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RECONSTRUCTION OF THE MASTICATORY APPARATUS OF THE HOLOTYPE OF THE RHYNCHOSAUR *HYPERODAPEDON SANJUANENSIS* FROM THE LATE TRIASSIC OF ARGENTINA: IMPLICATIONS FOR THE DIAGNOSIS OF THE SPECIES

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Abstract. Rhynchosaurs are a clade of robust, quadruped, and herbivorous stem-archosauromorph diapsids restricted to the Triassic Period. Most species have a specialized masticatory apparatus composed of a blade-and-groove occlusion and multiple longitudinal tooth rows. Rhynchosaurs are the most numerically abundant tetrapods of the Upper Triassic Ischigualasto Formation of NW Argentina. However, there is currently a single nominal species, *Hyperodapedon sanjuanensis*, described for this unit and the entire country. Though the dental morphology constitutes one of the most important sources of taxonomic and phylogenetic information of the group, this anatomical region remains undescribed in the holotype of *Hyperodapedon sanjuanensis*. The full occlusion of the skull and lower jaw obscures most of the morphology of the masticatory apparatus in this specimen. Here we present the first description of the maxillary tooth plate and dentary dentition of this specimen based on CT scan data and a three-dimensional rendering. The maxillary tooth plate of the holotype of *Hyperodapedon sanjuanensis* possesses two tooth-bearing areas that are separated by a single longitudinal groove. The lateral tooth-bearing area of the maxilla is wider than the medial one. The dentary possesses a single cutting blade and tooth row. Both maxilla and dentary lack lingual dentition. The information gathered here was used to emend the diagnosis of the species, review the taxonomy of some specimens, and check the dental scorings for *Hyperodapedon sanjuanensis*—based on the morphology of the holotype—in three independent phylogenetic data sets.

Key words. Archosauromorpha. Rhynchosauria. Ischigualasto Formation. Dentition. CT scan.

Resumen. RECONSTRUCCIÓN DEL APARATO MASTICATORIO DEL HOLOTIPO DEL RINCOSAURIO *HYPERODAPEDON SANJUANENSIS* DEL TRIÁSICO TARDÍO DE ARGENTINA: IMPLICANCIAS PARA LA DIAGNOSIS DE LA ESPECIE. Los rincosaurios son un clado de diápsidos stem-arcosauromorfos robustos, cuadrúpedos y herbívoros restringidos al Período Triásico. La mayoría de las especies tienen un aparato masticatorio especializado compuesto por una oclusión del tipo "hoja-y-surco" y numerosas hileras dentarias longitudinales. Los rincosaurios son los tetrápodos más abundantes numéricamente de la Formación Ischigualasto del Triásico Superior del noroeste argentino. Sin embargo, actualmente hay una sola especie nominal, *Hyperodapedon sanjuanensis*, descrita para esta unidad y todo el país. A pesar que la morfología dentaria constituye una de las fuentes de información taxonómica y filogenética más importantes para el grupo, esta región anatómica no ha sido descrita en el holotipo de *Hyperodapedon sanjuanensis*. La oclusión completa del cráneo y la mandíbula oculta la mayor parte de la morfología del aparato masticatorio de este espécimen. Aquí presentamos la primera descripción de la placa dentaria maxilar y dentición del dentario del holotipo de *Hyperodapedon sanjuanensis* basada en una tomografía computada y una reconstrucción tridimensional. La placa dentaria maxilar posee dos áreas portadoras de dientes separadas por un único surco longitudinal, siendo la lateral más ancha que la medial. El dentario posee una única hoja cortante e hilera de dientes. El maxilar y dentario carecen de dientes linguales. La información recuperada aquí permitió emendar la diagnosis de la especie, revisar la taxonomía de algunos especímenes y chequear las codificaciones dentarias para *Hyperodapedon sanjuanensis*—basada en la morfología del holotipo—en tres conjuntos de datos filogenéticos independientes.

Palabras clave. Archosauromorpha. Rhynchosauria. Formación Ischigualasto. Dentición. Tomografía computada.

RHYNCHOSAURS are a clade of robust, quadruped, and herbivorous stem-archosauromorph diapsids restricted to the Triassic Period. The earliest members of the group are recorded in the lower most Triassic rocks of South Africa and subsequently become more globally distributed and taxonomically and numerically abundant, especially during

the early Late Triassic (Romer, 1963; Chatterjee, 1969; Carroll, 1976; Dilkes, 1998; Ezcurra *et al.*, 2016). Indeed, rhynchosaurs were the most abundant tetrapods in several continental ecosystems during these times (Romer, 1963; Langer, 2005; Martínez *et al.*, 2013). Rhynchosaurs acquired a unique cranial architecture among diapsids during their evolutionary history, with a broader than long subtriangular skull in dorsal view that possesses a downturned beak formed by highly modified edentulous premaxillae, and a blade-and-groove occlusion between the maxilla and dentary. The masticatory apparatus of rhynchosaurids is clearly distinct from that of other archosauromorphs, which is composed of multiple tooth rows that were added continuously during life on the occlusal surface and generally also on the lingual surface of the maxilla and dentary (Benton, 1984).

Rhynchosaurs have been recorded in all current continents except Asia (excluding India), Australia, and Antarctica (Ezcurra *et al.*, 2016). In particular, the Argentinean fossil record of the group is restricted to the uppermost Ladinian–lower Carnian Chañares (Marsicano *et al.*, 2016; Ezcurra *et al.*, 2017) and the upper Carnian–lowermost Norian Ischigualasto (Martínez *et al.*, 2011) formations of the Ischigualasto-Villa Unión Basin (Sill, 1970; Contreras, 1981; Ezcurra *et al.*, 2014, 2017). The rhynchosaur remains of the Chañares Formation are based on cranial and postcranial bones of a stenaulorhynchine rhynchosaurid (Ezcurra *et al.*, 2014, 2017). By contrast, 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). *Hyperodapedon sanjuanensis* (Sill, 1970) is the only nominal species currently known from this unit, but preliminary reports indicated the possible presence of a total of five rhynchosaur species in the Ischigualasto Formation (Contreras, 1981, 1993, 1999).

The dental morphology of rhynchosaurs has been broadly used in the diagnosis of species, as phylogenetically informative characters, and to explore broader macroevolutionary trends (*e.g.*, Chatterjee, 1974; Benton, 1983, 1990; Langer *et al.*, 2000a, b; Montefeltro *et al.*, 2010; Mukherjee and Ray, 2014; Ezcurra *et al.*, 2016). However, despite of its importance, the dental morphology of the holotype of *H. sanjuanensis* (MACN-Pv 18185) is currently fairly unknown (Fig. 1). Sill (1970, p. 350) described very briefly the maxillary tooth plate of *H. sanjuanensis*—based on a referred specimen—as "*triangular, with an anteriorly directed apex, and divided asymmetrically by a groove*", and he did not provide any information about the dental anatomy of the lower jaw. The dental anatomy of MACN-Pv 18185 is mostly obscured by the full occlusion of the skull and lower jaw, and the close blade-and-groove occlusion does not allow further mechanical preparation without compromising the specimen. Therefore, our aim is to describe for the first time the masticatory apparatus of MACN-Pv 18185, mainly based on the information gathered from a computed tomography (CT) scan. Here, this data is used to revise the original diagnosis of *H. sanjuanensis* and the taxonomy of some historically collected specimens of the Ischigualasto Formation, and discuss phylogenetically informative dental characters in the holotype of this species.

Institutional abbreviations. **EXEMS,** Royal Albert Memorial Museum, Exeter, UK; **ISI,** Indian Statistical Institute, Kolkata, India; **MACN-Pv,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Paleovertebrados, Ciudad Autónoma de Buenos Aires, Argentina; **MCN,** Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; **MCZ,** Museum of Comparative Zoology, Cambridge, USA; **NHMUK PV,** Natural History Museum, Palaeontology Vertebrates, London, UK; **PVL,** Paleontología de Vertebrados 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; **WARMS,** Warwickshire Museum, Warwick, UK.

MATERIALS AND METHODS

The holotype of *Hyperodapedon sanjuanensis* (MACN-Pv 18185) was studied at first hand and a CT scan was conducted in the Clínica La Sagrada Familia (Buenos Aires) using a 64-channel axial medical computed tomograph. The scan resulted in 302 DICOM images (slice intervals= 1.25 mm) that were processed using the software 3D Slicer version 4.7 (Fedorov *et al.*, 2012).

