological disparity of rhynchosaurs in northwest Argentina and southwestern Pangaea.
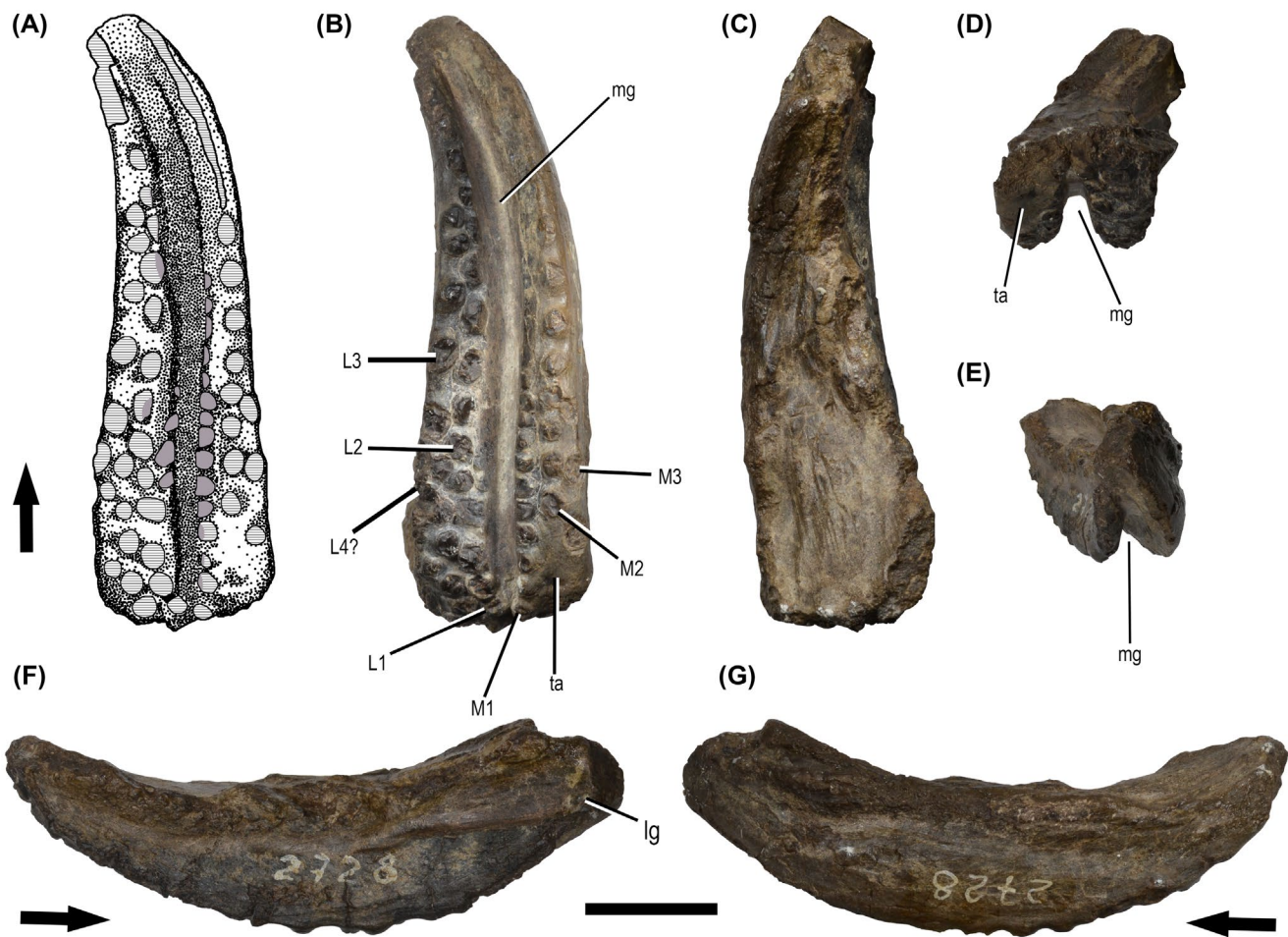
Introduction

