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ARTICLE

JUVENILE GLYPTODONT (MAMMALIA, CINGULATA) FROM THE MIOCENE OF PATAGONIA, ARGENTINA: INSIGHTS INTO MANDIBULAR AND DENTAL CHARACTERS

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ABSTRACT—The earliest complete glyptodonts (Glyptodontidae, Cingulata) found belong to the Propalaehoplophorinae from Santa Cruz Formation (late early Miocene, Burdigalian) in Patagonia, Argentina. Although several skulls and mandibles have been described from this formation, and assigned to five genera (*Propalaehoplophorus* Ameghino, *Cochlops* Ameghino, *Asterostemma* Ameghino, *Eucinepeltus* Ameghino, and *Metopotoxus* Ameghino), the fossil record and knowledge of juvenile specimens of glyptodonts are still poor. Here, we provide a detailed morphological description of a mandible of a juvenile propalaehoplophorinae glyptodont from the Santa Cruz Formation, using micro-computed tomography and scanning electron microscopy images. We compare the juvenile mandible with adult specimens and discuss the taxonomic assignment, the juvenile and adult mandibular and dental characters, and dental eruption and tooth wear.

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INTRODUCTION

We focus here on one specimen of the Cingulata, which along with the Pilosa (Tardigrada + Vermilingua) forms the major clade Xenarthra within placental mammals (Engelmann, 1985). The Cingulata is composed of the Dasypodidae, Peltephilidae, Pampatheriidae, Palaeopeltidae, and Glyptodontidae (McKenna and Bell, 1997), all easily recognized by the presence of armor consisting of articulated osteoderms covering most of the body of the animal (Hoffstetter, 1958; Engelmann, 1985). The traditional familiar arrangement of cingulates has been debated in the last years, due to changes within glyptodonts (Fernicola, 2008), the recognition of the Pachyarmatheriidae (Fernicola et al., 2018), and mainly by recent analyses that proposed the recognition of only two major clades of cingulates, Dasypodidae and Chlamyphoridae (to which glyptodonts belong) (Delsuc et al., 2016; Gibb et al., 2016; Mitchell et al., 2016).

Glyptodonts (sensu McKenna and Bell, 1997) are known from the late Eocene to the early Holocene of South, Central, and North America (see Zurita et al., 2016). Their fossil record is represented mainly by disarticulated osteoderms during the Eocene and Oligocene (Ameghino, 1902; McKenna et al., 2006), and the oldest known skull remains are from the early Miocene (Ameghino, 1889, 1898; Scott, 1903; Gaudin and Croft, 2015). Glyptodont skulls are relatively well known from the early Miocene through the earliest Holocene (Soibelzon et al., 2012) when glyptodonts became extinct. The oldest known glyptodont skulls belong to the Propalaehoplophorinae (sensu McKenna and Bell, 1997; Propalaehoplophoridae sensu Fernicola, 2008) from the Santa Cruz Formation (late early Miocene) in Patagonia, Argentina (Ameghino, 1898; Scott, 1903), and to Glyptodontidae incertae sedis from the Chucal Formation (early Miocene) in the Chilean Altiplano (Croft et al., 2007).

For the Santa Cruz Formation, several skulls and mandibles have been described and assigned to five traditionally recognized genera (*Propalaehoplophorus* Ameghino, 1887; *Cochlops* Ameghino, 1889; *Asterostemma* Ameghino, 1889; *Eucinepeltus* Ameghino, 1891a; and

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Metopotoxus Ameghino, 1898), and although we have information about the phylogeny, taxonomic issues, body mass, locomotion, mastication, and feeding habits of these glyptodonts (see Ameghino, 1898; Scott, 1903; Hoffstetter, 1958; Croft et al., 2007; Fernicola, 2008; González Ruiz, 2010; Vizcaíno et al., 2012a), our knowledge on the juvenile stages is still poor.

Juvenile specimens of Miocene propalaehoplophorinae glyptodonts were mentioned by Ameghino (1895–1920), Scott (1903), and Tauber (1994), but never described in detail. Additional information of Pliocene and Pleistocene juvenile glyptodonts appeared in different publications (Burmeister, 1870–1874; Ameghino, 1889; Lydekker, 1895; Castellanos, 1940; Vinacci Thul, 1945; Gillette and Ray, 1981; Oliveira et al., 2010; Carranza-Castañeda and Gillette, 2011; Chimento, 2012; Gillette et al., 2016). Other contributions exclusively referred to the description of juvenile specimens of Pliocene and Pleistocene glyptodonts are mostly based on isolated osteoderms or teeth (Rinderknecht, 2000; Zurita et al., 2009, 2011; Luna and Krapovickas, 2011; Zamorano et al., 2014; Luna et al., 2018), with the remarkable exception of the fetal specimen of *Glyptodon* Owen, 1839, described by Zurita et al. (2009).

In this setting, the objective of this contribution is to describe, both internally and externally, a newly recovered mandible belonging to a juvenile specimen of a propalaehoplophorinae glyptodont, collected by our team in field work carried out during 2015 in Santa Cruz Province, Argentina, to discuss the mandibular and dental characters of glyptodonts.

GEOLOGICAL SETTING

The specimen was collected at the cliffs of the estuary of the Gallegos River (51°34′15.80″S, 69°25′28.00″W) in the property of Killik Aike Norte farm, Santa Cruz Province (Patagonia, Argentina) (Fig. 1A). The locality of Killik Aike Norte, where the Santa Cruz Formation crops out, has been known since 1845 (Marshall, 1976; Brinkman, 2003; Vizcaíno et al., 2012b) and is dated in this area from ca. 18 to 16 Ma (Burdigalian, late early Miocene) (Fleagle et al., 2012; Perkins et al., 2012).

Three fossiliferous levels were described for Killik Aike Norte, which are placed at the base of the section: two of sandstone (NF1, NF3) and one tufaceous (NF2) interbedded. The most abundant fossiliferous level (NF2) has been dated to ca. 17.0 Ma, and all the fossil levels (NF1, NF2, NF3) are below a guide level of the Santa Cruz Formation, the white tuff (TB, 'Toba Blanca') dated to ca. 16.89 Ma (Tauber et al., 2004a, 2004b; Tejedor et al., 2006; Fleagle et al., 2012; Perkins et al., 2012) (Fig. 1B, C).

The new specimen was found in an isolated fragmentary rock, filled and surrounded by a matrix of volcanic ashes, of massive structure, probably coming from the NF2 (ca. 17.0 Ma) or any of the potentially fossiliferous upper levels of ash, ranging from ca. 16.4 to ca. 16.9 Ma. This specimen increases the numerous fossil vertebrates known for Killik Aike Norte (e.g., Ameghino, 1889; Scott, 1903–1928; Martin, 1904; Riggs, 1926; Brinkman, 2003; Tauber et al., 2004a, 2004b; Tejedor et al., 2006; Degrange and Tambussi, 2011), especially the cingulate association represented by *Peltephilus* Ameghino, 1887, *Stegotherium*, Ameghino, 1887, *Prozaedyus* Ameghino, 1891a, *Stenotatus* Ameghino, 1891b, *Proeutatus* Ameghino, 1891a, and *Eucinepeltus* Ameghino, 1891a (González Ruiz et al., 2015b, 2017).

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, U.S.A.; **CORDPZ**, Museo de Paleontología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina; **FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **KUVP**, University of Kansas Museum of Natural History, Vertebrate Paleontology, Lawrence, Kansas, U.S.A.; **MACNA**, Colección Ameghino, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MPEFPV**, Colección Paleontología de Vertebrados, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; **MPMPV**, Museo Regional Provincial 'Padre Manuel Jesús Molina,' Paleontología Vertebrados, Río Gallegos, Argentina.

Additional Abbreviations—Mf, upper molariform; **mf**, lower molariform; **HI**, hypsodonty index.

