

FIRST RECORD OF SUPERNUMERARY TEETH IN GLYPTODONTIDAE (MAMMALIA, XENARTHRA, CINGULATA)

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The presence of extra teeth, defined as the presence of teeth in excess of the normal expected number in any of the dental arcades, has been reported for nearly all orders of extant mammals (among others, Wolsan, 1984; Colyer, 1990; Dixon et al., 2005; Natsume et al., 2005; Martin, 2007; Zinoviev, 2010) but are rarely recorded for fossil mammals (Wilson, 1955; McKenna, 1960; Fine, 1964; Wang and Wu, 1976; Rose and Smith, 1979; Fordyce, 1982; Arnal and Vucetich, 2011). These extra teeth occur in both sexes, in wild and captive individuals, in all tooth classes and both tooth generations, in both upper and lower series, both bilaterally and unilaterally, and in the right or left side. They are situated either within a tooth row, as peripheral or intercalated teeth, or outside it, internally or externally (Wolsan, 1984). These teeth are categorized as (1) supplemental teeth that resemble teeth of the normal series in both crown and root morphology, although not always in size; (2) haplodont supernumerary teeth with simple, usually conical, crowns and single roots; and (3) tuberculate extra teeth with complex crowns that have what can be called an occlusal surface bearing several tubercles (Colyer, 1990). Several explanations have been proposed to account for the occurrence of extra teeth in mammals: (1) persistence of deciduous teeth; (2) excessive development in skull size; (3) return to a lost primitive condition (i.e., atavism); (4) mutation producing new tooth germs; and (5) a complete splitting and development of a tooth germ (Wood and Wood, 1933; Wolsan, 1984; Colyer, 1990; De Moraes et al., 2001).

Within the Xenarthra (orders Cingulata and Pilosa), the records of supernumerary teeth are scarce. There are isolated records in Pilosa Megalonychidae (McDonald, 1978; McAfee and Naples, 2012) and in Cingulata Dasypodidae (Scott, 1903; Cattoi, 1966; Wetzel, 1985; Ciancio et al., 2012); however, no supernumerary teeth have been reported in Cingulata Glyptodontidae (sensu McKenna and Bell, 1997).

The Glyptodontidae (Cingulata) (late Eocene–early Holocene) (Scillato-Yané, 1977; Carlini and Scillato-Yané, 1999) comprise a clade of armored herbivorous xenarthrans and, like the rest of Xenarthra, have a particular and distinct dentition from other mammals; they are characterized by being homodont, monophodont, and euhypsodont (Gillette and Ray, 1981). The molariform teeth of glyptodonts lack enamel (like most xenarthrans) and are structurally composed of a central axis (with or without branches of osteodentine), surrounded by a matrix of orthodentine and an external layer of orthodentine hardened by minerals (Ferigolo, 1985; McDonald, 2003; Vizcaíno, 2009; Kalthoff, 2011). Most glyptodonts have eight trilobed and molariform teeth in each hemimaxilla and eight in each dentary (Mf 8/mf 8), none of them located in the premaxillary bone. In

some taxa, the first two or three have a simpler morphology (i.e., not evidently lobed or trilobed) and the Mf1s have been called incisoriforms by several authors, although without implying homologies but function (Ameghino, 1889; Scott, 1903; Hoffstetter, 1958; Paula Couto, 1979; Pujos and De Iuliis, 2007). A reduction in the number of teeth ($n = 32$), relative to the typical eutherian ($n = 54$) and placental ($n = 44$) dental formulas, occurs in Glyptodontidae (Gillette and Ray, 1981; Ji et al., 2002; O’Leary et al., 2013). Despite ongoing work, tooth homologies for this group (i.e., Xenarthra) have not been established. This is because the most basal forms have a peculiar dentition that does not correspond with, or show a known homology to, the typical dental classification used for mammals (i.e., incisors, canines, premolars, and molars) (Ciancio et al., 2012; McAfee and Naples, 2012). The dentition of Xenarthra is unique among mammals and does not retain the tribosphenic condition (Gillette and Ray 1981; Engelmann, 1985; Fariña, 1985; Fariña and Vizcaíno, 2001; McDonald, 2003; Vizcaíno, 2009). Recently, a new dental nomenclature has been proposed for Tardigrada teeth, although their homology with those of other mammals is still unclear (see Pujos et al., 2011, and references therein).