Rhynchosaurs are a clade of early archosauromophs that lived during the Triassic Period and became globally distributed and very abundant during the Late Triassic (Romer 1963; Chatterjee 1969; Carroll 1976; Dilkes 1998; Ezcurra et al. 2016). Rhynchosaurs are found in all continents with the exception of Australasia and Antarctica (Ezcurra et al. 2016). Several rhynchosaur species have been reported in Middle-Upper Triassic rocks of Brazil and Argentina, namely *Brasinorhynchus mariantensis*, *Hyperodapedon huenei*, *Teyumbaita sulcognathus*, *Hyperodapedon mariensis*, and *H. sanjuanensis* (Tupí-Caldas 1933; Sill 1970; Langer and Schultz 2000a; Montefeltro et al. 2010; Schultz et al. 2016). In Argentina, rhynchosaurs are currently restricted to the Middle-Upper Chañares Formation (Ezcurra et al. 2014, 2017) and the Upper Triassic Ischigualasto Formation (Sill 1970), both units belonging to the Ischigualasto-Villa Unión Basin. The fossil record of the group is considerably richer in the younger Ischigualasto Formation, being represented by more than 400 specimens (Martínez et al. 2013) and *H. sanjuanensis* (Sill 1970) is the only nominal species currently known from this unit. However, there are some preliminary reports that indicate the possible presence of up to five different rhynchosaur species in the Ischigualasto Formation (Contreras 1981, 1997, 1999).

The maxillary tooth plates, which form part of the complex masticatory apparatus that characterise Middle and Late Triassic rhynchosaurs, are the remains most commonly preserved. This portion of the maxilla has been widely used by previous authors for taxonomy and as part of the character lists of phylogenetic analyses focused on rhynchosaurs (*e.g.* Chatterjee 1969; Benton 1983, 1990; Langer and Schultz 2000a; Langer et al. 2010; Montefeltro et al. 2010; Mukherjee and Ray 2014; Ezcurra et al. 2016; Gentil and Ezcurra 2017). Here we report on an isolated partial maxilla from the Ischigualasto Formation that possesses a morphology that differs from those of other South American rhynchosaur species, including the Argentinian species *H. sanjuanensis*, as well as probably other known rhynchosaurs worldwide. Therefore, this specimen expands the morphological disparity of rhynchosaurs, at least, in South America.

Materials and methods

PVL 2728 (Figure 1) was studied at first hand and mechanically reprepared with a widia tip under a binocular microscope. Measurements of this specimen and other 56 rhynchosaur maxillary tooth plates (Supplementary Information) were taken with a digital calliper with a maximum deviation of 0.02 mm, but values

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Figure 1. Hyperodapedontinae indeterminate (PVL 2728). **A**, Drawing of right maxilla in ventral view, and photographs of the same bone in **B**, ventral; **C**, dorsal; **D**, posterior; **E**, anterior; **F**, lateral; **G**, medial views. The arrows indicate anterior direction. Abbreviations: **L1–4**, first to fourth lateral tooth row; **M1–3**, first to third medial tooth row; **lg**, lateral groove; **mg**, main groove; **ta**, toothless area. Scale bar equals 20 mm.

were rounded to the nearest 0.1 millimetre, or were taken from the published literature. We used only complete measurements –widths at the posterior end of the tooth plate– and no measure was estimated based on other specimens. All these measurements belong to specimens of *Hyperodapedon gordoni*, *H. mariensis*, *H. sanjuanensis*, *Hyperodapedon tikiensis*, *Hyperodapedon huxleyi*, *H. huenei*, *Supradapedon stockleyi*, *H.* sp., *Isalorhynchus genovefae*, and *T. sulcognathus* (see Supplementary Information for the criteria used for taxonomic assignments). The measurements were normalized and transformed logarithmically following the protocol described by Lleonart et al. (2000) to remove information related to body size, including absolute size and allometric effects. We used a function written for R by Ezcurra and Butler (2014): supplementary information) to implement this normalization protocol. This function normalizes measurements following the equation of Lleonart et al. (2000) only if the results of the allometric regression are significant ($p < 0.05$); if not, it normalizes measurements by dividing them by the independent variable (here, the maximum width of the maxillary tooth plate). These measurements were included in bivariate and trivariate (ternary) graphics to generate morphospace plots of the hyperodapedontine tooth plates. The bivariate plot uses the widths of the lateral and medial tooth-bearing areas and the ternary plot also includes the maximum anteroposterior depth of the

largest occlusal tooth. Specimens with two longitudinal maxillary grooves were excluded from the ternary plot in order to focus the graphic in the morphospace occupied by specimens with a single longitudinal groove (e.g. PVL 2728). Specimens in which the largest tooth could not be measured were also excluded from this plot. These measurements were used to conduct T-tests to determine if the width of the lateral and medial tooth-bearing areas and anteroposterior depth of the largest tooth of PVL 2728 significantly differ from those of the other specimens with a single groove from the Ischigualasto and the Brazilian Santa Maria formations. In the case of having the measurements of maxillae from both sides of the same individual, we used the mean of both measurements for the statistical analyses in order to avoid dependency generated by measures taken from the same individual. The plots and statistical analyses were conducted in R (R Core Development Team 2008).