MATERIALS AND METHODS

Measurements and Images

All linear measurements are expressed in mm. Measurements larger than 5 mm were taken with a Mitutoyo digital vernier caliper, and those shorter than 5 mm and angles were taken with a Fiji caliper (Schindelin et al., 2012). Images were taken using a Nikon D5200 camera with a Nikon AF-S Micro-Nikkor 105 mm 1:2.8G ED lens, in a light box with fluorescent tubes. Scanning electron microscopy (SEM) images were taken on the scanning electron microscope (JEOL JSM-6460) at ALUAR (Aluminios Argentinos, Puerto Madryn, Argentina). We used micro-computed tomography (µ-CT) scans acquired on a SkyScan 1173 instrument in Y-TEC (YPF Tecnología, Buenos Aires, Argentina) to obtain a three-dimensional (3D) model and segmentation of the specimen at the 3D imaging facilities of the UMR 7207 CR2P (MNHN CNRS UPMC, Paris, France). The data were reconstructed using phoenix datos|x 2.0 reconstruction software, then exported into a 16-bit TIFF image stack and segmented with Mimics Innovation Suite 18 (Materialise), and exported with 3D object rendering. The hypsodonty index was calculated, following Vizcaíno et al. (2011), as the depth (dorsoventral diameter) of mandible at mf6 divided by the length (anteroposterior diameter) of the tooth row (here, from mf1 to mf7).

General Terminology of the Glyptodont Dentition

Descriptions follow Evans (1994) and De Iuliis and Pulerà (2011) for general anatomy, Smith and Dodson (2003) and Hillson (2005) for general tooth and mandible terminology, and Gillette and Ray (1981), Wible and Gaudin (2004), Croft et al. (2007), Kalthoff (2011), and Gaudin and Lyon (2017) for glyptodont and cingulate anatomical terminology. The accepted dental formula for glyptodonts is eight teeth in each maxilla and eight teeth in each dentary (8/8), with a total of 32 teeth (Ameghino, 1889; Gillette and Ray, 1981). There are some questioned cases of atrophied incisors, some exceptional cases of supernumerary teeth, and no evidence of tooth replacement (Cabrera, 1944; Gillette and Ray, 1981; González Ruiz et al., 2015a). Croft et al. (2007) indicated that some anterior molariforms resemble a tribosphenic tooth, but the highly specialized teeth of Xenarthra have never been correlated to the tribosphenic dentition of most other mammals (McDonald, 2003; Pujos et al., 2012). Although some authors suggested homologies with the eutherian dental formula (Lydekker, 1895; Hoffstetter, 1958; Thenius, 1989), these interpretations were based on the simplified trilobate anatomy of the anterior-most upper and lower teeth observed in some glyptodonts, sometimes called incisiforms (Paula Couto, 1979; Pujos and De Iuliis, 2007). Because all teeth are confined to the parallel portions of the palate and the mandible, Gillette and Ray (1981) concluded that the upper and lower anterior teeth, i.e., the incisiforms and the caniniforms, were always absent; thus, all teeth are considered molariforms. Glyptodont molariforms are hypselodont (high-crowned, rootless, and ever growing) (Mones, 1982; Ciancio et al., 2014), formed by an internal layer of osteodentine, a middle layer of orthodentine, and an external layer of hypermineralized orthodentine. The internal and the external layers are harder than the middle layer, forming an internal band and external crests of higher relief, with lower areas of the middle layer forming most of the molariform occlusal surface (Kalthoff, 2011; Green and Kalthoff, 2015).

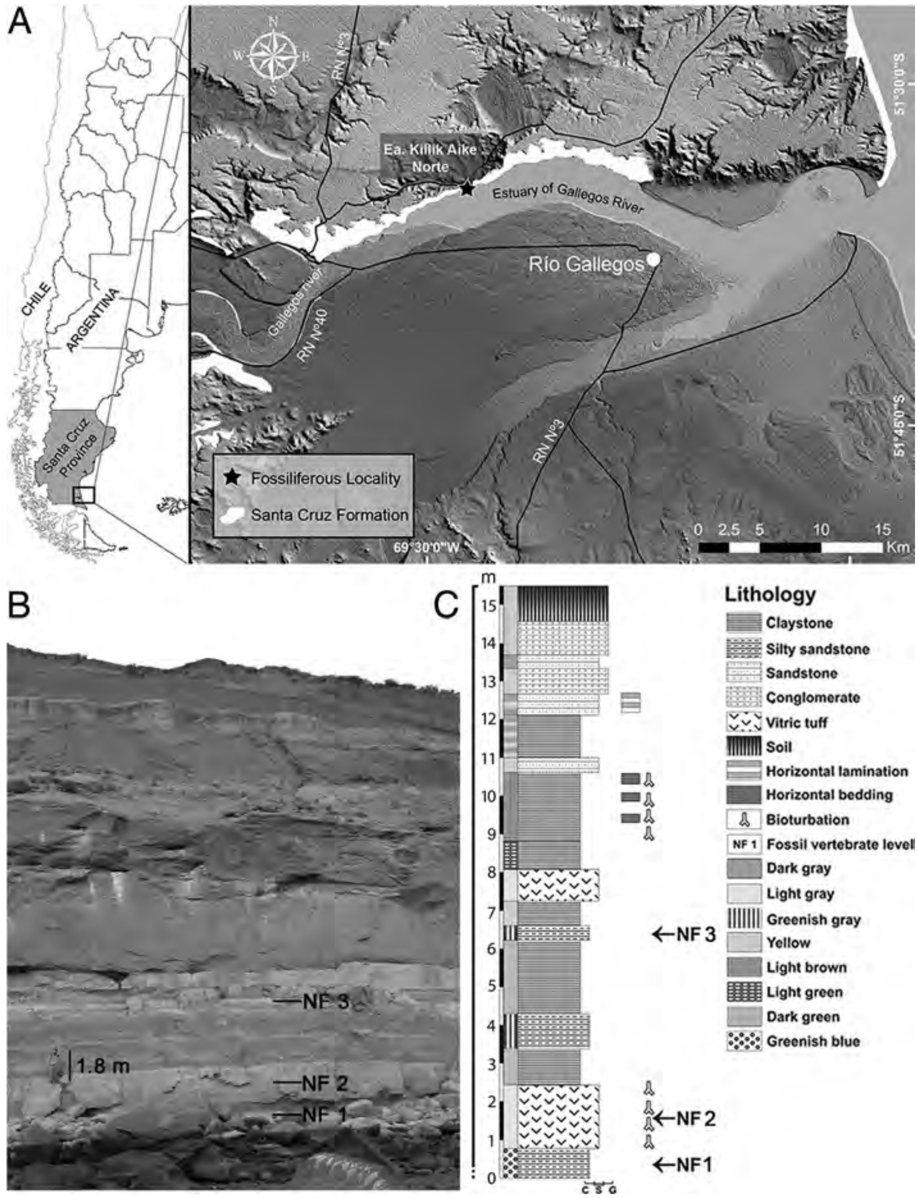

FIGURE 1. **A**, location map of the fossiliferous locality Killik Aike Norte, with the Santa Cruz Formation indicated; **B**, photograph of the profile; **C**, generalized geological profile.

Juvenile and Adult Specimens of Propalaehoplophorinae

The late early Miocene glyptodonts from the Santa Cruz Formation are represented by five genera formally recognized and described: *Propalaehoplophorus*, *Cochlops*, *Asterostemma*, *Eucinepeltus*, and *Metopotoxus*. Because the new specimen is a mandibular fragment, we made comparisons only with confidently assigned adult specimens from the Santa Cruz Formation (see Ameghino 1889, 1891a, 1898; Scott, 1903; Croft et al., 2007; Fernicola, 2008; González Ruiz, 2010; Fernicola et al., 2018), such as *Propalaehoplophorus* (MLP 16-15, MACN A 4755, and MACN A 4757) and *Eucinepeltus* (MPEF PV 1383, MACN A 4760, MACN A 4761, KUVP 594, and FMNH 12065). Therefore, three genera were excluded from the comparisons for following reasons: (1) *Cochlops*: there are several references to mandibular specimens of *Cochlops* (Ameghino, 1891a, 1898; Scott, 1903; Croft et al., 2007; González Ruiz, 2010; Vizcaíno et al., 2012a), but their attributions, as well as the mandibular diagnostic characters compared with those of *Propalaehoplophorus*, were neither clearly assessed nor published (Scott, 1903; Croft et al., 2007; González Ruiz, 2010); (2) *Asterostemma*: only Ameghino (1895–1920) briefly described (without providing collection number or figures) at least one mandibular specimen that we could not find stored in the Ameghino collection or in the collection catalog; in addition, the validity of this genus has been questioned (Scott, 1903; Paula Couto, 1979; González Ruiz, 2010); and (3) *Metopotoxus*: there is no reference to mandibular specimens of this genus, and its validity has been questioned by several authors (Simpson, 1947; González Ruiz, 2010; Vizcaíno et al., 2012a).