We agree with previous authors in considering 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; Ben-

ton, 1983, 1984, 1990; Dilkes, 1995; Langer and Schultz, 2000a, b; Langer *et al.*, 2000a; Nesbitt and Whatley, 2004; Whatley, 2005; Montefeltro *et al.*, 2010). 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.

The dental morphology of the holotype of *H. sanjuanensis* was compared with that of some isolated maxillae (MACN-Pv 18526a, b; MCZ 3618–3620) and a partial skull (PVL 3432) from the Ischigualasto Formation that were available here for comparison. In particular, two of these specimens (MCZ 3618—Sill, 1970: plate III e, but mistakenly quoted in that contribution as MCZ 3619—and PVL 3432) were considered as referred specimens of *H. sanjuanensis* by Sill (1970). The isolated maxillae are hereafter quoted as "*Hyperodapedon* sp. from the Ischigualasto Formation" (see Discussion).

SYSTEMATIC PALEONTOLOGY

ARCHOSAUROMORPHA von Huene, 1946
RHYNCHOSAURIA Osborn, 1903
RHYNCHOSAURIDAE Huxley, 1859
HYPERODAPEDONTINAE Chatterjee, 1974

Hyperodapedon Huxley, 1859

Type species. *Hyperodapedon gordoni* Huxley, 1859.

Hyperodapedon sanjuanensis (Sill, 1970)
= "*Scaphonyx*" *sanjuanensis* Sill, 1970
Figures 1–3

Holotype. MACN-Pv 18185, partial skeleton that includes a fairly complete skull—partially reconstructed with plaster—and lower jaw (Figs. 1–3), presacral and sacral vertebral series, probably the first two caudal vertebrae, and partial pectoral and pelvic girdles, and fore- and hindlimbs.

Type 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). This specimen was collected in 1958 during a joined fieldwork conducted by the Museo Argentino de Ciencias Naturales (Buenos Aires) and the University of Harvard (Boston). Sill (1970) did not inform the precise geographic locality or stratigraphic level of MACN-Pv 18185. An intensive sampling conducted in the last decades showed that rhynchosaurs are stratigraphically restricted to the lower half (*Scaphonyx-Exaeretodon-Herrerasaurus* biozone *sensu* Martínez *et al.*, 2011) of the Ischigualasto Formation—La Peña, Cancha de Bochas, and lower Agua de la Peña members (Martínez *et al.*, 2013). As a result, it is likely that the holotype of *Hyperodapedon sanjuanensis* comes from one of these members.

Emended diagnosis. *Hyperodapedon sanjuanensis* is a rhynchosaur that differs from other hyperodapedontines in the following unique combination of dental character-states observable in the holotype (autapomorphies are indicated with an asterisk): maxillary tooth plate with a single longitudinal groove (two grooves are present in *Teyumbaita sulcognathus* (Azevedo and Schultz, 1987), *Hyperodapedon huenei* Langer and Schultz, 2000a, some specimens of *Hyperodapedon tikiensis* Mukherjee and Ray, 2014, and an unnamed form from Ischigualasto preliminary reported by Contreras [1981]) that divides a lateral tooth-bearing area distinctly broader than a medial area (medial area broader or subequal to the lateral area in *T. sulcognathus*, *H. huenei*, *Hyperodapedon gordoni* Huxley, 1859, *Hyperodapedon stockleyi* (Boonstra 1953), and the unnamed form from Ischigualasto), with a cushion-shaped lateral tooth-bearing area (crest-shaped lateral tooth-bearing area in *T. sulcognathus* and apparently *H. tikiensis sensu* Mukherjee and Ray [2014]), and without lingual teeth (maxillary lingual teeth present in *T. sulcognathus* and *H. huenei*); dentary with a single longitudinal cutting blade bearing one tooth row (two cutting blades are present in *T. sulcognathus* and the unnamed form from Ischigualasto) and without lingual teeth* (lingual teeth are present in the dentary of other rhynchosaurid rhynchosaurs, including *T. sulcognathus*, *H. huenei*, *H. gordoni*, *H. tikiensis*, *Hyperodapedon huxleyi* (Chatterjee, 1974), *Hyperodapedon mariensis* (Tupi-Caldas, 1933), and the unnamed form from Ischigualasto).

Nomenclatural note. Martínez *et al.* (2013) claimed that

Langer and Schultz (2000a) combined "*Scaphonyx fischeri*" from Brazil and "*S.*" *sanjuanensis* from Argentina as the new combination *H. sanjuanensis*. Martínez *et al.* (2013) decided to not follow this nomenclatural change because they did not accept such hypothesis of synonym. However, this new combination was not a result of a synonym but a consequence of considering "*S. fischeri*" a *nomen dubium* because the holotype of the species, which is composed of a cervical and a dorsal centrum and a pedal digit with four phalanges and a pedal ungual (Woodward, 1908), is not diagnostic (Langer, 1996, 1998; Langer and Schultz, 2000a). "*Scaphonyx fischeri*" is the type species of the genus and, as a result, "*Scaphonyx*" is invalid. Langer and Schultz (2000a, b) found "*S.*" *sanjuanensis* as deeply nested within the genus *Hyperodapedon* and, as a result, they propose the new combination *H. sanjuanensis*. Therefore, the latter taxonomic nomenclature is followed here.

RESULTS

The description of the dental morphology of the holotype of *Hyperodapedon sanjuanensis* (MACN-Pv 18185) is mainly based on a volume rendering generated from the CT scan and complemented with observations on the actual specimen. The quality of the CT scan is good enough to digitally disarticulate the skull from the lower jaw and reconstruct most of the maxillary tooth plate and lower jaw dentition of the specimen (Figs. 2–3), but not for the detailed description of subtle details. Thus, the condition of