We follow previous authors who considered the lateral longitudinal groove of rhynchosaurs with two longitudinal grooves as homologous to the single longitudinal groove present in the maxillary tooth plate of several hyperodapedontine species (e.g. Chatterjee 1969, 1980; Benton 1983, 1984, 1990; Dilkes 1995; Langer and Schultz 2000a, 2000b; Langer et al. 2000; Nesbitt and Whatley 2004; Whatley 2005; Montefeltro et al. 2010; Gentil and Ezcurra 2017). The anatomical nomenclature for the description

of the arrangement of the maxillary tooth rows that flank the main groove follows that of Chatterjee (1974). Accordingly, the tooth rows laterally to the main groove are labelled as L1, L2, …, Ln, being L1 the row lying closer to the groove. Similarly, the rows that are medial to the main groove are labelled as M1, M2, …, Mn, being M1 the row lying closer to the groove.

Institutional abbreviations

EXEMS, Royal Albert Memorial Museum, Exeter, U.K.; **MACN-Pv**, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Colección Nacional de Paleovertebrados, Buenos Aires, Argentina; **MCN,** Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; **MCP**, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; **MCZ**, Museum of Comparative Zoology, Cambridge, U.S.A.; **NHMUK PV**, Natural History Museum, Palaeontology Vertebrates, London, U.K.; **PVL**, Paleontología de Vertebrados, Instituto Miguel Lillo, San Miguel de Tucumán, Argentina; **SAM-PK**, Iziko South African Museum, Cape Town, South Africa; **UFRGS**, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

SYSTEMATIC PALAEONTOLOGY

ARCHOSAUROMORPHA Huene, 1946
    RHYNCHOSAURIA Osborn, 1903
    RHYNCHOSAURIDAE Huxley, 1859
    HYPERODAPEDONTINAE Chatterjee, 1974
    Gen. et sp. indet.
    Figure 1

Material. PVL 2728, an isolated maxilla without the ascending process and the anterior tip of the bone (Figure 1).

Locality and horizon. Ischigualasto Formation, Agua de la Peña Group, Ischigualasto-Villa Unión Basin, upper Carnian–lowermost Norian (Martínez et al. 2011), Ischigualasto Provincial Park, San Juan Province, Argentina (Sill 1970). The precise geographic locality or stratigraphic level of PVL 2728 within the Ischigualasto Formation is unknown.

Results

General morphology

The maxilla PVL 2728 has a preserved length of 87.0 mm, but the anterior tip is broken (Figure 1), and a maximum width of 25.2 mm at its posterior end. The occlusal surface of the tooth plate is strongly convex ventrally (Figure 1(F, G)) and subtriangular (Figure 1(A, B)), tapering towards the anterior end, and strongly laterally curved in occlusal view (Figure 1(A–C)). The dorsal surface of the maxilla (Figure 1(C)) is concave, but severely damaged; therefore, the longitudinal groove for reception of the anterior process of the jugal is not preserved. The preserved lateral surface (Figure 1(F)) is also concave and seems to have been overprepared. This surface possesses a longitudinal, crescent groove that deepens anteriorly and is dorsal to the alveolar margin, as occurs in other hyperodapedontines (e.g. *Hyperodapedon sanjuanensis*: MACN-Pv 18185; *H. huenei*: UFRGS-PV-0132T; *H. mariensis*: MCN PV 1867). The posterolateral corner of the

maxilla expands slightly laterally (Figure 1(D)), resembling the laterally inflated surface that is laterally overlapped by the jugal in other hyperodapedontines (e.g. *Teyumbaita sulcognathus*: UFRGS-PV-0232T; *H. huenei*: UFRGS-PV-0132T). The preserved medial surface of the maxilla (Figure 1(G)) is convex and smooth. A shallow, longitudinal groove occurs around the mid-length of the bone. However, it is not clear if this feature is a result of overpreparation.

The occlusal surface of the maxilla is subdivided by a single, deep longitudinal groove (=main groove) that runs along all the preserved occlusal surface, dividing it into medial and lateral tooth-bearing areas, as occurs in *Su. stockleyi* (SAM-PK-11704; Boonstra 1953; Langer et al. 2017), *H. huxleyi* (Chatterjee 1974), *H. gordoni* (Benton 1983), *H. sanjuanensis* (Sill 1970; Gentil and Ezcurra 2017), *H. mariensis* (MCN PV1867), some specimens of *H. tikiensis* (Mukherjee and Ray 2014), and *I. genovefae* (Buffetaut 1983) (Figure 2(B–H)). By contrast, *Stenaulorynchus stockleyi* (NHMUK PV R9275, R9276, R9278–R9281), *Brasinorhynchus mariantensis* (Schultz et al. 2016), *Mesodapedon kuttyi* (Chatterjee 1980), *Fodonyx spenceri* (EXEMS 60/1985.292), and the hyperodapedontines *H. huenei* (Langer and Schultz 2000a) (Figure 2(I)) and *T. sulcognathus* (Montefeltro et al. 2010) (Figure 2(J)) possess two longitudinal grooves that define three tooth-bearing areas. The main groove of PVL 2728 reaches its maximum depth around the mid-length of the tooth plate and shallows towards the anterior and posterior ends. The main groove becomes slightly transversely broader towards the anterior end of the bone (Figure 1(A, B)), resembling the condition of most hyperodapedontines (Chatterjee 1974; Langer and Schultz 2000a; Montefeltro et al. 2010; Mukherjee and Ray 2014; MCP-PV-4104; SAM-PK 11704; MACN-Pv 18185).