Juvenile specimens of Propalaehoplophorinae were never described in detail. Ameghino (1895–1920) briefly described the eruption sequence of the mf1 for Propalaehoplophorinae based on an ontogenetic sequence of three specimens. Although we discuss Ameghino's (1895–1920) observations (see Discussion), he did not describe, figure, or provide collection numbers to identify the specimens in his collection (MACN A). Scott (1903) assigned one right mandibular specimen (MACN A 4752) published by Ameghino (1891a, 1898) as corresponding to a young individual based on the original description (Ameghino, 1891a); according to Scott (1903), compared with other specimens, it is slightly smaller and slenderer and has small alveoli for atrophied incisors placed anterior to the mf1. Although the specimen is somewhat different from other specimens, the development of the occlusal surfaces of the preserved teeth (mf1–mf7) is complete (being flat like an adult specimen), so it could be considered to be a young adult, in agreement with Scott (1903). Tauber (1994) described and assigned a skull of a Propalaehoplophorinae (CORDPZ 1371) as a juvenile because of the small size, the lesser development of the occlusal surfaces of Mf2 and Mf3, and the porosity of the frontal and maxillary bones. Finally, we found an isolated juvenile tooth of a Propalaehoplophorinae from Santa Cruz Province at the MLP collections (MLP 68-VI-25-437), but its position in the tooth row and whether it is upper or lower are difficult to determine, besides, its stratigraphic provenance is unknown.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
XENARTHRA Cope, 1889
CINGULATA Illiger, 1811
GLYPTODONTIDAE Gray, 1869
PROPALAEHOPLOPHORINAE Ameghino, 1891b
EUCINEPELTUS Ameghino, 1891a

Type Species—*Eucinepeltus petesatus* Ameghino, 1891a; from Santa Cruz Formation, Monte Observación (Cerro Observatorio), Santa Cruz Province, Argentina.

cf. *EUCINEPELTUS* Ameghino, 1891a
(Figs. 2–6)

Referred Specimen—MPM PV 17408, fragment of mandible (left dentary) with most of the horizontal ramus (corpus mandibularis), the mandibular symphysis, mf1–mf7, and the external wall of the alveoli corresponding to the mf8. The mf8 and most of the upper region of the vertical ramus (ramus mandibularis) are not preserved.

Geographic and Stratigraphic Provenance—Killik Aike Norte, Santa Cruz Province, Argentina, late early Miocene (Burdigalian Age), Santa Cruz Formation (Flynn and Swisher, 1995; Tauber et al., 2004a; Fleagle et al., 2012; Perkins et al., 2012).

DESCRIPTION

Dentary

The preserved portion measures 73 mm in length. The horizontal ramus is elongate; the posterior half is regularly curved, convex labially, and flat lingually, and the anterior half is ventrolingually curved and anteroventrally expanded, forming the symphyseal area (Fig. 2A–C). The vertical ramus is not preserved. In occlusal view, there is an almost complete, short predental zone ('spout') of 4.1 mm, only slightly everted, followed posteriorly by the tooth row (Fig. 2A–C). In lateral view (Fig. 2A), anteriorly, there is no labial depression (for the descending process of the zygomatic arch) and there are three mental foramina: the anterior-most below the mf2, a second small mental foramina below the mf2–mf3, and the posterior-most below the mf3. Posteriorly, the base of the ascending ramus is preserved, represented by the base of the coronoid process at the anterior face of the mf7. In medial view (Fig. 2B), anteriorly, the mandibular symphysis extends dorsally from the rostral tip of the mandible ahead of the mf1 to the posterior margin of the mf3 ventrally and exhibits a rough surface and a rounded anteroventral lingual edge. The symphysis extends slightly below the ventral margin of the horizontal ramus. The mandibular/dental canal is ventral to mf2 (Fig. 3A, B), and lingual to the mf3–mf7 (Fig. 3C, D) because the roots of mf4–mf7 extend ventrally almost to the ventral margin of the mandibular ramus (Fig. 4A, B), which is broken lingual to the mf6 where the mandibular/dental canal is present (Fig. 2B).

Molariforms

There are seven molariforms (mf1–mf7). In occlusal view (Fig. 2C), mf1–mf3 are oriented obliquely to the longitudinal axis of the tooth row, whereas mf4–mf7 are oriented in the same longitudinal axis. In lateral view, all molariforms are conical, with the base ventral and the lateral faces oblique to the plane of the dental series. The preserved tooth row measures 57.4 mm in length. Molariforms have the long axis anteroposteriorly oriented, increasing in size from mf1 to mf5 and decreasing from mf5 to mf7 (Table 1). The mf1–mf4 are simpler than mf5–mf7, with increasing complexity of the development of lobes and grooves from mf1 to mf5, and mf5–mf7 are subequal in complexity.

The mf1 has a reniform outline (Fig. 5A), lingually convex and labially concave, with no deep grooves clearly delimiting lobes. The mf2 is more distinctly reniform than mf1 in outline (Fig. 5B), with two shallow grooves not reaching the tip of the tooth, one lingual anterior and one labial central defining two lobes, thus making an asymmetrical bilobed outline. The mf3 is reniform and sigmoid in outline (Fig. 5C), similar to mf2 although larger, with a lingual deep anterior groove and a labial deep central groove not reaching the tip of the tooth and defining an anterior lobe and a larger posterior one; the central groove has two inner, shallow and narrow grooves, which do not reach the tip of the tooth and define the incipient middle labial lobe (Figs. 2A, 4A), absent in mf1–mf2, indicating a lingual bilobed outline and an incipient labial trilobed outline. The mf4 is reniform and sigmoid in outline (Fig. 5D), with a deep anterior groove lingually and a shallow, narrow posterior groove, both reaching the tip of the tooth and defining an incipient middle lobe from the larger posterior lobe, and two deep, narrow grooves labially that reach the tip of the tooth and define anterior and posterior larger lobes and a small middle lobe, indicating a more trilobed outline than mf3 but less than mf5. The mf5–mf7 have the typical trilobed outline (Fig. 5E–G), with anterior, middle, and posterior lobes limited by two labial and two lingual deep and wide grooves, one anterior and one posterior in each case, all reaching the tip of the tooth. The lobes are rounded (Fig. 5E–G); the anterior and middle lobes are symmetrical, and the posterior lobe is asymmetrical with the labial half larger; the posterior face of the tooth is flat and oblique to the long axis. All molariforms retain the external observable outline from the top to the base (Fig. 4), having open roots (Fig. 4D).

The occlusal surfaces of the mf1–mf2 are blunt and lack wear facets (Figs. 5A, B, 6A), having a central rounded cusp. The mf3 has a central rounded cusp similar to that of mf1–mf2 (Fig. 5C), and a posterolingual, subcircular, small facet oblique to the horizontal plane of the horizontal ramus (Fig. 6C, D), occupying a small part of the occlusal surface. The mf4 has one anterior small, oval facet and one posterior large, reniform facet occupying most of the occlusal surface (Fig. 6E, F); both facets are perpendicularly oriented, and together produce a beveled occlusal surface. The anterior (smaller) and the posterior (larger) facets are mesioventrally and distoventrally oriented, respectively, oblique to the plane of the horizontal ramus. The mf5–mf7 have a single, trilobed, and almost flat facet (Figs. 5E–G, 6G),