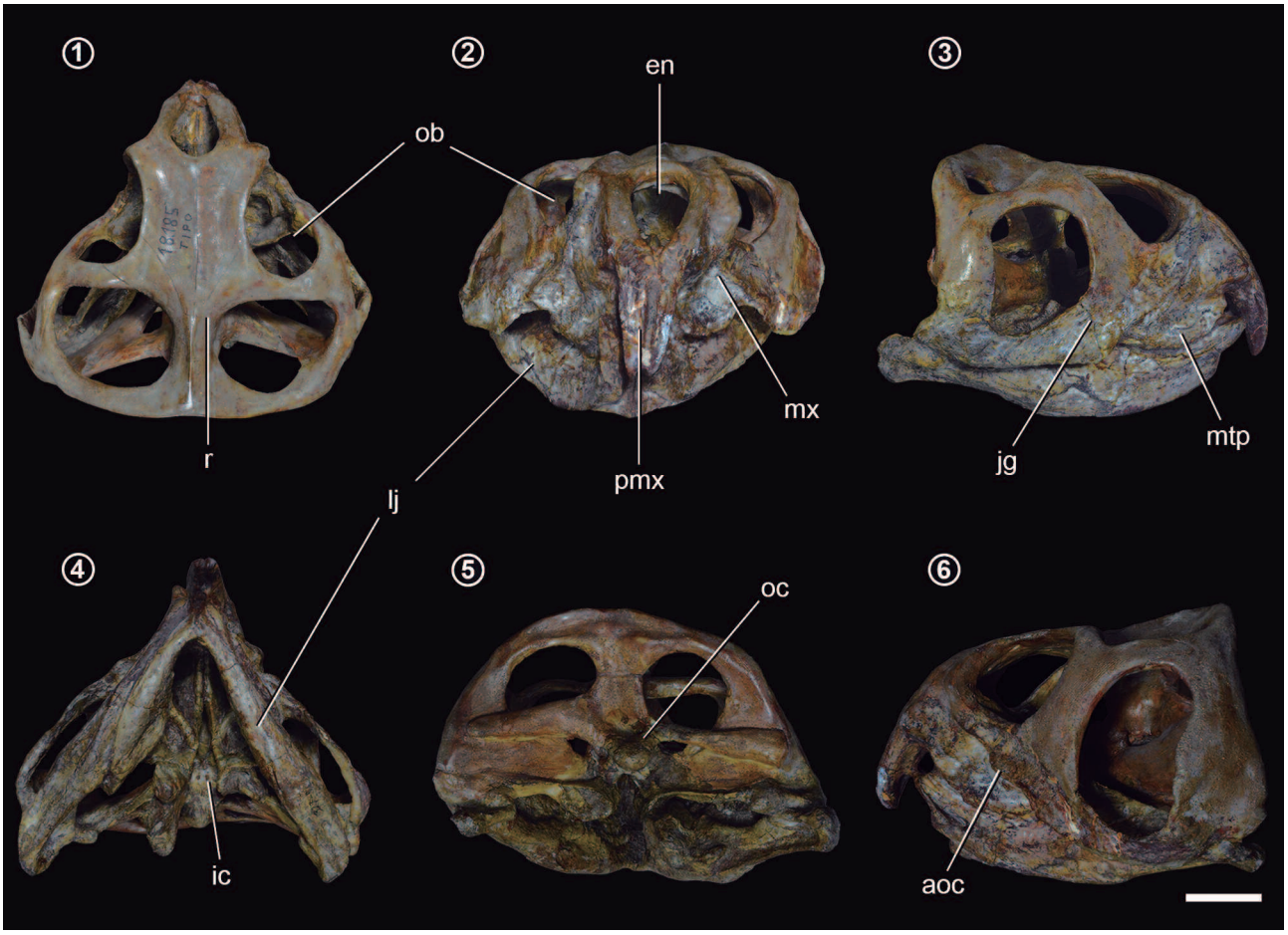

Figure 1. Skull of the holotype of ***Hyperodapedon sanjuanensis*, MACN-Pv** 18185. **1,** Dorsal view; **2,** anterior view; **3,** right lateral view; **4,** ventral view; **5,** posterior view; **6,** left lateral view. Abbreviations: **aoc,** anguli oris crest; **en,** external naris; **ic,** passage of internal carotids; **jg,** jugal; **lj,** lower jaw; **mtp,** maxillary tooth plate, **mx,** maxilla; **ob,** orbit; **oc,** occipital condyle; **pmx,** premaxilla; **r,** reconstructed area. Scale bar= 5 cm.

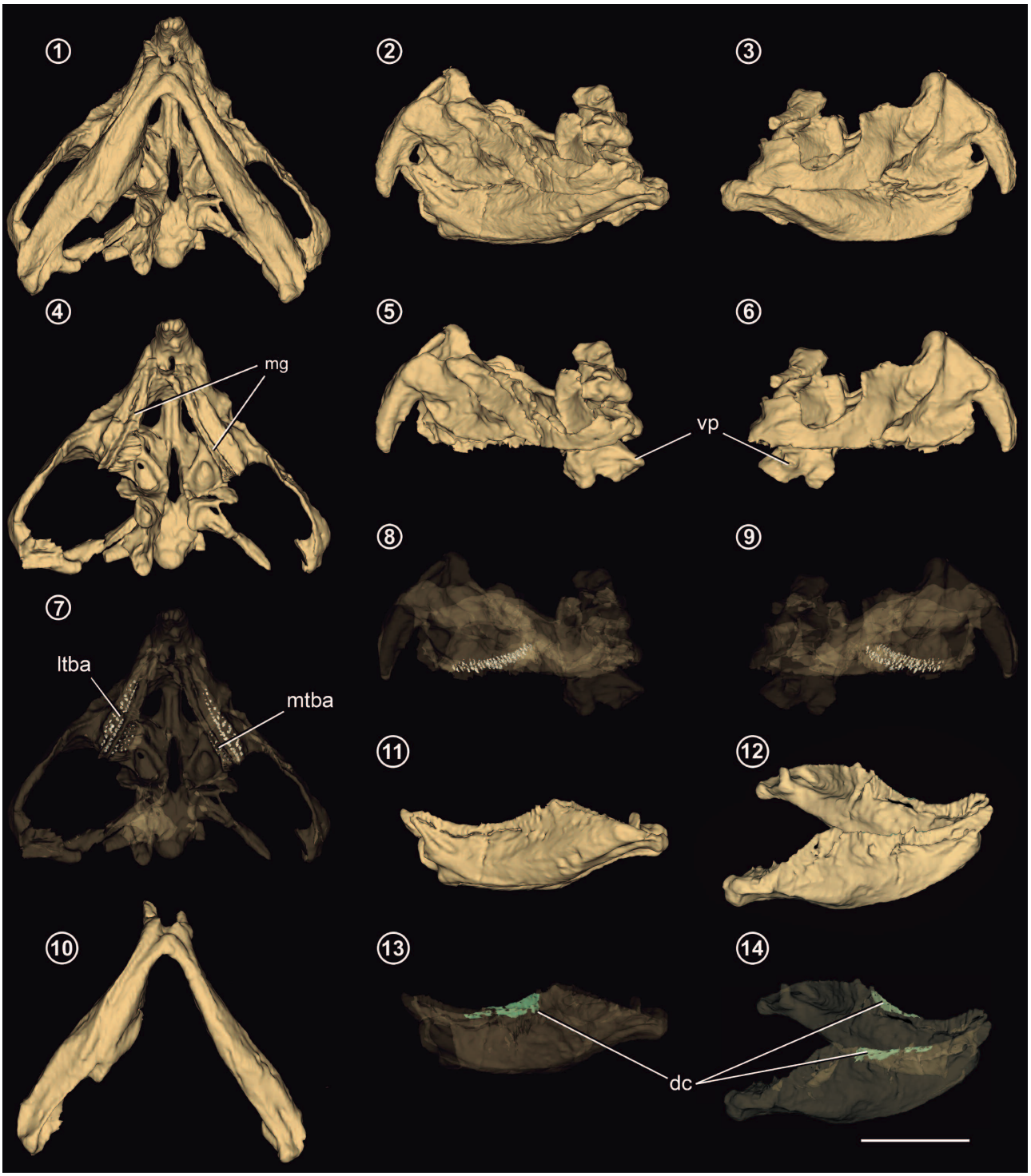

Figure 2. Three-dimensional rendering of the holotype of ***Hyperodapedon sanjuanensis*, MACN-Pv** 18185. **1–3,** Complete skull; **4–9,** skull without lower jaw; **10–14,** lower jaw in **1, 4, 7,** ventral view; **2, 5, 8, 11, 13,** left lateral view; **3, 6, 9,** right lateral view; **12, 14,** right dorsolateral view. **7–9, 13, 14,** Transparent bone to show the position of the teeth. Abbreviations: **dc,** dentary crest; **ltba,** lateral tooth-bearing area; **mg,** main groove; **mtba,** medial tooth-bearing area; **vp,** "ventromedial projection". Scale bar= 10cm.

some character-states should be taken with caution (*e.g.*, anterior extension of tooth rows, tooth crown shapes and wear facets). The general morphology of the masticatory apparatus of MACN-Pv 18185 resembles that of most other Late Triassic rhynchosaurs (Benton, 1984). In this regard,the premaxillae form a single, strongly downturned, edentulous beak and the dentary possesses a single tooth-bearing cutting blade that fits in a longitudinal, edentulous groove on the occlusal surface the maxilla.