The lateral and medial tooth-bearing areas of PVL 2728 are cushion-shaped, as occurs in most hyperodapedontines (Langer and Schultz 2000a), with the exception of the crest-shaped lateral tooth-bearing area of *T. sulcognathus* (Montefeltro et al. 2010) and the lateral and medial tooth-bearing areas of the *Hyperodapedon* from Nova Scotia (Langer et al. 2017). The lateral and medial tooth-bearing areas of PVL 2728 have maximum widths of 11.8 and 11.7 mm, respectively. This strong degree of symmetry between the lateral and medial tooth-bearing areas (<0.4% of the total width of the tooth plate) is not common among hyperodapedontines, but it also occurs in an indeterminate *Hyperodapedon* specimen from southern Brazil (UFRGS-PV-0324T) and a referred specimen of *H. gordoni* (Benton 1983: NUGD B) (Figure 2(E)). A sub-symmetry between the widths of both tooth-bearing areas (differences between 1−2 mm) occurs in other specimens of *H. gordoni* (Benton 1983: NUGD A, EM 1926.6), a referred specimen of *I. genovefae* (Langer and Schultz 2000a: MAL-1996 4), and a referred specimen of *H. tikiensis* (Mukherjee and Ray 2014: IITKGPR35). The other studied and measured hyperodapedontine maxillae with one main groove possess a lateral tooth-bearing area distinctly wider than the medial one (e.g. *H. mariensis*: MCN PV1867, UFRGS-PV-0149T; *H. sanjuanensis*: MACN-Pv 18185; *H. huxleyi*: ISIR 17; *Su. stockleyi*: Langer et al. 2017; *H*. sp. from the Ischigualasto Formation: MACN-Pv 18526b, 20065) (Figure 2(B–D)). By contrast, the widest tooth-bearing area is always the medial one in rhynchosaurs
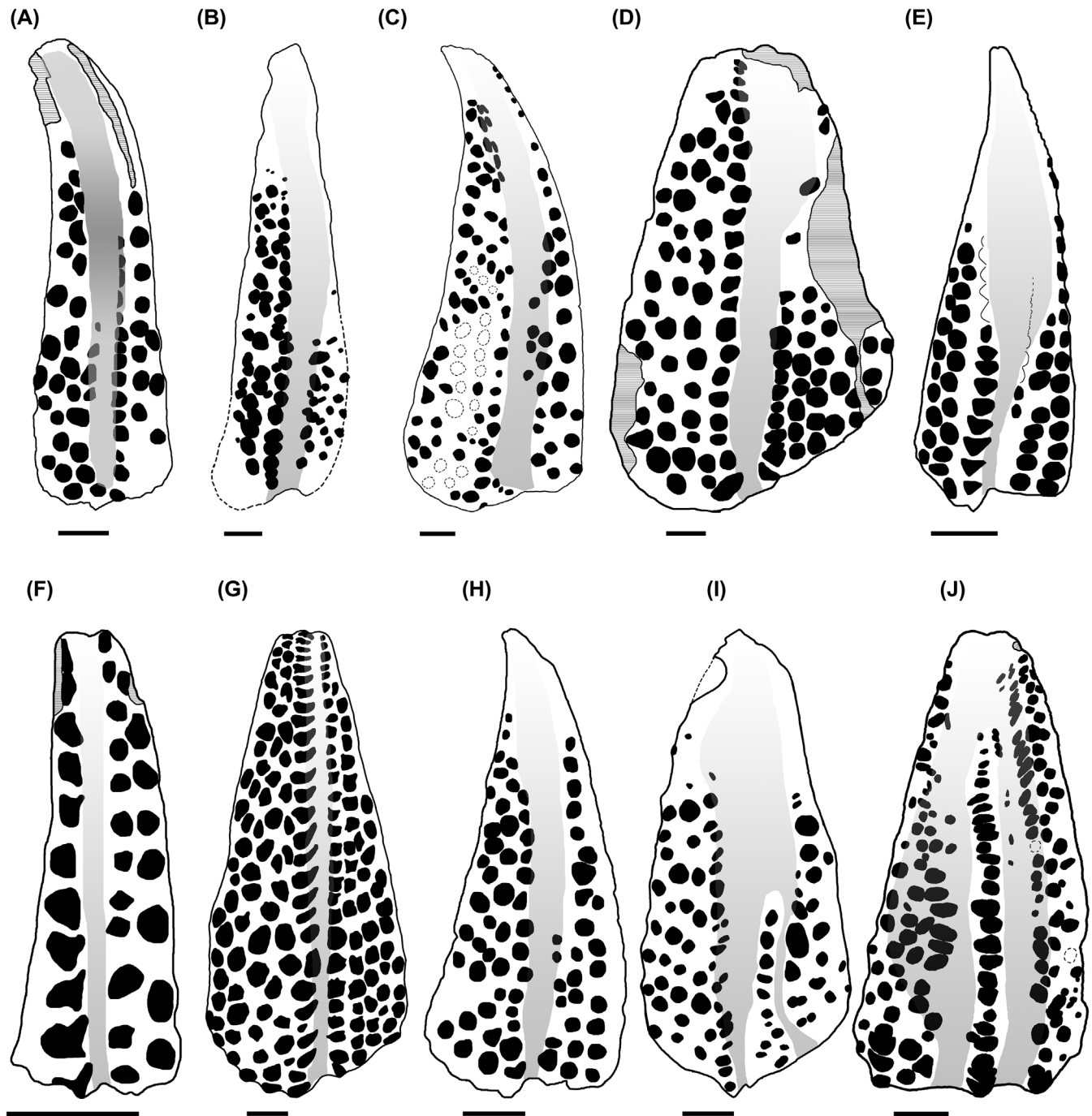
Figure 2. Schematic drawings of the maxillary tooth plate of Late Triassic hyperodapedontine rhynchosaurs. **A**, PVL 2728; **B**, *Hyperodapedon sanjuanensis* (MACN-Pv 18185, holotype); **C**, *Hyperodapedon mariensis* (UFRGS-PV-0408T, reversed); **D**, *Supradapedon stockleyi* (redrawn from Langer et al. 2017; SAM 11704, holotype, reversed); **E**, *Hyperodapedon gordoni* (redrawn from Benton 1983; NUGD B, reversed); **F,** *Isolarhynchus genovefae* (redrawn from Langer et al. 2000; MDE-R18, holotype, reversed); **G**, *Hyperodapedon huxleyi* (redrawn from Chatterjee 1974; ISIR 17); **H,** *Hyperodapedon tikiensis* morphotype 1 (redrawn from Mukherjee and Ray 2014, IITKGPR36, holotype, reversed); **I**, *Hyperodapedon huenei* (UFRGS-PV-0132T, holotype); and **J,** *Teyumbaita sulcognathus* (UFRGS-PV-0298T). Scale bars equal 10 mm.