In this contribution, we describe the first case of supernumerary teeth for a glyptodont (Glyptodontidae, Xenarthra) and discuss possible explanations for its occurrence.

Institutional Abbreviations—**GCF**, Grupo Conservacionista de Fósiles, Museo Paleontológico ‘Fray Manuel Torres,’ San Pedro, Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A.

Anatomical Abbreviations—**Mf**, upper molariform tooth; **mf**, lower molariform tooth; **Mfs**, upper molariform teeth; **sMf**, supernumerary upper molariform tooth; **TI**, total length; **Tlds**, total length of the dental series.

Description and Comments

The specimen under study (UCMP 38104) corresponds to an adult *Boreostemma acostae* (Villarroel, 1983), collected by J. Royo y Gómez in 1945 in La Venta (Huila, Colombia), specifically from the Villavieja Formation ‘Monkey Unit.’ The ‘Monkey Unit’ is located at the base of Villavieja Formation (ca. 12.9–11.5 Ma) (middle Miocene) of the Honda Group (Flynn et al., 1997) (Fig. 1). The mammal fauna of the Honda Group characterizes the Laventan Age/Stage or ‘Laventan Land Mammal Age’ (Madden et al., 1997). *Boreostemma acostae* (Villarroel, 1983) was described based upon a large fragment of dorsal carapace and originally assigned to Glyptodontidae Propalaeohoplorinae. Recently, the species was redescribed with added cranial and carapace characters and consecutively reinterpreted as a basal Glyptodontinae (Carlini et al., 2008; Zurita et al., 2013).

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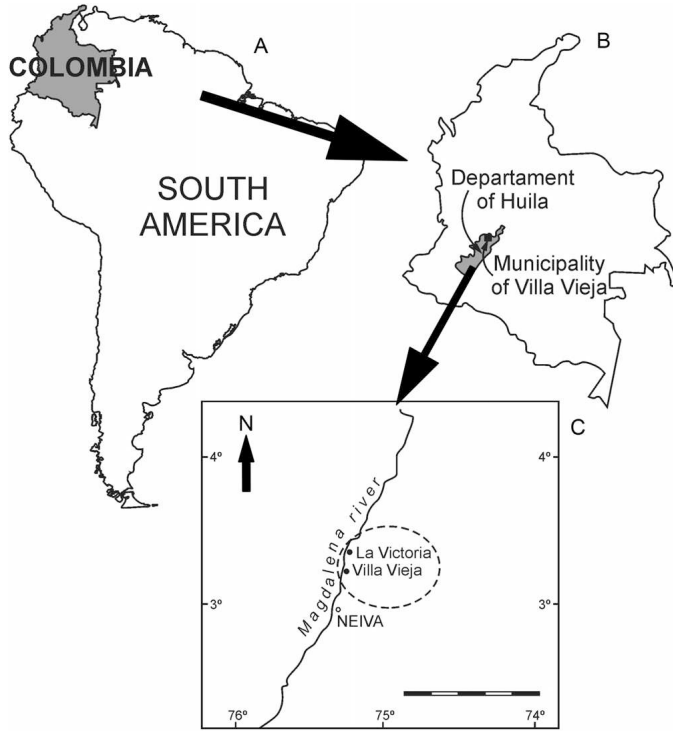


FIGURE 1. Location map showing the area where UCMP 38104 was found. **A**, South America; **B**, Department of Huila, Colombia; **C**, Honda Group outcrops. Scale bar equals 100 km.