Maxillary dentition

The occlusal surface of the maxillary tooth plate is strongly convex ventrally. This surface has a length of 12 cm and a maximum transverse width on the posterior end of 4 cm in the right maxilla and 3 cm in the left maxilla—which probably has a damaged medial margin. The tooth plate is divided by a single, deep longitudinal groove (= main groove) that arches slightly laterally (Fig. 4.1). The anterior half of the main groove becomes shallower towards the anterior end of the bone and its anterior quarter broadens slightly transversely. There are two tooth-bearing areas separated by the main groove, as occurs in *H. gordoni* (Huxley, 1859), *H. mariensis* (MCN PV 1867, UFRGS PV 0149T), *H. stockleyi* (SAM-PK-11704; Boonstra, 1953), *H. huxleyi* (Chatterjee, 1974), some specimens of *H. tikiensis* (Mukherjee and Ray, 2014), *Isalorhynchus genovefae* (Buffetaut, 1983), *Ammorhynchus navajoi* (Nesbitt and Whatley, 2004), a referred specimen of *H. sanjuanensis* (PVL 3432), and the isolated maxillae of *Hyperodapedon* sp. from the Ischigualasto Formation (MCZ 3618–3620, MACN-Pv 18526a) (Figs. 4–5). By contrast, *H. huenei* (Langer and Schultz, 2000a) (Fig. 5.4), *Teyumbaita sulcognathus* (Montefeltro *et al.*, 2010) (Fig. 5.8), *Fodonyx spenceri* (EXEMS 60/1985.292; Benton, 1990), *Stenaulorynchus stockleyi* (NHMUK PV R9275, R9276, R9278–R9281; von Huene, 1938), *Mesodapedon kuttyi* (Chatterjee, 1980), *Brasinorhynchus mariantensis* (Schultz *et al.*, 2016), and the unnamed form from Ischigualasto (Contreras, 1981, 1993) possess two longitudinal grooves that define three tooth-bearing areas. The lateral tooth-bearing area of MACN-Pv 18185 is cushion-shaped, as occurs in most hyperodapedontines (Langer *et al.*, 2000a), with the exception of the crest-shaped lateral tooth-bearing area of *T. sulcognathus* (Montefeltro *et al.*, 2010) and apparently *H. tikiensis* (Mukherjee and Ray, 2014). The lateral tooth-bearing area of MACN-Pv 18185 is transversely broader than the medial one, which has a transverse width of 1.5 cm. This is a result of a medially placed main groove with respect to the center of the tooth plate, as in *H. huxleyi* (Chatterjee, 1974), *H. mariensis* (MCN PV 1867, UFRGS PV 0149T), *H. tikiensis* (Mukherjee and Ray, 2014), most specimens of *Isalorhynchus genovefae* (Langer *et al.*, 2000a), a referred specimen of *H. sanjuanensis* (PVL 3432), and the isolated maxillae of *Hyperodapedon* sp. (MCZ 3618–3620, MACN-Pv 18526a). By contrast, the medial and lateral tooth-bearing areas are subequal in width in *H. gordoni* (Benton, 1983) and *H. stockleyi* (SAM-PK-11704) or the medial area is broader in *T. sulcognathus* (Montefeltro *et al.*, 2010), *H. huenei* (Langer and Schultz, 2000a), *F. spenceri* (EXEMS 60/1985.292), *S. stockleyi* (NHMUK PV R9275, R9276, R9278–R9281), *M. kuttyi* (Chatterjee, 1980), *B. mariantensis* (Schultz *et al.*, 2016), and the unnamed form from Ischigualasto (Contreras, 1981, 1993).

The medial tooth-bearing area of the left maxilla of MACN-Pv 18185 is transversely narrower (transverse width= 6 mm) than the same area in the right maxilla (transverse width= 10 mm), in which the former possesses

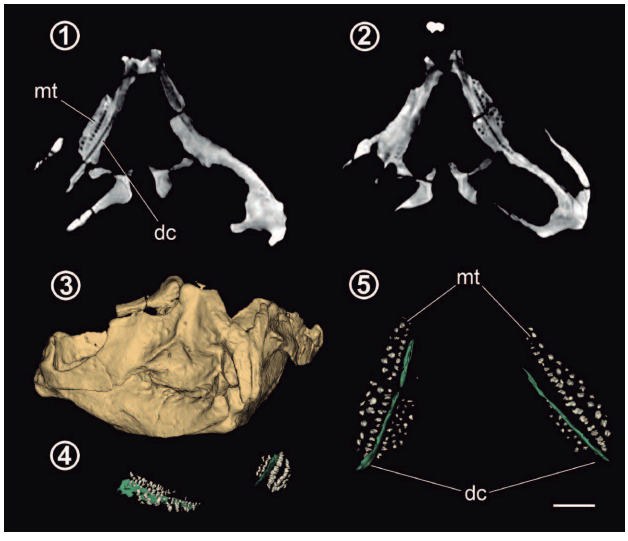

Figure 3. Original CT scan data and three-dimensional rendering of the holotype of ***Hyperodapedon sanjuanensis*, MACN-Pv** 18185. **1–2,** Coronal section of the skull; **3,** skull in right anterolateral view; **4–5,** maxillary and dentary teeth arranged in full occlusion in **4,** right anterolateral view and **5,** occlusal view. Abbreviations: **dc,** dentary crest; **mt,** maxillary teeth. Scale bar= 2cm.

two tooth rows and the latter three (Figs. 2.4, 2.7, 3.5). The right and left maxillary medial tooth-bearing areas have different widths in the digitally reconstructed specimen, but the width of the posterior halves of both maxillary tooth plates are similar in the real specimen. The medial surface is complete in both maxillary tooth plates and, as a result, the difference observed in the digitally reconstructed specimen is interpreted as a probable artefact of the CT scan and/or volume rendering. Similarly, there is an apparent ventromedial expansion on the posteromedial corner of the occlusal surface of the right maxillary tooth plate (Fig. 2.4). However, the teeth are placed distinctly dorsal to this expansion. This putative bony development is the result of the lack of contrast between the bone and remaining matrix in this part of the specimen, immediately dorsal to the contact between the maxilla and the palatine.

The maxillary teeth are relatively large (Figs. 2.7, 3.1–2, 4.1), resembling the condition in *Rhynchosaurus articeps* (NHMUK PV R1236; Benton, 1990), *F. spenceri* (EXEMS 60/1985.292), and other hyperodapedontine rhynchosaurs (Benton, 1984; Schultz *et al.*, 2016). By contrast, the stenaulorhynchines *S. stockleyi* and *B. mariantensis* possess proportionally smaller maxillary teeth with a greater number of tooth positions in each longitudinal row (Schultz *et al.*, 2016). The resolution of the CT scan does not allow determining confidently the tooth crown shape in MACN-Pv 18185 (*i.e.*, conical versus pyramidal types; *sensu* Benton, 1984). The lateral tooth-bearing area possesses three clear longitudinal tooth rows (L1–L3). This count of lateral tooth rows falls within the variation observed in similar-sized maxillary tooth plates of the isolated maxillae of *Hyperodapedon* sp. of the Ischigualasto Formation, which possess three (MACN-Pv 18526a), four (MACN-Pv 18526b, MCZ 3618, 3619) (Fig. 4.3), or even five (MCZ 3620) (Fig. 4.2) longitudinal tooth rows in the lateral tooth-bearing area. The teeth of L1 and L2 seem to be larger in cross-section than those of L3 in the posterior half of the left tooth plate. Nevertheless, the tooth crowns of the lateral tooth-bearing area in the right maxilla are similar in size in the three longitudinal rows, resembling the condition in the isolated maxillae of *Hyperodapedon* sp. from Ischigualasto (MCZ 3618–3620, MACN-Pv 18526a, b). As a result, it is possible

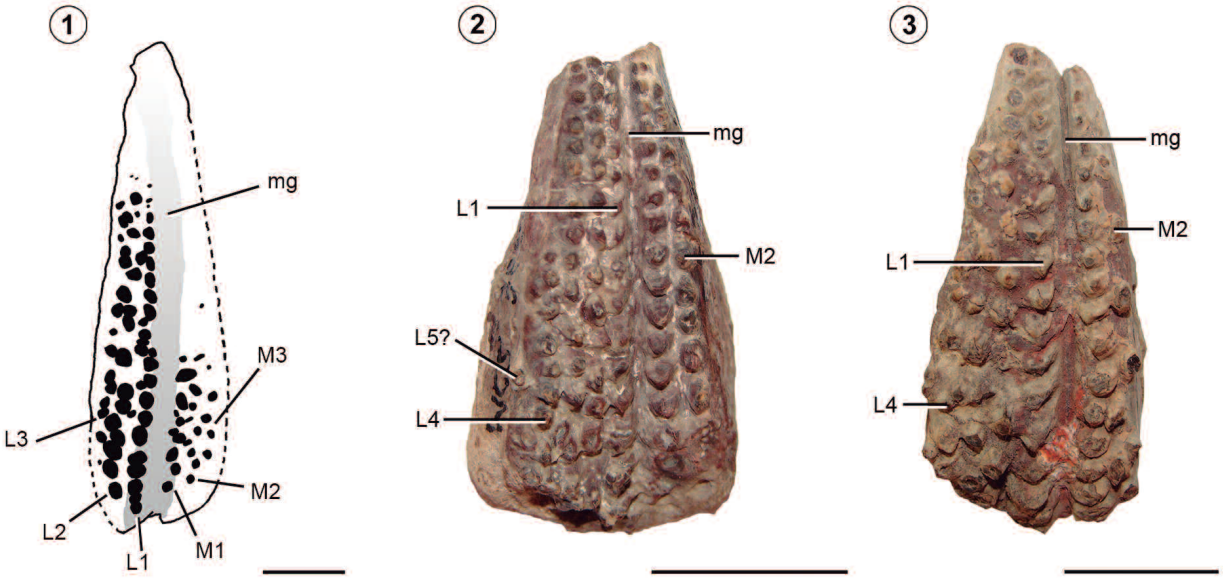

Figure 4. Maxillae of hyperodapedontines from the Ischigualasto Formation in occlusal views. **1,** Interpretative reconstruction from both maxillae of **MACN-Pv** 18185; **2, MCZ** 3620 (left maxilla of *Hyperodapedon* sp., reversed); **3, MCZ** 3618 (right maxilla of *Hyperodapedon* sp.). Abbreviations: **L1–5,** first to fifth lateral tooth row; **M1–3,** first to third medial tooth row; **mg,** main groove. Scale bars= 2 cm.