with two maxillary grooves (e.g. *H. huenei*: Langer and Schultz 2000a; *T. sucolgnathus*: Montefeltro et al. 2010) (Figure 2(I, J)).

Two types of tooth crowns are identified in the posterior region of the tooth plates –in unworn teeth– of Late Triassic rhynchosaurs, anteroposteriorly compressed pyramidal crowns with an elliptical cross-section section and conical crowns with a circular cross-section (Chatterjee 1974; Benton 1984; Langer and Schultz 2000a; Mukherjee and Ray 2014). The very base of the tooth crowns of PVL 2728 is circular in cross-section, but the rest of the crowns are missing or heavily worn (Figure 1(A,

B)). As a result, it cannot be determined if the tooth crowns were pyramidal or conical. All the teeth have a similar diameter at the base of the crowns, with a maximum anteroposterior diameter of 4.2 mm, and they are widely spaced from each other, resembling the condition in *I. genovefae* (Whatley 2005), *Su. stockleyi* (SAM-PK-11704), and *H. sanjuanensis* (PVL 3432). The lateral tooth-bearing area of PVL 2728 possesses three clear longitudinal tooth rows and a putative fourth one (Figure 1(B)). The tooth crowns of L1 are heavily worn to their base and to the level of the bone surface on the lateral wall of the main groove. These