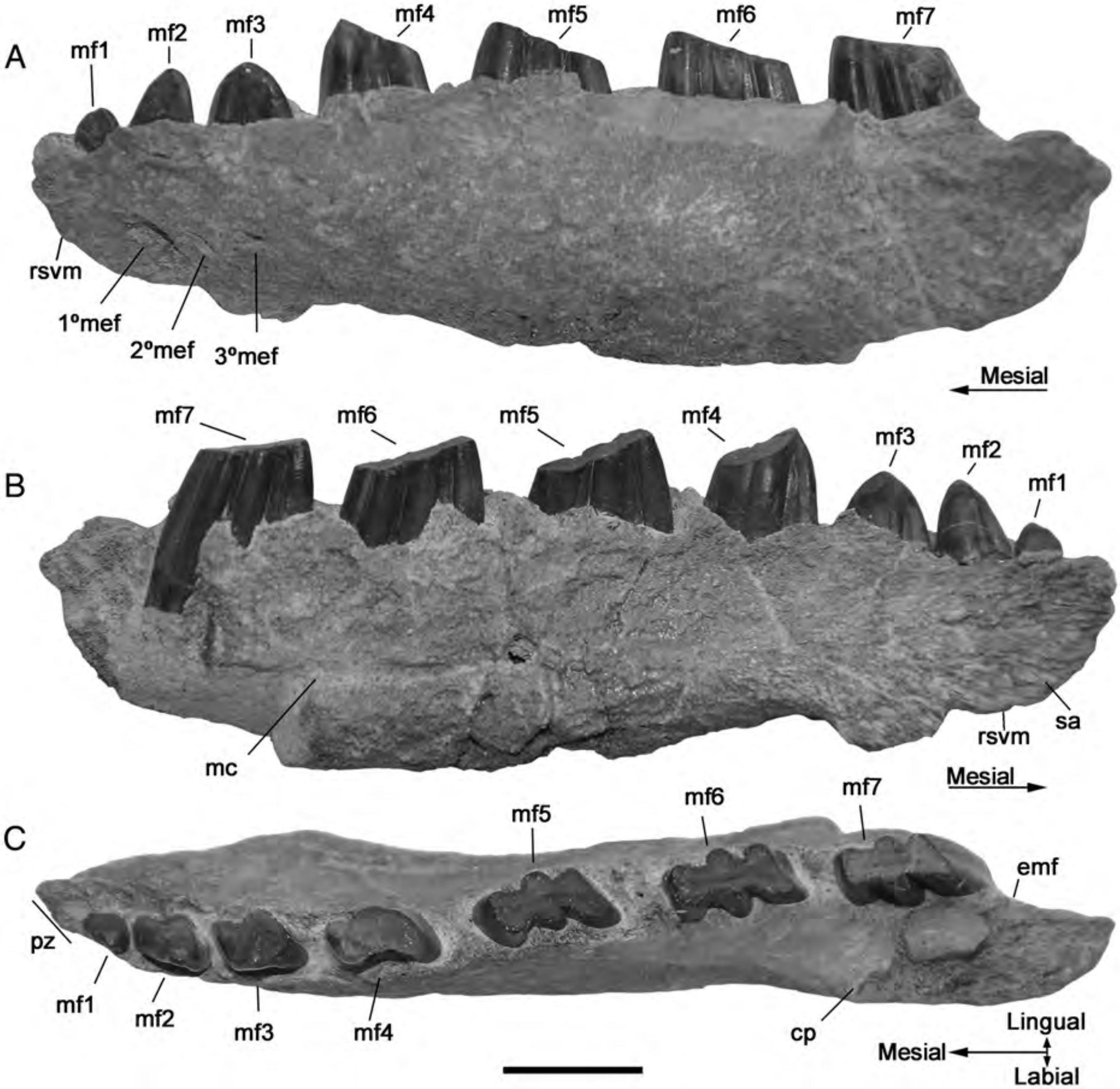

FIGURE 2. MPM PV 17408, cf. *Eucinepeltus*, left hemimandible in **A**, labial, **B**, lingual, and **C**, occlusal views. **Abbreviations**: **cp**, base of the coronoid process; **emf**, external wall of the mf8 alveoli; **mc**, mandibular canal; **mef**, mental foramina; **mf**, molariform; **pz**, predental zone; **rsvm**, rounded symphyseal ventral margin; **sa**, symphyseal area. Scale bar equals 10 mm.

oblique distoventrally to the plane of the horizontal ramus, which occupies all the occlusal surface of the tooth.

The mf1 and mf2 have no attrition facets, and the external layer of orthodentine covers all the molariform; in the posterior facet of mf3 and in the anterior facet of mf4, the external and the middle layers of orthodentine are observable, whereas the internal osteodentine layer is not; in the posterior facet of mf4 and in the facets of mf5–mf7, the external and the middle orthodentine layers and the internal osteodentine layer are observable (Fig. 5E–G). In the facets, the external orthodentine and the internal osteodentine (when observable) layers are elevated with respect to the middle orthodentine layer. The external orthodentine layer stands out as a rim in all facet outlines, and the internal osteodentine layer forms a straight, elevated, central line without branching, extending from the center of the anterior lobe to the posterior lobe where it is inclined labially (Fig. 6G).

In the external layer of orthodentine, all molariforms have transverse, rounded, regularly spaced long-period incremental lines in the dentine ('Andresen lines') around the tooth and from the base to the tip. These 'Andresen lines' are parallel or subparallel to the horizontal plane of the horizontal ramus, but

TABLE 1. Measurements (in mm) of MPM PV 17408, cf. *Eucinepeltus*, molariforms.

Molariform	Longitudinal diameter	Transverse diameter
mf1	3.3	1.7
mf2	4.8	2.7
mf3	5.1	3.0
mf4	6.4	3.7
mf5	8.6	4.1
mf6	8.3	4.0
mf7	8.1	3.5

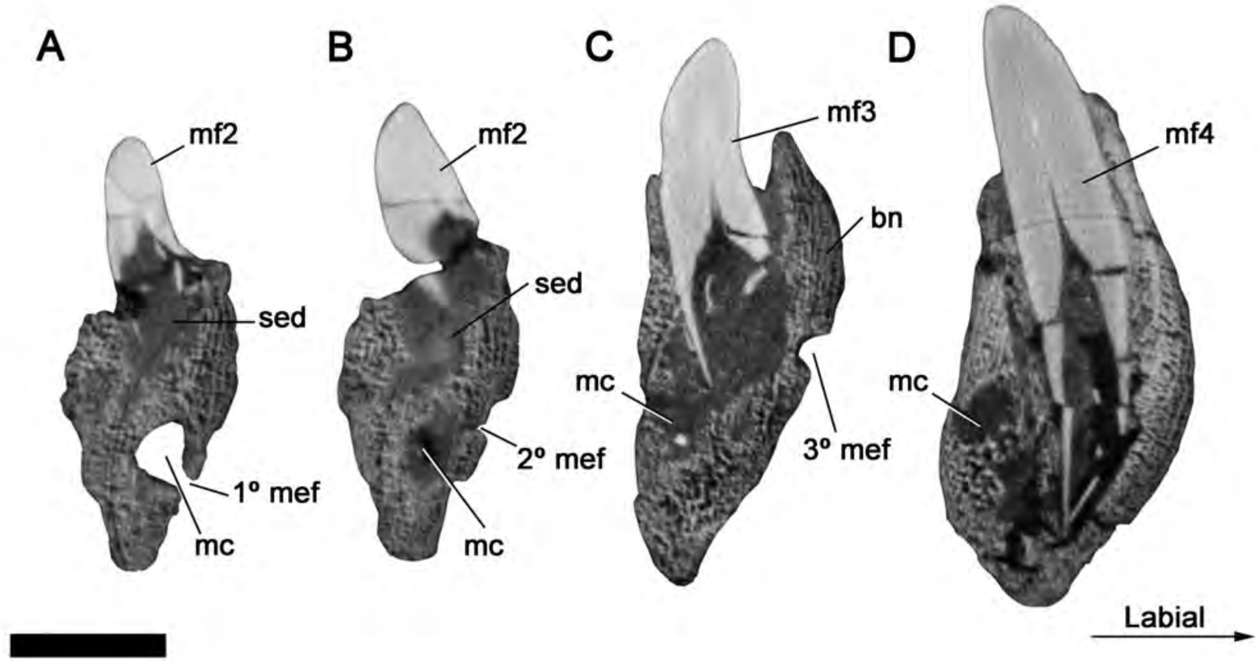

FIGURE 3. MPM PV 17408, cf. *Eucinepeltus*, left hemimandible, digital transverse sections. **A**, at mf2 level (first mental foramina); **B**, at mf2 level (second mental foramina); **C**, at mf3 level; **D**, at mf4 level. **Abbreviations**: **bn**, bone; **mc**, mandibular canal; **mef**, mental foramina; **mf**, molariform; **sed**, sediment. Scale bar equals 5 mm.

some of them, especially those of the labial face of the posterior lobe, are oblique; in the mf5 (Fig. 6G, H), we counted 17 per 50 mm.