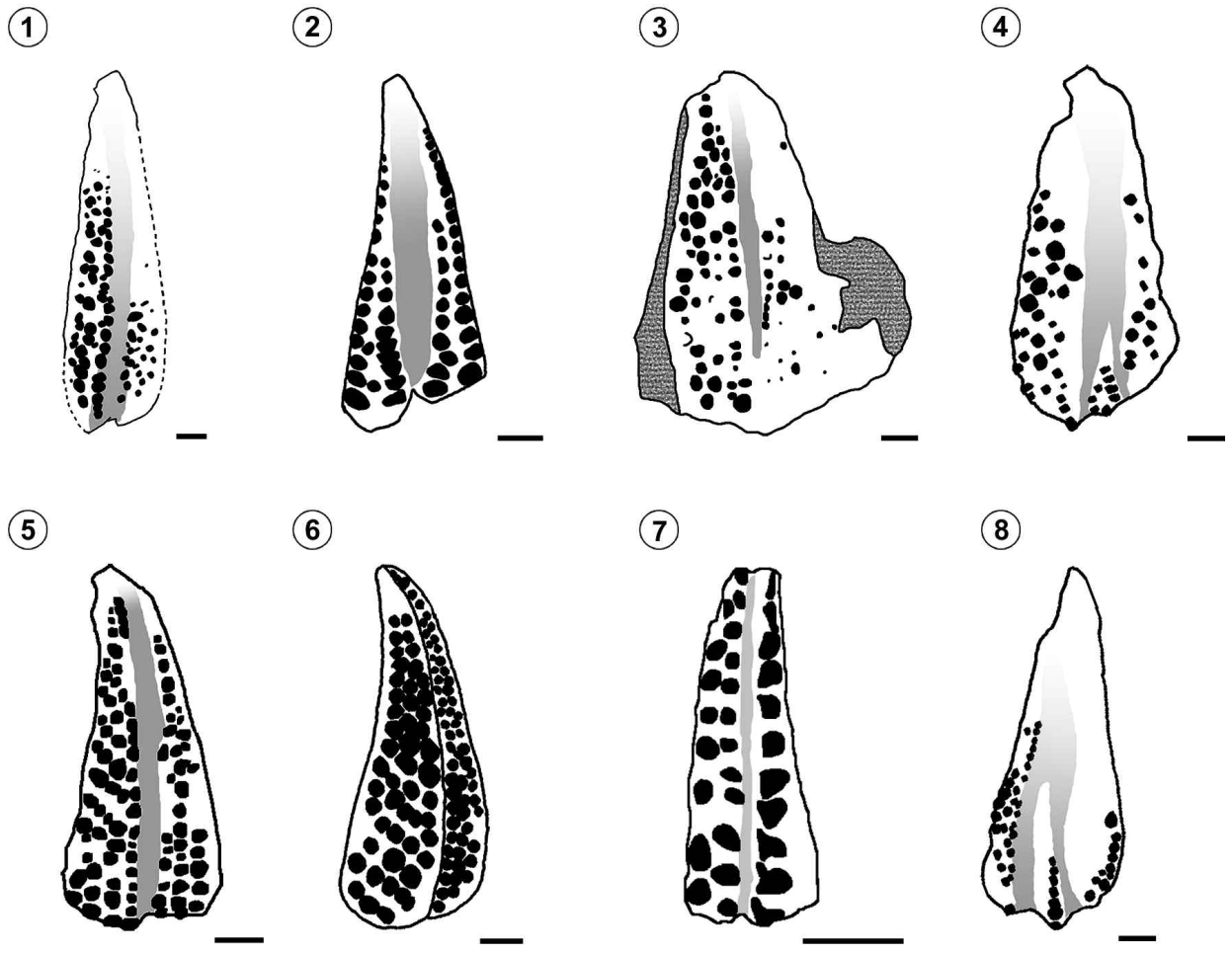

Figure 5. Schematic drawings of the maxillary tooth plate of Late Triassic rhynchosaurs. **1,** ***Hyperodapedon sanjuanensis*** (holotype); **2,** ***Hyperodapedon gordoni*** (redrawn from Benton, 1983); **3,** ***Hyperodapedon stockleyi*** (redrawn from Boonstra, 1953, reversed); **4,** ***Hyperodapedon huenei*** (redrawn from Langer and Schultz, 2000a); **5,** ***Hyperodapedon tikiensis*** morphotype 1 (redrawn from Mukherjee and Ray, 2014, reversed); **6,** ***Hyperodapedon huxleyi*** (redrawn from Chatterjee, 1974); **7,** ***Isolarhynchus genovefae*** (redrawn from Buffetaut, 1983); **8,** ***Teyumbaita sulcognathus*** (redrawn from Montefeltro *et al.*, 2010). Scale bars= 1cm.

that the smaller size of the teeth of L3 in the left maxilla is a result of an artefact of the CT scan or volume rendering. The size of the teeth of L1–L3 decreases anteriorly in MACN-Pv 18185 and the isolated maxillae of *Hyperodapedon* sp. from Ischigualasto (MCZ 3618–3620). In particular, the size of the teeth of L1 decreases more abruptly than those of L2.

The teeth of L1 are more closely packed than those of L2 and L3 and become more separated from each other gradually towards the anterior end of the tooth plate (Figs. 2.7, 3.5, 4.1). This condition seems to be variable among the isolated maxillae of *Hyperodapedon* sp. from Ischigualasto (MACN-Pv 18526a, b, MCZ 3618–3620) (Fig. 4). L1 extends from the posterior-most part of the maxilla and reaches, at least, the beginning of the anterior third of the tooth plate. L2 starts anteriorly to L1 in the posterior end of the tooth plate and extends anteriorly up to approximately the same level as L1. A more posteriorly extended L1 than L2 also occurs in the isolated maxillae of *Hyperodapedon* sp. from Ischigualasto (MCZ 3618–3620, MACN-Pv 18526a). L3 is the shortest row of the lateral tooth-bearing area in the reconstruction, bearing between 6–8 teeth. The reconstruction generated from the CT scan data is probably missing the most anterior teeth of the longitudinal rows because in

the isolated maxillae of *Hyperodapedon* sp. from Ischigualasto the rows reach the anterior end of the plate (*e.g.*, MCZ 3619) (Fig. 4.3). By contrast, a more posteriorly restricted L3 than L1 and L2 may be a real condition because it occurs, at least, in some the isolated maxillae of *Hyperodapedon* sp. from Ischigualasto (MCZ 3618). The longitudinal rows of the lateral tooth-bearing area are gradually more ventrally placed from medial to lateral, resembling the condition in the isolated maxillae of *Hyperodapedon* sp. from Ischigualasto (*e.g.*, MCZ 3620, MACN-Pv 18526a).

The medial tooth-bearing area preserves three longitudinal tooth rows (M1–M3) in the right maxilla and two in the left maxilla (see above) (Fig. 3.5). The isolated maxillae of *Hyperodapedon* sp. from Ischigualasto of similar size to that of MACN-Pv18185 possess two or three longitudinal medial tooth rows (MACN-Pv 18526a, b, MCZ 3618–3620). As reconstructed, the medial tooth rows of MACN-Pv 18185 are shorter than the lateral ones, being restricted to the posterior third of the tooth plate. However, the shortness of the medial tooth rows is probably a result of the lack of contrast in the CT scan, strong tooth wear, or poor preservation. For example, the medial tooth rows reach the anterior end of the tooth plate in the isolated maxillae of *Hyperodapedon* sp. from Ischigualasto (MACN-Pv 18526a, MCZ 3618–3620). The teeth of the medial tooth-bearing area are smaller in cross-section than those of the lateral area. This condition is variable in the studied isolated maxillae of *Hyperodapedon* sp. from Ischigualasto, but generally the lateral and medial teeth are subequal in size in these specimens. M1 starts slightly anterior to L1 in the posterior end of the tooth plate and M2 and M3 start gradually more anteriorly from lateral to medial, respectively, in the posterior margin of the plate. This condition resembles that of other hyperodapedontine rhynchosaurs (*e.g.*, the isolated maxillae of *Hyperodapedon* sp. from Ischigualasto, MCZ 3618–3620; *H. stockleyi*, SAM-PK-11704; *H. huxleyi*, Chatterjee, 1974).