worn crowns can be seen in the posterior half of the tooth plate (Figure 1(A)). The most posterior tooth crown of L1 is placed immediately posterolaterally to the main groove and approximately to the same level of the most posterior tooth of L2. L2 is the longest row, starting from the posterior margin of the lateral tooth-bearing area and extending anteriorly immediately before the broken margin of the tooth plate. Most of the tooth crowns of this row are not heavily worn, with the exception of the crowns of the middle region, which possess an extensive lingual wear facet where the main groove is deeper. The broadest teeth of L2 are placed in the posterior third of the row, whereas the size of the teeth is similar in the posterior region of the three lateral longitudinal rows. L3 is the most lateral distinct row on the occlusal surface; its posterior end is placed anterior to that of L1 and L2 and L3 extends anteriorly beyond L1. Anteriorly, the crowns of L3 are slightly smaller than those of L2 at the same level, and are also the most complete, preserving their conical base. Some fragments of a possible tooth crown on the transition between the occlusal and lateral surfaces may indicate the presence of an anteroposteriorly short L4 (Figure 1(A, B)).

The medial tooth-bearing area has also three longitudinal tooth rows. The teeth of M1 are slightly smaller than those of the lateral tooth-bearing area. M1 extends along the posterior two-thirds of the tooth plate, with the most posterior tooth placed posteromedially to the posterior end of the main grove. The tooth crowns of M1, with exception of the most posterior tooth, are heavily worn on their medial surface, showing an extensive and planar wear facet. The most anterior tooth crowns of M1 are worn to their base, being restricted to the medial wall of the main groove. M2 extends considerably more anteriorly than M1 and posteriorly it is placed 10 mm anterior to the posterior margin of the plate. The complete anterior extension of M2 cannot be determined because the occlusal surface of the anterior portion of the medial tooth-bearing area is damaged. M3 is the most medial tooth row and is restricted to the posterior third of the occlusal surface of the bone, being only composed of three well-spaced teeth. The most posterior tooth of M3 is placed posterior to the end of M2, but rather anterior to the posterior margin of the maxillary tooth plate and M1. This region between the posterior margin of the tooth plate and the beginning of M2 and M3 is edentulous and it is not a preservational artefact because this area is well preserved, not covered with sediment, and without signs of wear. This condition differs from that of other hyperodapedontine specimens studied by us, but it is reminiscent to an edentulous area on the posterior end of the medial tooth-bearing area of a large maxilla referred to *I. genovefae* (Whatley 2005: Figure 1–3(f)). The medial surface of the maxilla, immediately above the alveolar margin, is complete and lacks lingual teeth.

The diameter of the maxillary teeth is proportionally large, resembling the condition in non-stenaulorhynchine rhynchosaurids (Schultz et al. 2016), such as *Rhynchosaurus articeps* (NHMUK PV R1236), *F. spenceri* (EXEMS 60/1985.292), *I. genovefae* (Langer and Schultz 2000a; MDE-R18), and other hyperodapedontine rhynchosaurs (Benton 1984; Schultz et al. 2016). Despite *H. sanjuanensis*, *H. mariensis*, and *H. gordoni* have also proportionally large teeth, they are proportionally smaller than those of PVL 2728 (see below).