DISCUSSION

Taxonomic Assignment

The predental zone of the mandible is short and slightly everted in MPM PV 17408 and *Eucinepeltus* (Figs. 7A, B, 8A, B, 9A, B), whereas it is long and strongly everted in *Propalaehoplophorus* (Figs. 7C, 8C, 9C). The horizontal ramus has no labial depressions and the ventral margin is regularly curved in MPM PV 17408 and *Eucinepeltus* (Fig. 7A, B), whereas the labial depressions are present and the ventral margin is more convex in *Propalaehoplophorus* (Fig. 8C). The HIs in MPM PV 17408 (0.338) and in adult *Eucinepeltus* (0.369) are lower than in adult *Propalaehoplophorus* (0.470) (Table 2), as a result of a shallow horizontal ramus in the first two.

TABLE 2. Measurements (in mm) and hypsodonty indices (HIs) of cf. *Eucinepeltus*, *Propalaehoplophorus*, and *Eucinepeltus*.

Specimen	Mandibular depth at mf6	Length of tooth row (mf1–mf7)	HI: mandibular depth at mf6/ length tooth row
cf. *Eucinepeltus* MPM PV 17408	19.2	57.4	0.338
Propalaehoplophorus MLP 16-15	37.8	80.5	0.470
Eucinepeltus MACN A 4760	42.9	116.2	0.369

The mf4 of MPM PV 17408 is more similar to the mf1–mf3 than to the mf5–mf7 (Fig. 9A), especially in the reniform and sigmoid outlines, with a marked labial concavity and lingual convexity; mf4 has also a small labial middle lobe but no lingual middle lobe, producing an incipient labial trilobed outline and a lingual bilobed outline (Fig. 9A). This morphology is similar to that of adult specimens of *Eucinepeltus* (Fig. 9B) but differs from *Propalaehoplophorus* (Fig. 9C) as described by Ameghino (1887, 1889, 1895–1920, 1898), Scott (1903), and Croft et al. (2007).

Considering that we do not know the complete morphological variations during propalaehoplophorinae glyptodont ontogeny, and that *Eucinepeltus* has three described species from the Santa Cruz Formation (*E. petesatus* Ameghino, 1891a; *E. complicatus* Brown, 1903; and *E. crassus* Scott, 1903) with unresolved taxonomy (González Ruiz, 2010; González Ruiz et al., 2013), we assign the specimen to cf. *Eucinepeltus* following Matthews' (1973) and Bengtson's (1988) recommendations on open nomenclature.

Juvenile and Adult Mandibular and Dental Characters

The preserved portion of the dental series (mf1–mf7) measures 57.4 mm in length, ca. 49% of the same portion in an adult (116.2 mm) of *Eucinepeltus*. In a complete hemimandible of an unborn specimen of *Glyptodon*, it represents 27% of an adult (Zurita et al., 2009). The anteroventral edge of the mandibular symphysis is lingually rounded in juvenile (Fig. 8A) and straight in adult (Fig. 8B) specimens of *Eucinepeltus* and *Propalaehoplophorus* (Fig. 8C); the dorsal margin is less distinctly marked in the juvenile than in the adults, and well developed and straight in the latter; the posteroventral margin of the juvenile extends to the mf3–mf4 boundary (Fig. 8A), to the middle of the mf4 in adults of *Eucinepeltus* (Fig. 8B), and to the mf3–mf4 boundary or the middle of

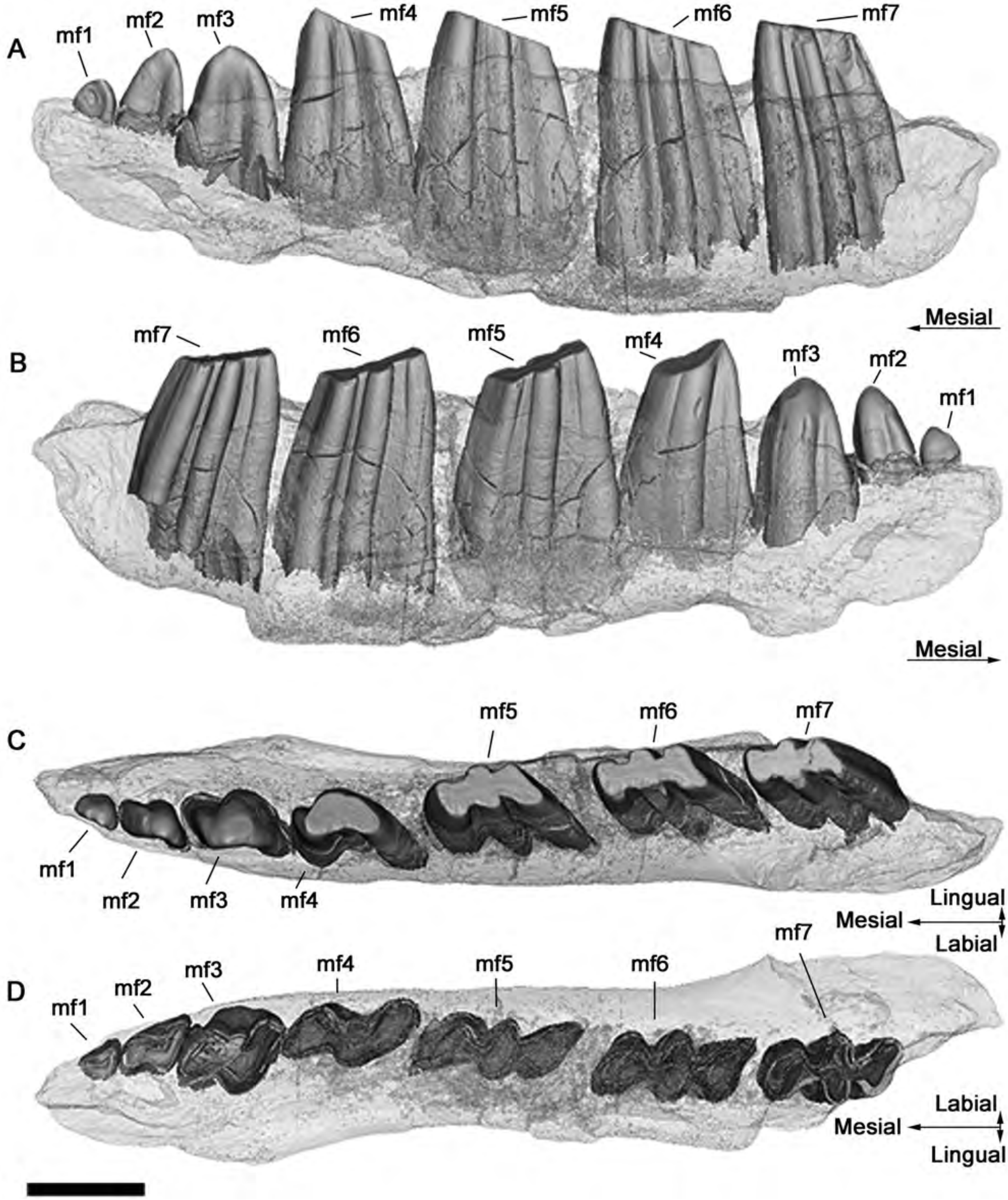

FIGURE 4. MPM PV 17408, cf. *Eucinepeltus*, left hemimandible, digital rendering in **A**, labial, **B**, lingual, **C**, occlusal, and **D**, ventral views. Bone is transparent. **Abbreviation**: **mf**, molariform. Scale bar equals 10 mm.