Dentary dentition

All the dentary teeth are implanted on the top of a single longitudinal cutting blade (Figs. 2.13–14, 3.4–5), which fits in the main groove of the maxillary tooth plate. This condition also occurs in all hyperodapedontine rhynchosaurids with the exception of *T. sulcognathus*, which possesses two longitudinal tooth-bearing cutting blades in the dentary (Montefeltro *et al.*, 2010). The cutting blade is continuously dorsally concave in lateral or medial view, as occurs in other rhynchosaurids (Benton, 1984). There is no lingual tooth on the dentaries of MACN-Pv 18185, contrasting with the condition in all other valid rhynchosaurid species, in which teeth distinctly occur on the internal surface of the bone, ventral to the cutting blade (Langer and Schultz, 2000a; Langer *et al.*, 2000a, b). The longitudinal tooth rows of both hemimandibles extend posterior to the maxillary teeth as preserved and do not reach anteriorly the level of the teeth of the maxillary lateral tooth-bearing area. Indeed, the most anterior region of the dentary shows no evidence of teeth (Fig. 2.13–14). This could mean that this region is edentulous, the teeth are heavily worn to the point that no distinct crown is shown in the CT scan–resembling the condition in the specimen UFRGS-PV-0232T of *T. sulcognathus* (Montefeltro *et al.*, 2010)–or the CT scan does not have enough contrast/resolution to identify unworn teeth. The dentary teeth cannot be generally individualized from each other in the reconstruction because they seem to be heavily packed, very small, and circular in cross-section (Fig. 3.1–2).

DISCUSSION

Sill (1970) described the dental morphology of *Hyperodapedon sanjuanensis* in the original description of the species based on the anatomy of referred specimens (*e.g.*, MCZ 3618; Sill, 1970, plate III e). However, this description was very short (see Introduction) and, as a result, here we present the first detailed description of the dental anatomy of this species. The maxillary tooth plates here reconstructed for the holotype of this species (MACN-Pv 18185) are congruent with those described very briefly by Sill (1970), sharing the presence of a single longitudinal groove that separates a lateral tooth-bearing area from a narrower medial area. This combination of features is also present in the other maxillary tooth plates from the Ischigualasto Formation that were available here for comparison (MCZ 3618, 3620, MACN-Pv 18526a, b, PVL 3432). In addition, our observations confirm previous claims that *H. sanjuanensis* differs from other rhynchosaurids in the absence of lingual teeth on the dentary (Langer *et al.*, 2000a).

The description of the masticatory apparatus of MACN-Pv 18185 shows that *H. sanjuanensis* can be distinguished

from other rhynchosaur species based on a unique combination of dental character-states. As a result, we provide an emended diagnosis for the species based on the dental characters analyzed here (see Systematic Paleontology). In the case of *H. mariensis* and *H. huxleyi*, these species can be distinguished from *H. sanjuanensis* in the presence of lingual teeth in the dentary (Chatterjee, 1974; Langer and Schultz, 2000a). However, the maxillary tooth plate of MACN-Pv 18185 cannot be distinguished from those of *H. mariensis* (*e.g.*, MCN PV 1867, UFRGS PV 0149T), sharing the presence of a medially displaced main groove and absence of lingual teeth. As a result, the isolated maxillae from the Ischigualasto Formation used here for comparisons (MCZ 3618–3620, MACN-Pv 18526a, b; including MCZ 3618, which was previously referred to *H. sanjuanensis* by Sill [1970]) possess a morphology congruent with that of *H. sanjuanensis* and *H. mariensis*, and therefore are here referred to *Hyperodapedon* sp.. Similarly, the maxillary tooth plates of PVL 3432—a fairly complete skull originally referred to *H. sanjuanensis* by Sill (1970)—cannot be distinguished from the *Hyperodapedon* species mentioned above. However, this specimen and the holotype of *H. sanjuanensis* share the presence of an infratemporal fenestra as anteroposteriorly long as the orbit and the absence of lingual teeth in the dentary, contrasting with *H. mariensis* and *H. huxleyi*. Thus, these character-states allow distinguishing PVL 3432 and the holotype of *H. sanjuanensis* from all the other hyperodapedontine species and as a consequence the former specimen is retained as referable to *H. sanjuanensis*.

The dental morphology of MACN-Pv 18185 and those of the isolated maxillae of *Hyperodapedon* sp. from Ischigualasto show subtle dental variations among them, in which the most conspicuous difference is the number of tooth rows in the lateral tooth bearing area. This difference in the number of lateral tooth rows can be explained by ontogenetic variation, in which additional tooth rows appear during the ontogeny of hyperodapedontine rhynchosaurs (Langer *et al.*, 2000b). As a consequence, this difference does not support a taxonomic distinction between these specimens. However, all these specimens (MCZ 3618–3620, MACN-Pv 18526a, b, 18185) seem to distinctly differ from the probable second rhynchosaur species from the Ischigualasto Formation—which has two longitudinal grooves in the maxillary tooth plate—preliminary reported by Contreras (1981, 1993).

The dentition of rhynchosaurs has provided a substantial number of phylogenetically informative characters in analyses that tested the relationships among the species of the clade. For example, the phylogenetic datasets of Langer and Schultz (2000a), Hone and Benton (2008), and Mukherjee and Ray (2014) are composed of *ca.* 28%, 18%, and 24% dental characters, respectively. The scorings of the dental characters of these three datasets were checked here for the holotype of *H. sanjuanensis* based on the dental morphology described here for this specimen (Appendix I). We found that the vast majority of the scorings agree with the anatomy observed in the actual specimen and digital reconstruction of MACN-Pv 18185. Indeed, we detected only one difference. The width of maxillary dental battery (**DBW**) versus length of the maxillary dental battery (**DBL**) ratio in the right maxillary tooth plate of MACN-Pv 18185 is *ca.* 0.25 based on the measurements taken from the three-dimensional rendering. However, this value distinctly differs from the scoring of Mukherjee and Ray (2014)—state 2 (*i.e.*, 0.4)— for *H. sanjuanensis*.

We expect that the information gathered from this study represents a step forward towards a more comprehensive revision of the taxonomy of the rhynchosaur assemblage of the Ischigualasto Formation, which may be represented by more than a single species (Contreras, 1981, 1993, 1999).

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REFERENCES

Azevedo, S.A., and Schultz, C.L. 1987. *Scaphonyx sulcognathus* (sp. nov.), um novo rincossaurideo do neotriassico do Rio Grande do Sul, Brasil. *Proceedings of X Congresso Brasileiro de Paleontologia* (Rio de Janeiro), *Anais*: 99–113.

Benton, M.J. 1983. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society B: Biological Sciences* 302: 605–718.

Benton, M.J. 1984. Tooth form, growth, and function in Triassic

rhynchosaurs (Reptilia, Diapsida). *Palaeontology* 27: 737–776.

Benton, M.J. 1990. The species of *Rhynchosaurus*, a rhynchosaur (Reptilia, Diapsida) from the Middle Triassic of England. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 328: 213–306.

Boonstra, L.D. 1953. A note on some rhynchosaurian remains from Tanganyika Territory. *Annals of the South African Museum* 42: 1–4.

Buffetaut, E. 1983. *Isalorhynchus genovefae*, n. g. n. sp.(Reptilia, Rhynchocephalia), un nouveau Rhynchosaure du Trias de Madagascar. *Neues Jahrbuch für Geologie und Paläontologie* 1983: 465–480.

Carroll, R.L. 1976. *Noteosuchus*—the oldest known rhynchosaur. *Annals of the South African Museum* 72: 37–57.

Chatterjee, S. 1969. Rhynchosaurs in time and space. *Proceedings of the Geological Society of London* 1658: 203–208.

Chatterjee, S. 1974. A rhynchosaur from the Upper Triassic Maleri formation of India. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 267: 209–261.

Chatterjee, S. 1980. The evolution of rhynchosaurs. *Mémoires de la Société Géologique de France, Nouvelle Série* 139: 57–65.