Quantitative analysis

The bivariate plot (medial versus lateral tooth-bearing area widths) (Figure 3(A)) shows a clear distinction in both axes between hyperodapedontines with two longitudinal grooves (i.e. *T. sulcognathus* [yellow dots], *H. huenei* [orange dots],
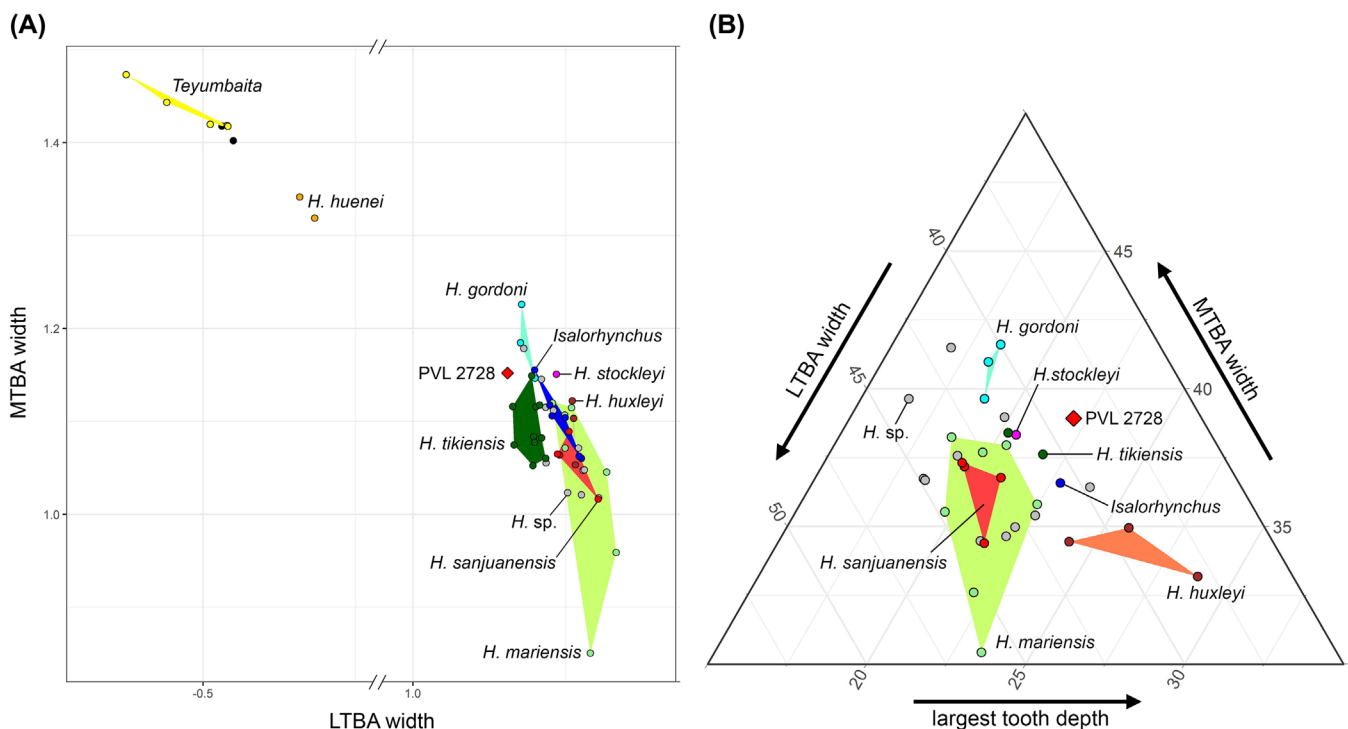
Figure 3. Morphospace of hyperodapedontine rhynchosaur tooth plates. A, Bivariate plot of the medial versus lateral tooth-bearing area widths; and **B**, ternary plot of the medial and lateral tooth-bearing area widths and largest tooth anteroposterior depth.

and indeterminate hyperodapedontines from the Ischigualasto Formation [black dots]; left upper quadrant of the plot) and those with a single longitudinal groove in the maxillary tooth plate (right inferior quadrant of the plot). Within the latter group, *H. mariensis* occupies the largest area of morphospace (light green area) and the sampled specimens of *H. sanjuanensis* are restricted within this area (Figure 3(A): red area). The morphospaces of *I. genovefae* (Figure 3(A): dark blue area) and *H. huxleyi* (Figure 3(A): brown dots) partially overlap that of *H. mariensis*, whereas the morphospaces of *H. gordoni* (Figure 3(A): light blue area) and *H. tikiensis* (Figure 3(A): dark green area) do not overlap it. The maxillae referred to *H.* sp. (Figure 3(A): grey dots) are distributed within or very close to the morphospaces of *H. mariensis*, *H. sanjuanensis*, *H. tikiensis*, *H. gordoni*, and *I. genovefae*. *Supradapedon stockleyi* (Figure 3(A): magenta dot) and PVL 2728 (Figure 3(A): red rhomb) occur in a region of the morphospace close to, but well separated from, that occupied by the above mentioned species and specimens.

The ternary plot (medial and lateral tooth-bearing area widths, and largest tooth anteroposterior depth) (Figure 3(B)) show a further distinction between the hyperodapedontine species with a single longitudinal groove. As occurred in the bivariate plot, the area occupied by the sampled specimens of *H. sanjuanensis* is restricted within the morphospace of *H. mariensis*. The morphospaces of *H. huxleyi*, *H. gordoni*, and *I. genovefae* are rather well-separated from each other as well as from that of *H. mariensis*. One of the plotted specimens of *H. tikiensis* and the holotype of *Su. stockleyi* are placed close to each other and to the edge of the morphospace of *H. mariensis*. The specimens referred to *H.* sp. are widely distributed in the morphospace and several of them occur within the morphospace of *H. mariensis*. PVL 2728 lies in a region of the morphospace not occupied by hyperodapedontine species or other indeterminate specimens and differs from them in the width of the lateral tooth-bearing area and size of the largest tooth crown.

The *T*-tests found significant differences in the widths of the lateral and medial maxillary tooth-bearing areas and the anteroposterior depth of the largest tooth crown of PVL 2728 with those of the other specimens from the Ischigualasto Formation and from all South America (i.e. the Ischigualasto and Santa Maria formations), respectively ($p < 0.001$). By contrast, there were not significant differences among any of the three variables between specimens of *H. sanjuanensis* and *H. mariensis* ($p > 0.1$).