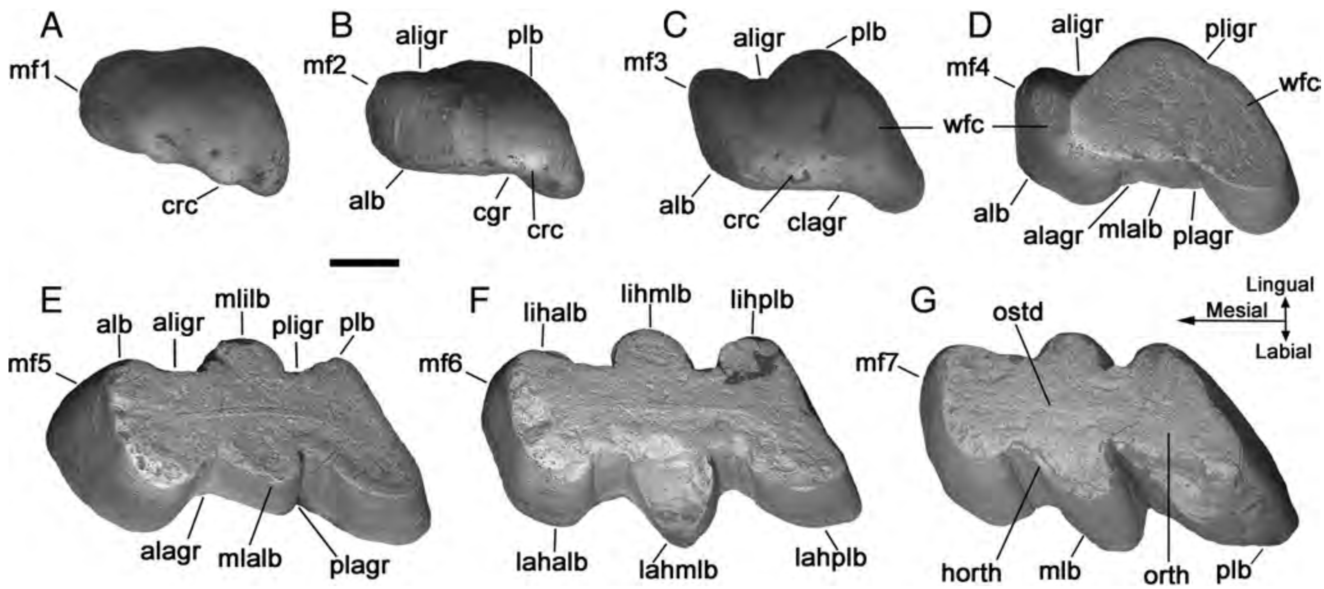

FIGURE 5. MPM PV 17408, cf. *Eucinepeltus*, left lower molariforms, digital renderings in occlusal view. **A**, mf1; **B**, mf2; **C**, mf3; **D**, mf4; **E**, mf5; **F**, mf6; **G**, mf7. **Abbreviations**: **alb**, anterior lobe; **alagr**, anterior labial groove; **aligr**, anterior lingual groove; **clagr**, central labial groove; **cgr**, central groove; **crc**, central rounded cusp; **horth**, hypermineralized orthodentine; **lahalb**, labial half anterior lobe; **lahmlb**, labial half middle lobe; **lahplb**, labial half posterior lobe; **lihalb**, lingual half anterior lobe; **lihmlb**, lingual half middle lobe; **lihplb**, lingual half posterior lobe; **mf**, molariform; **mlalb**, middle labial lobe; **mlb**, middle lobe; **mlilb**, middle lingual lobe; **orth**, orthodentine; **ostd**, osteodentine; **plagr**, posterior labial groove; **plb**, posterior lobe; **pligr**, posterior lingual groove; **wfc**, wear facet. Scale bar equals 1 mm.

the mf4 in *Propalaehoplophorus* (Fig. 8C). The mandibular symphysis is not expanded lingually in the juvenile, being almost a flat rugged surface, indicating that the symphysis was not fused as in all adult glyptodonts (Fariña and Vizcaíno, 2001; but see Croft et al., 2007).

In MPM PV 17408, the space at occlusal surfaces between molariforms is wider than in adults (Fig. 9A–C), as in juvenile specimens of *Glyptotherium* (Gillette et al., 2016). The morphology of the molariforms in lateral view is conical (Figs. 4A, B, 8A), but rectangular in adults of Propalaehoplophorinae (Fig. 8B, C) and in other glyptodonts. The main differences in the occlusal surfaces between juvenile and adult specimens occur in the mf1–mf4; in this case, the first two have rounded cusps, the third has a rounded cusp and a small facet, and the fourth has a beveled occlusal surface (Figs. 5A–D, 9A); all eight molariforms in adults have flat occlusal surfaces (Fig. 9B, C), similar to the mf5–mf7 in the juvenile (Figs. 5E–G, 9A), suggesting a stepwise dental eruption.

The ‘Andresen lines’ (Green and Kalthoff, 2015) observed in the external orthodentine layer of the molariforms were interpreted by Carranza-Castañeda and Gillette (2011) as probable growth lines in juvenile specimens of the glyptodont *Glyptotherium* Osborn, 1903, but they counted 16 per 100 mm, whereas we counted 17 per 50 mm, which could indicate a slow down of

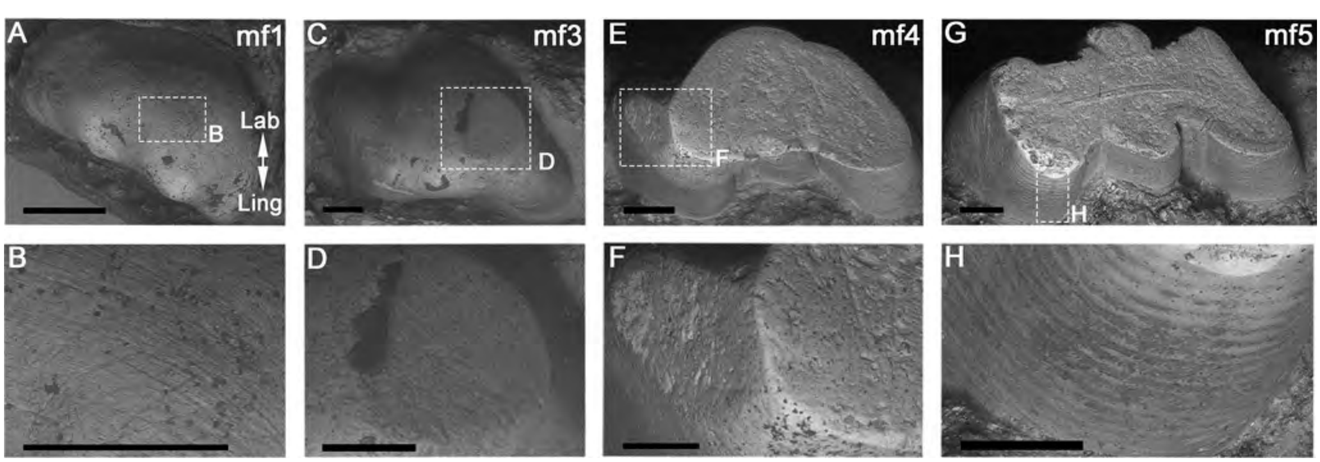

FIGURE 6. MPM PV 17408 (cf. *Eucinepeltus*), mf1, mf3, mf4, and mf5 of left hemimandible, digital renderings. **A**, mf1 in occlusal view; **B**, detail of microwear in nonchewing region of mf1; **C**, mf3 in occlusal view; **D**, detail of the wear facet of mf3; **E**, mf4 in occlusal view; **F**, detail of the beveled wear facets of mf4; **G**, mf5 in occlusal view; **H**, detail of the growth lines of mf5. **Abbreviations**: **mf**, molariform; **Lab**, labial; **Ling**, lingual. Scale bars equal 1 mm.