Contreras, V.H. 1981. Datos preliminares sobre un nuevo rincosaurio (Reptilia, Rhynchosauria) del Triásico Superior de Argentina. *Anais do II Congresso Latino-Americano de Paleontologia* (Porto Alegre), *volume* 1: 289–294.

Contreras, V.H. 1993. Un nuevo rincosaurio (Reptilia: Rhynchosauria) del Triásico Superior sudamericano. *Ameghiniana* 30: 326.

Contreras, V.H. 1999. Rhynchosaurs from Ischigualasto Formation (Upper Triassic, Late Carnian), San Juan, Argentina. *VII° International Symposium of Mesozoic Terrestrial Ecosystems* (Buenos Aires), *Abstracts*: 18–19.

Dilkes, D.W. 1995. The rhynchosaur *Howesia browni* from the Lower Triassic of South Africa. *Palaeontology* 38: 665–686.

Dilkes, D.W. 1998. The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 353: 501–541.

Ezcurra, M.D., Trotteyn, M.J., Fiorelli, L.E., Baczko, M.B. von, Taborda, J.R.A., Iberlucea, M., and Desojo, J.B. 2014. The oldest rhynchosaur from Argentina: a Middle Triassic rhynchosaurid from the Chañares Formation (Ischigualasto–Villa Unión Basin, La Rioja Province). *Paläontologische Zeitschrift* 88: 453–460.

Ezcurra, M.D., Montefeltro, F., and Butler, R.J. 2016. The early evolution of rhynchosaurs. *Frontiers in Ecology and Evolution* 3: 142.

Ezcurra, M.D., Fiorelli, L.F., Martinelli, A.G., Rocher, S., Baczko, M.B. von, Ezpeleta, M., Taborda, J.R.A., Hechenleitner, E.M., Trotteyn, M.J., and Desojo, J.B. 2017. Deep faunistic turnovers preceded the rise of dinosaurs in southwestern Pangaea. *Nature Ecology and Evolution* 1: 1477–1483.

Fedorov, A., Beichel, R., Kalpathy-Cramer, J., Finet, J., Fillion-Robin, J.C., Pujol, S., and Buatti, J. 2012. 3D Slicer as an image computing platform for the Quantitative Imaging Network. *Magnetic Resonance Imaging* 30: 1323–1341.

Hone, D.W., and Benton, M.J. 2008. A new genus of rhynchosaur from the Middle Triassic of south-west England. *Palaeontology* 51: 95–115.

Huene, F. von. 1938. *Stenaulorhynchus*, ein Rhynchosauridae der ostafrikanischen Obertrias. *Nova Acta Leopoldina, Neue Folge* 6: 83–121.

Huene, F. von. 1946. Die grossen Stämme der Tetrapoden in den geologischen Zeiten. *Biologisches Zentralblatt* 65: 268–275.

Huxley, T.H. 1859. Postscript: Murchinson, R.I. On the sandstones of Morayshire (Elgin & c.) containing reptilian remains, and their relations to the Old Red Sandstone of that Country. *Quarterly Journal of the Geological Society* 15: 435–436.

Langer, M.C. 1996. [Rincossaurossul-brasileiros histórico e filogenia. Dissertação de Maestrado, Instituto de Geociências, Universidad Federal do Rio Grande do Sul, Porto Alegre, 361 p. Unpublished.].

Langer, M.C. 1998. Gilmoreteiidae new family and *Gilmoreteius* new genus (Squamata, Scincomorpha): replacement names for Macrocephalosauridae Sulimski, 1975 and *Macrocephalosaurus* Gilmore, 1943. *Comunicações do Museu de Ciências e Tecnologia da PUCRS, Série Zoologia Porto Alegre* 11: 13–18.

Langer, M.C. 2005. Studies on continental Late Triassic tetrapod biochronology. II. The Ischigualastian and a Carnian global correlation. *Journal of South American Earth Sciences* 19: 219–239.

Langer, M.C., and Schultz, C.L. 2000a. A new species of the Late Triassic rhynchosaur *Hyperodapedon* from the Santa Maria Formation of south Brazil. *Palaeontology* 43: 633–652.

Langer, M.C., and Schultz, C.L. 2000b. Rincossauros – herbívoros cosmopolitas do Triássico. In: M. Holz, and L.F. De Ros (Eds.), *Paleontologia do Rio Grande do Sul*. Ediitora da Universidade, CIGO/UFRGS, Porto Alegre, p. 246–272, 397.

Langer, M.C., Boniface, M., Cuny, G., and Barbieri, L. 2000a. The phylogenetic position of *Isalorhynchus genovefae*, a Late Triassic rhynchosaur from Madagascar. *Annales de Paléontologie* 86: 101–127.

Langer, M.C., Ferigolo, J., and Schultz, C.L. 2000b. Heterochrony and tooth evolution in hyperodapedontine rhynchosaurs (Reptilia, Diapsida). *Lethaia* 33: 119–128.

Marsicano, C.A., Irmis, R., Mancuso, A., Mundil, R., and Chemale, F. 2016. The precise temporal calibration of dinosaur origins. *Proceedings of the National Academy of Sciences* 113: 509–513.

Martínez, R.N., Sereno, P.C., Alcober, O.A., Colombi, C.E., Renne, P.R., and Montañez, I.P. 2011. A basal dinosaur from the dawn of the dinosaur era in southwestern Pangaea. *Science* 331: 206–210.

Martínez, R.N., Apaldetti, C., Alcober, O.A., Colombi, C.E., Sereno, P.C., Fernández, E., Malnis, P.S., Correa, G.A., and Abelin, D. 2013. Vertebrate succession in the Ischigualasto Formation. *Society of Vertebrate Paleontology Memoir* 12: 10–30.

Montefeltro, F.C., Langer, M.C., and Schultz, C.L. 2010. Cranial anatomy of a new genus of hyperodapedontine rhynchosaur (Diapsida, Archosauromorpha) from the Upper Triassic of Southern Brazil. *Earth and Environmental Sciences Transaction of the Royal Society of Edinburgh* 101: 27–52.

Mukherjee, D., and Ray, S. 2014. A new *Hyperodapedon* (Archosauromorpha, Rhynchosauria) from the Upper Triassic of India: implications for rhynchosaur phylogeny. *Palaeontology* 57: 1241–1276.

Nesbitt, S.J., and Whatley, R.L. 2004. The first discovery of a rhynchosaur from the Upper Moenkopi Formation (Middle Triassic) of northern Arizona. *PaleoBios* 24: 1–10.

Osborn, H.F. 1903. The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. *Memoirs of the American Museum of Natural History* 1: 451–507.

Romer, A.S. 1963. La evolución explosiva de los rhynchosaurios del Triásico. *Revista Museo Argentino de Ciencias Naturales Bernardino Rivadavia e Instituto Nacional de Investigación de las Ciencias Naturales (Ciencias Zoológicas)* 8: 1–14.

Schultz, C.L., Langer, M.C., and Montefeltro, F.C. 2016. A new rhynchosaur from south Brazil (Santa Maria Formation) and rhynchosaur diversity patterns across the Middle-Late Triassic boundary. *Paläontologische Zeitschrift* 90: 593–609.

Sill, W.D. 1970. *Scaphonyx sanjuanensis*, nuevo rincosaurio (Reptilia)

de la Formación Ischigualasto, Triásico de San Juan, Argentina. *Ameghiniana* 7: 341–354.

Tupi-Caldas, J.L. 1933. Contribuição ao estudo do fóssil da Alemoa, Municipio de Santa Maria, Rio Grande do Sul. In: J.L. Tupi-Caldas (Ed.), *Curso Geral de Mineralogia e Geologia, aplicada ao Brasil. 2da.ed.* Edições da Livraria do Globo, Porto Alegre, p. 333–339.

Whatley, R.L. 2005. [Phylogenetic relationships of *Isalorhynchus genovefae*, the rhynchosaur (Reptilia, Archosauromorpha) from Madagascar. Ph.D. dissertation, University of California, Santa Barbara, 276 p. Unpublished.].

Woodward, A.S. 1908. III. On some Fossil Reptilian Bones from the State of Rio Grande do Sul, Brazil 2. *Geological Magazine* 5: 251–255.

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APPENDIX I

List of dental characters whose scorings were checked in the holotype of *Hyperodapedon sanjuanensis* (MACN-Pv 18185):

- *Tooth implantation: subthecodont or thecodont (0), ankylothecodont (1) (Hone and Benton, 2008: character 39).* The actual specimen possesses an ankylothecodont tooth implantation, in agreement with the scoring of Hone and Benton (2008).