Discussion

The quantitative analyses conducted here reinforce the idea that the dental morphology of hyperodapedontine rhynchosaurs allows distinguishing several species from others, as is the case between *H. mariensis*, *H. huxleyi*, and *H. gordoni*, and bolsters its importance in hyperodapedontine taxonomy (e.g. Benton 1983; Langer and Schultz 2000a; Montefeltro et al. 2013; Mukherjee and Ray 2014; Gentil and Ezcurra 2017). However, our morphospace plots also show that the South American species *H. sanjuanensis* and *H. mariensis* possess a very similar maxillary dental anatomy to each other (Figure 3) –at least for the combination of variables sampled here–. This result agrees with the conclusion of Gentil and Ezcurra (2017), based on qualitative observations, that these two species cannot be distinguished from each other

based on isolated maxillary tooth plates. Similarly, the holotype of *Su. stockleyi* falls in a region of the morphospace very close to that of a specimen of *H. tikiensis*. These similitudes in the maxillary tooth plates may be phylogenetically informative and would be interesting to include them as continuous characters in future phylogenetic analyses.

The qualitative and quantitative comparisons –based on both graphical and statistical evidences– indicate that the maxilla PVL 2728 from the Ischigualasto Formation can be distinguished from other rhynchosaurs based on its dental morphology. There is currently a single named rhynchosaur species in the Ischigualasto Formation –*Hyperodapedon sanjuanensis*– (Sill 1970), but Contreras (1981, 1993, 1997, 1999) reported up to four other possible species, but without collection numbers, that may occur in this unit, namely '*Scaphonyx fisheri*', pug-nosed rhynchosaur, *Hyperodapedon* sp. cf. *H. gordoni*, and ? '*Scaphonyx*' *sulcognathus* (Contreras 1997, 1999). PVL 2728 differs from *H. sanjuanensis* and the '*Scaphonyx fisheri*' reported by Contreras (1997) in the presence of a centrally placed longitudinal groove, and also from the former species in its proportionally bigger teeth (Figure 3). The new specimen described here can be distinguished from the pug-nosed rhynchosaur of Ischigualasto (sensu Contreras 1997) in the presence of a proportionally narrower tooth plate and from the putative ? '*Scaphonyx*' *sulcognathus* of the same formation (sensu Contreras 1997) in the absence of two maxillary longitudinal grooves (Contreras 1993). Finally, the morphology of PVL 2728 is consistent with that briefly described for the *Hyperodapedon* sp. cf. *H. gordoni* of the Ischigualasto Formation (sensu Contreras 1997, 1999), but because of the absence of detailed information about the latter form we cannot determine if they belong to the same species.

The position in the morphospace of PVL 2728 departs from that of other hyperodapedontines, including several specimens sampled in the Late Triassic of southern Brazil (*H. mariensis* and *H.* sp.) and outside South America (e.g. *H. gordoni*). During the transformation and normalization of the complete data-set (i.e. tooth plates with one and two grooves) it was found that the size of the largest maxillary tooth has a very strong negative allometry (allometric coefficient = 0.2699), though only marginally significant and with a low proportion of predictable variance ($R^2 = 0.095$, $p = 0.0464$), with respect to the maximum width of the tooth plate. Conversely, the widths of the lateral and medial tooth-bearing areas of the maxillary tooth plates with a single groove were significantly correlated with the maximum width of the bone (lateral: $R^2 = 0.9117$, $p < 0.0001$; medial: $R^2 = 0.8325$, $p < 0.0001$), but with allometric coefficients close to 1 –isometric growth– (lateral = 0.9466, medial = 0.9557). As a result, it seems that the observed differences between PVL 2728 and other South American rhynchosaurs are not a consequence of ontogenic variation because the data was normalized using these allometric components and therefore at least most of the absolute size and allometric effects were removed (Lleonart et al. 2000).

Our results indicate that PVL 2728 increases the morphological disparity of the rhynchosaur tooth plates of South America and probably also for the group as a whole. This specimen sheds light on the poorly known Argentinian rhynchosaur assemblage and bolsters previous claims of a high rhynchosaur species richness in the Ischigualasto Formation (Contreras 1981, 1993, 1999). Although we have evidence that PVL 2728 may represent

a distinct rhynchosaur taxon (with the possible exception of the briefly reported *Hyperodapedon* sp. cf. *H. gordoni* of the Ischigualasto Formation sensu Contreras 1997, 1999) we refrain of erecting a new species based on this specimen because of its fragmentary condition. A new species based on such fragmentary specimen would complicate future taxonomic assignments of new specimens to this or other morphotypes if there are no available overlapping bones with PVL 2728.

Disclosure statement

No potential conflict of interest was reported by the authors.

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