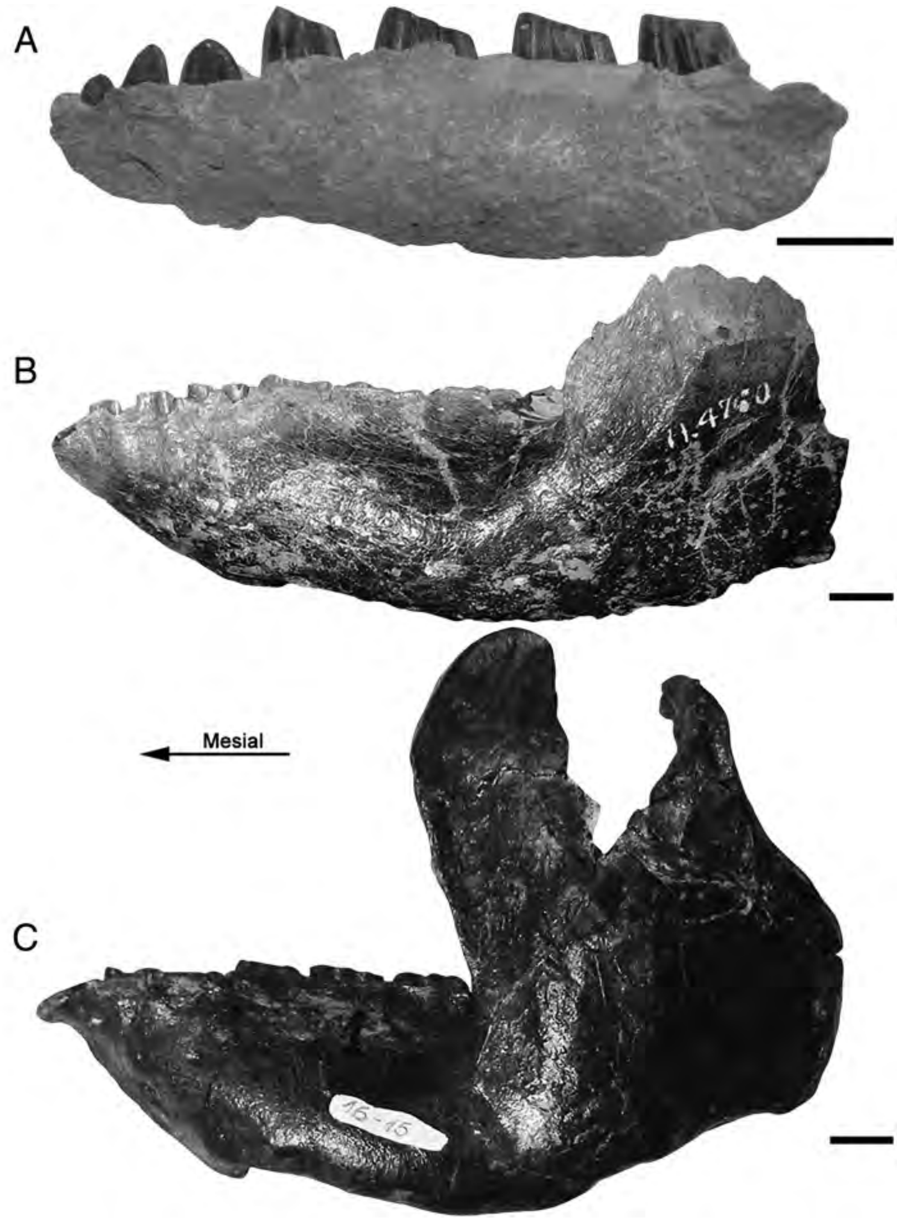

FIGURE 7. Glyptodont left hemimandibles in labial view. **A**, MPM PV 17408, cf. *Eucinepeltus*; **B**, MACN A 4760, *Eucinepeltus*; **C**, MLP 16-15, *Propalaehoplophorus*. Scale bars equal 10 mm.

growth toward adulthood. The relation of the transverse bands with the relative age of the specimens needs to be explored with more specific techniques and a larger sample of specimens.

Dental Eruption

Ameghino (1895–1920) described the eruption sequence of anterior lower molariforms in propalaehoplophorinae glyptodonts based on an ontogenetic sequence of three mandibles, and he observed, from the youngest to oldest: (1) two germs of incisors, the mf1 not erupted, and the mf2 erupted and unworn; (2) two or three semipartitioned cavities in front of mf1 attributed to probable abortive incisors, and the mf1 not erupted; and (3) three small alveoli of the incisors and the mf1 completely erupted and worn. Ameghino (1895–1920) concluded that the dental germs are in an alveolar canal that closes progressively, the incisors never erupt, and anterior-most molariforms erupt successively, with the mf1 the last. Unfortunately, the specimens mentioned by Ameghino (1895–1920) were not found in collections; they were published without collection numbers or figures, and only the first one was clearly assigned by Ameghino to *Asterostemma* (see Juvenile and Adult Specimens of Propalaehoplophorinae); in addition, the presence of alveoli of atrophied incisors in glyptodonts has not yet been corroborated (Mercerat, 1981; Lydekker, 1895; González Ruiz et al., 2015a). Gillette and Ray (1981) and Gillette et al. (2016) found no evidence of the complete eruption sequence in *Glyptotherium*, but they identified a relative late eruption of the Mf8 in one specimen, in which the occlusal surface is somewhat shorter than the alveolar portion and the Mf8 is smaller than Mf7, and in a second specimen they found an apparent later eruption of mf2 and mf3; unfortunately, there are no records of juvenile specimens with the mf8.

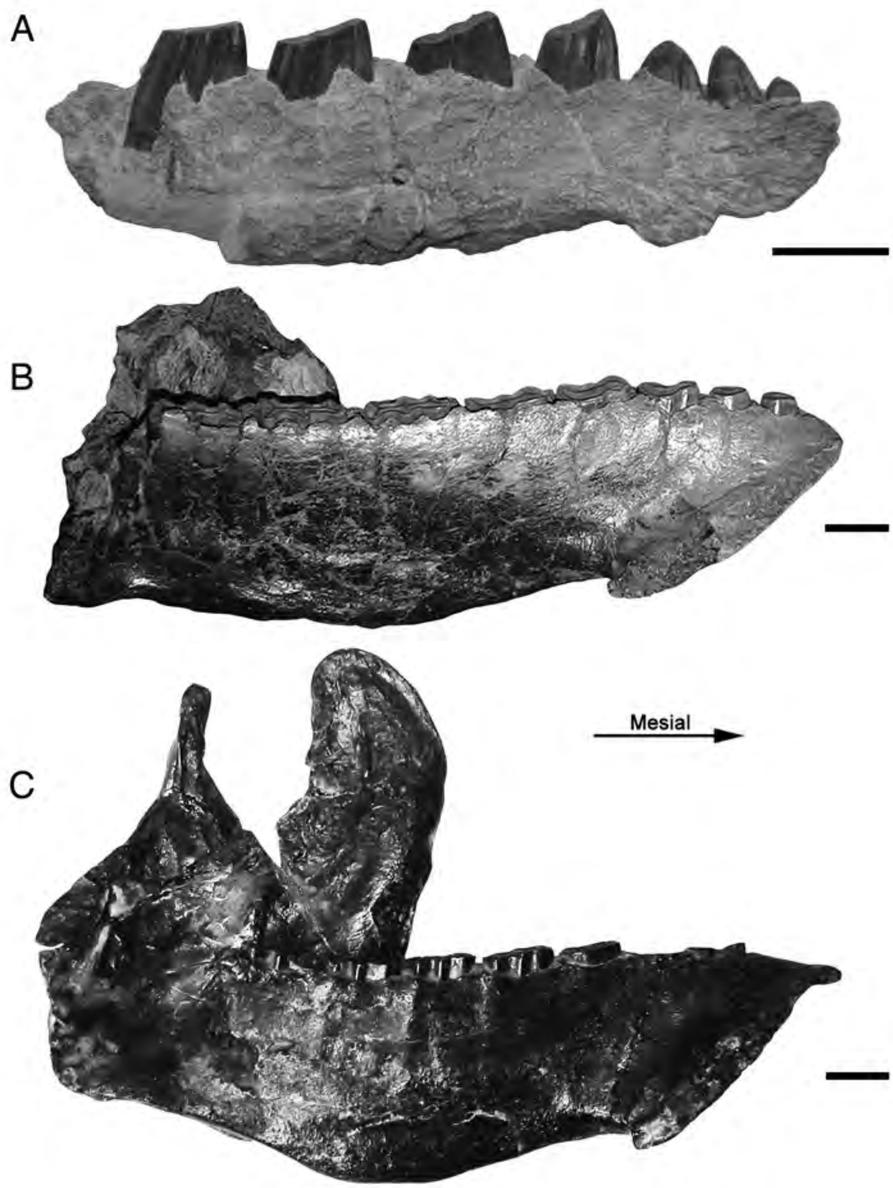

FIGURE 8. Glyptodont left hemimandibles in lingual view. **A**, MPM PV 17408, cf. *Eucinepeltus*; **B**, MACN A 4760, *Eucinepeltus*; **C**, MLP 16-15, *Propalaehoplophorus.* Scale bars equal 10 mm.