- *Premaxillary teeth: present (0), absent (1) (Hone and Benton, 2008: character 40; Mukherjee and Ray, 2014: character 32).* MACN-Pv 18185 has an edentulous premaxilla, matching the scorings in the datasets of previous authors.

- *Maxillary grooves: absent (0), present (1) (Mukherjee and Ray, 2014: character 35).* Mukherjee and Ray (2014) scored the presence of a maxillary groove in *H. sanjuanensis*, which agrees with the morphology observed in the rendering of MACN-Pv 18185.

- *Tooth occlusion: single sided overlap (0), flat occlusion (1), blade and groove jaw apparatus, where dentary blade(s) fit precisely into maxillary groove(s) (2) (Hone and Benton, 2008: character 42; Mukherjee and Ray, 2014: character 43).* Based on the three-dimensional rendering, we agree with the scorings of previous authors in the presence of a blade and groove jaw occlusion in *H. sanjuanensis* (Fig. 2).

- *Number of maxillary grooves: two (0), one (1) (Langer and Schultz, 2000a: character 14); none (0), one (1), two (2) (Hone and Benton, 2008: character 43).* MACN-Pv 18185 possesses a single maxillary groove, as scored for *H. sanjuanensis* by Langer and Schultz (2000a) and Hone and Benton (2008) (Figs. 4.1, 5.1).

- *Combination of maxillary groove and dentary blade: two grooves-two blades (0); two grooves-one blade (1), one groove-one blade (2) (Mukherjee and Ray, 2014: character 36).* This character is partially dependant from the previous one, but it also includes the morphology of the dentary tooth-bearing area. The holotype of *H. sanjuanensis* possesses one groove in the maxilla and one blade in the dentary, which agrees with the scoring of Mukherjee and Ray (2014).

- *Number of rows of teeth on maxilla: single row (0), multiple rows (batteries) of teeth (1) (Hone and Benton, 2008: character 41; Mukherjee and Ray, 2014: character 34).* MACN-Pv 18185 has 5–6 tooth rows in the maxilla, matching the scorings of previous authors (Fig. 3.4, 3.5).

- *Proportion of maxillary tooth plate: width at posterior end (DBW)/length (DBL) ≤ 0.2 (0), c.0.3 (1), 0.4(2), ≥ 0.5 (3) (Mukherjee and Ray, 2014: character 33).* The DBW/DBL ratio in the right maxillary tooth plate of MACN-Pv 18185 is ca. 0.25 based on the measurements taken from the three-dimensional rendering. This value distinctly differs from the scoring of Mukherjee and Ray (2014)—state 2 (*i.e.,* 0.4)—for *H. sanjuanensis*.

- *Relative width of the tooth-bearing areas lateral and medial to the maxillary main groove: medial tooth-bearing area wider (0), lateral tooth-bearing area wider (1) (Langer and Schultz, 2000a: character 15; Hone and Benton, 2008: character 44). Maxillary tooth-bearing area lateral to the main longitudinal groove (LDS) relative to the medial dentigerous space (MDS): LDS/MDS < 1 (0), LDS/MDS = 1 (1), 1 < LDS/MDS < 1.5 (2), LDS/MDS > 1.5 (3) (Mukherjee and Ray, 2014: character 37).* The lateral tooth-bearing area of MACN-Pv 18185 is wider than the medial one, as scored for *H. sanjuanensis* by Langer and Schultz (2000a) and Hone and Benton (2008). Mukherjee and Ray (2014) quantified the difference between the widths of both tooth-bearing areas (LDS/MDS). We calculated the LDS/MDS ratio in the right maxilla of MACN-Pv 18185 as 1.4, in agreement with the scoring of Mukherjee and Ray (2014).

- *Maxillary cross-section lateral to main groove: crest-shaped (0), cushion-shaped (1) (Mukherjee and Ray, 2014: character 38).* A cushion-shaped lateral tooth-bearing area is observed in the DICOM images and the volume rendering of MACN-Pv 18185, matching the scoring of Mukherjee and Ray (2014).

- *Number of tooth rows on LDS: 1 (0)≥ 2 (1) (Mukherjee and Ray, 2014: character 39). Maxillary lateral tooth-bearing area: one or two teeth in a transverse section (0), more than two teeth in a transverse section (1) (Langer and Schultz, 2000a: character 16).* MACN-Pv 18185 possesses three tooth rows in both LDSs, in agreement with the scoring of Langer and Schultz (2000a) and Mukherjee and Ray (2014) (Figs. 3.5, 4.1, 5.1).

- *Medial maxillary groove: present and reaching the anterior half of the maxilla (0), present but not reaching the anterior half of the maxilla (1), absent (2) (Mukherjee and Ray, 2014: character 40).* As occurs in most species of *Hyperodapedon* (see above), the rendering of MACN-Pv 18185 shows no medial groove and agrees with the scoring of Mukherjee and Ray (2014) for *H. sanjuanensis*.

- *Number of tooth rows on MDS (area medial to the primary longitudinal groove): ≤ two rows (0), three or more tooth rows (1) (Mukherjee and Ray, 2014: character 41).* MACN-Pv 18185 possesses two and three tooth rows in the MDS, but the lack of one row in the left maxilla is interpreted as an artefact. Thus, we agree with the scoring of Mukherjee and Ray (2014) as state 1.

- *Maxillary lingual teeth: present (0), absent (1) (Langer and Schultz, 2000a: character 17); absent (0), present (1) (Hone and Benton, 2008: character 45); absent (0), single (1), few and scattered (2), multiple rows of teeth (3) (Mukherjee and Ray, 2014: character 42).* In the rendering of MACN-Pv 18185 all the maxillary teeth are placed on the oc-

clusal surface, with no evidence of lingual teeth. This observation is congruent with the scorings of previous authors.

- *Shape of dentary teeth: only conical (0), conical and laterally compressed (1), only laterally compressed (2) (Mukherjee and Ray, 2014: character 45).* This character could not be identified confidently in the three-dimensional rendering of MACN-Pv 18185.

- *Number of posterior dentary teeth: more on the anterior half of the mandible (0), more on the posterior half of the mandible (1) (Langer and Schultz, 2000a: character 18; Hone and Benton, 2008: character 48).* The quality of the CT scan does not allow a clear individualization of the dentary teeth. However, the anterior third of the dentary seems to be edentulous, matching with the scoring as state 1 of Langer and Schultz (2000a) and Hone and Benton (2008).

- *Number of rows of teeth on dentary: one (0), two (1), more than two full rows (2) (Hone and Benton, 2008: character 46).* The dentary possesses a single tooth row. This observation agrees with the scoring of Hone and Benton (2008) for *H. sanjuanensis* (Fig. 2.13, 2.14).

- *Number of dentary cutting blades: two (0), one (1) (Langer and Schultz, 2000a: character 19).* MACN-Pv 18185 possesses a single dentary cutting blade, which agrees with scoring of Langer and Schultz (2000a) (Fig. 2.11–2.14).

- *Teeth on the lingual face of the dentary: present (0), absent (1) (Langer and Schultz, 2000a: character 20); absent (0), present (1) (Hone and Benton, 2008: character 47); absent (0); primary lingual dentary teeth present (1); loss of primary lingual teeth and presence of lingual teeth (2); loss of lingual teeth (3) (Mukherjee and Ray, 2014: character 46).* Langer and Schultz (2000a) and Hone and Benton (2008) described and scored an absence of lingual teeth in the dentary of *H. sanjuanensis*. This observation in confirmed here based on the holotype of the species.

- *Primary lingual teeth on the dentary: present (0), absent (1) (Langer and Schultz, 2000a: character 21).* The scoring of Langer and Shultz (2000a) agrees with the absence of lingual teeth observed in MACN-Pv 18185.

- *Vomerine teeth: present (0), absent (1) (Hone and Benton, 2008: character 49; Mukherjee and Ray, 2014: character 47). Palatine teeth: present (0), absent (1) (Hone and Benton, 2008: character 50; Mukherjee and Ray, 2014: character 48). Pterygoid teeth: present (0), absent (1) (Hone and Benton, 2008: character 51; Mukherjee and Ray, 2014: character 49).* We concluded that MACN-Pv 18185 lacks palatal teeth based on the observation of the real specimen and CT scan data. This condition matches with the scorings of previous authors and also occurs in other hyperodapedontine rhynchosaurs (Ezcurra *et al.*, 2016).