Although the preserved molariforms appear to be erupted in the new specimen MPM PV 17408, the alveolar dorsal margin of the horizontal ramus is not fully preserved (Fig. 2A, B). This implies the possibility that mf1–mf3 are not fully erupted, especially mf1–mf2, which are unworn. This new specimen supports the view of Ameghino (1895–1920), who observed that the mf1 is the last tooth to erupt, or at least the last to be functional. This condition of MPM PV 17408, as well as that observed in *Glyptotherium* by Gillette and Ray (1981) and Gillette et al. (2016), indicates an eruption progression from the center (mf5–mf7) to the anterior region (mf1–mf3), and also probably to the posterior region of the tooth row (mf8); unfortunately, the mf8 was not preserved in the new specimen. This also agrees in part with Ciancio et al. (2012) in that the eruption of the permanent dentition generally occurs from posterior to anterior in the armadillo *Dasypus* Linnaeus, 1758. Finally, beyond fragmentary segments of the mandibular/dental canal, we could not find evidence of internal structures (i.e., other mandibular canals), probably because of the low quality of preservation of MPM PV 17408, that may indicate the existence of teeth ahead of the mf1 as those found in other xenarthrans (Hautier et al., 2016; Ferreira-Cardoso et al., 2019), nor alveoli or dental germs of atrophied incisors as proposed by Ameghino (1895–1920), nor evidence of tooth replacement in any molariform.

Tooth Wear

Attrition is produced by tooth-to-tooth contact, which tends to form macrowear facets (see Ungar, 2015). In MPM PV 17408, attrition is absent in mf1–mf2 (Fig. 5A, B) but is evident in mf3 due to a small facet (Fig. 5C), as well as in

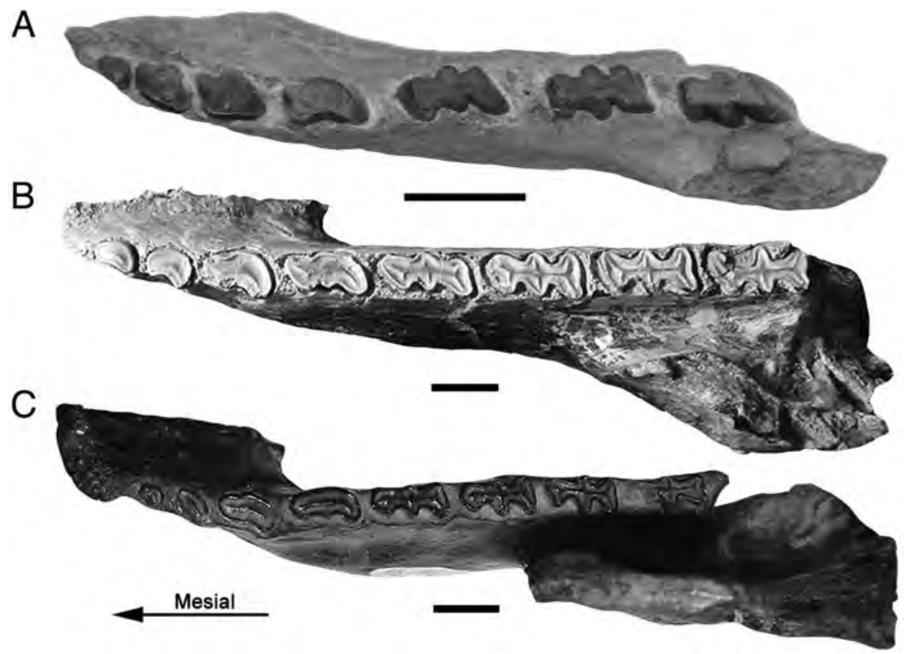

FIGURE 9. Glyptodont left hemimandibles in occlusal view. **A**, MPM PV 17408, cf. *Eucinepeltus*; **B**, MACN A 4760, *Eucinepeltus*; **C**, MLP 16-15, *Propalaehoplophorus.* Scale bars equal 10 mm.

mf4, which has two facets, one small and one large, forming a beveled occlusal surface (Fig. 5D); attrition is also seen in mf5–mf7, each with a complete and almost flat facet occupying all the molariform surface (Fig. 5E–G). All facets are at oblique angles with respect to the horizontal plane of the horizontal ramus, from ca. 20° in mf4 reducing progressively to ca. 5° in mf7 (Figs. 4A, B, 7A, 8A), whereas all occlusal surfaces are subparallel to the horizontal plane of the horizontal ramus in adults (Figs. 7B, C, 8B, C). The different degrees of development of the occlusal surfaces allow us to infer that mf5–mf7 are functional first, because they have all occlusal surfaces occupied by attrition facets like in adult specimens, and also because they erupted first (see Dental Eruption); then, the incorporation of molariforms in the masticatory process progresses anteriorly. This progression probably goes also posteriorly, as indicated by the presence of Mf8 with less development of the occlusal surfaces than the preceding Mf7, and so forth, as was indicated for juvenile specimens of *Glyptotherium* by Gillette and Ray (1981).

The beveled mf4 (Fig. 6E, F) of this specimen is unique in glyptodonts because all adult glyptodonts do not have beveled teeth; the flat occlusal surface is a synapomorphy of Glyptodontia (Fernicola, 2008). Beveled molariforms are present in armadillos due to the occlusion of the lower tooth between its immediate upper homologue and its more anterior neighbor, as reported by Ciancio et al. (2012) for *Dasypus.* Beveled teeth are present in the oldest known armadillos from the Eocene (*Utaetus* Ameghino, 1902; *Lumbreratherium* Herrera, Powell, Esteban, and Del Papa, 2017; and *Astegotherium* Ameghino, 1902), and in other armadillos, both extinct (e.g., *Prozaedyus*, *Proeutatus*, and *Eutatus* Gervais, 1867) and extant (e.g., *Dasypus*; and *Euphractus* Wagler, 1830) (Simpson, 1932; Gaudin and Wible, 2006; Vizcaíno, 2009; Ciancio et al., 2012, 2014; Herrera et al., 2017). In this sense, the temporary presence of this character in the juvenile specimen here reported could be a reflection of this beveled occlusal surface or the result of the masticatory movements (see Gillette and Ray, 1981; Fariña, 1985; Fariña and Vizcaíno, 2001).

Original microwear usually occurs on occlusal surfaces and does not extend to nonchewing regions of a molar or molariform tooth (Teaford, 1988). The incidence of indistinguishable microwear on both chewing and nonchewing regions of a single tooth has long been cautioned in the interpretation of the originality of microwear features (Teaford, 1988). The microscopic patterns of MPM PV 17408 are visible on occlusal surfaces and extend to all nonocclusal regions of the teeth in this particular mandibular series (Fig. 6B–D). The similarity is obvious under both low-magnification light microscopy and SEM. Therefore, we cannot reject the hypothesis that the visible scratches and pits in this specimen are a result of random, non-food-related causes. As such, we cannot objectively analyze the ecological potential of microwear on this specimen.

Eucinepeltus has been interpreted by Vizcaíno et al. (2011), on the basis of the hypsodonty index and the relative muzzle width index, as highly selective feeder in relatively closed habitats, living within the flora of the Santa Cruz Formation (late early Miocene) on the Atlantic coast represented by a mixture of open, semiarid temperate forests and humid warm-temperate forests (Brea et al., 2012, 2013). Unfortunately, the relative muzzle width could not be calculated for cf. *Eucinepeltus* because the skull was not preserved, so the niche requirements could not be inferred, although at least the HI is similar to that of an adult *Eucinepeltus.*

CONCLUSIONS

We described in detail one of the few and oldest known juvenile specimen of a Miocene (Burdigalian Age) glyptodont from Patagonia (Argentina).

The assignment as cf. *Eucinepeltus* is based on (1) mandibular predental zone not much everted, almost straight and subparallel to the molariform series; (2) horizontal ramus with no labial depressions, and with the ventral margin regularly curved; and (3) mf4 more similar to mf1–mf3 than to mf5–mf7.

The preserved portion of the dental series (mf1–mf7) represents ca. 49% of the same portion in an adult of *Eucinepeltus*, and the HI is similar between the new specimen (0.338) and an adult *Eucinepeltus* (0.369). The main juvenile characters were found at the symphysis (not expanded lingually, rounded anteroventral edge, dorsal margin less distinctly marked, and posteroventral margin extends to the mf3–mf4 boundary) and at the molariforms (conical in lateral view, mf1–mf2 with rounded cusps, mf3 with a rounded cusp and a small facet, and mf4 with a beveled occlusal surface).

In cf. *Eucinepeltus*, the mf1 is the last erupted tooth, or at least the last to be functional, and the eruption progresses from the center (mf5–mf7) to the anterior region (mf1–mf3) of the tooth row. Attrition is absent in mf1–mf2 and is evident from mf3 to mf7. The beveled mf4 of this specimen is unique because adult glyptodonts do not have beveled teeth.

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