This specimen (UCMP 38104) has all the diagnostic characters of *B. acostae*: (1) rostral area very much extended anteriorly, similar to that observed in Cingulata Pamphathiidae; (2) ventral half of the descending process of the maxillae evidently less dorsoventrally elongated than that of Propalaeohoplophorinae, with its main axis at an angle of about 90° with respect to the palatal plane; and (3) Mf1 lobate (Zurita et al., 2013). The new specimen described herein corresponds to an almost complete skull (without mandible), with most of the dentition preserved, although slightly deformed by taphonomic processes (Fig. 2). The upper right dental series is composed of nine well-preserved Mfs. On the left dental series, the presence of eight Mfs is inferred by the preservation of the first four Mfs and the four alveoli of the last four Mfs (Fig. 2B).

The Mfs increase in size from Mf1 to Mf5 and decrease from Mf5 to Mf8 (Table 1). The Mf1 is 'D'-shaped, with the major axis oriented transversely to the longitudinal axis of the dental series and with its anterior margin convex and with two perpendicular grooves, which makes it incipiently lobed (Fig. 3B). The sMf is located between Mf1 and Mf2, with its major axis oriented transversely to the longitudinal axis of the tooth series (Fig. 3B). It has a very slightly marked lobation, with no labial central lobe and with two small labial lobes; as in Mf1, the anterior face is convex and the posterior is concave. This extra tooth falls into Colyer's (1990) category 1 (i.e., supplemental teeth that resemble teeth of the normal series in both crown and root morphology, although not always in size). From Mf2, the Mfs have their major axis along the longitudinal axis of the tooth series. The Mf2 is slightly trilobed, with a well-developed labial central lobe and a poorly developed lingual central lobe; both of the lobes are defined by two perpendicular grooves on the labial and lingual sides, respectively. The Mf3–8 are completely trilobed, with the lingual face of the anterior lobe more developed. The Mf5–6 have a perpendicular groove that results in an irregular curvature (i.e., not smooth) of the posterior lobe. The Mf7–8 do not have

this perpendicular groove in the posterior lobe, and the posterior lobe of Mf8 is smaller than that of Mf7.

The high level of lobation of the molariforms in *B. acostae* is noteworthy, and goes from a very incipient trilobation observed in Mf2 to a progressive and well-developed trilobation in Mf3–8 (Fig. 3B). There is more lobation than early Miocene Propalaeohoplophorinae (e.g., *Propalaeohoplophorus* spp.), in which the lobation starts in Mf2–3 and the trilobation in Mf4–8 (Fig. 3A). The species of glyptodonts from the middle Miocene are mostly known by remains of dorsal carapaces and caudal armors (González Ruiz et al., 2011), a situation that precludes a dental comparison with specimens from similar age. Compared with Glyptodontidae 'Hoplophorini' from the late Miocene–early Pliocene (e.g., *Eosclerocalyptus* spp.), *B. acostae* shows a high level of lobation; trilobation in *Eosclerocalyptus* spp. starts at Mfs 3–4. *Boreostemma acostae* has less developed trilobation than specimens of Glyptodontinae from the Pliocene (e.g., *Paraglyptodon* sp.), in which marked trilobation starts at Mf2, Mf1 being elongated (not 'D'-shaped like *B. acostae*). Finally, *B. acostae* shows less lobation than the most derived Pleistocene forms (i.e., the 'Panochthini' *Panochthus* spp. and the Glyptodontinae *Glyptodon* spp. and *Glyptotherium* spp.), in which Mf1s are already both lingually and labially trilobed (Fig. 3C) (Scott, 1903; Gillette and Ray, 1981; Fericola, 2008; Zurita et al., 2009, 2013; Zamorano and Brandoni, 2013).

Discussion

Several authors have mentioned the presence of one to three foramina in the premaxillary and the corresponding part of the mandible in Propalaeohoplophorinae, which have been interpreted as alveoli for deciduous incisors (Ameghino, 1889, 1891, 1895, 1898; Scott, 1903; Paula Couto, 1979; Hoffstetter, 1958). However, other authors indicated that these are palatal foramina because they are not in homologous positions in different specimens (Mercerat, 1891; Lydekker, 1894). These perforations seem like foramina (where vessels and nerves pass into the buccal cavity), although it cannot be rejected that, in some cases, they might correspond to alveoli, which could correspond to atrophied incisors (not to deciduous incisors). This reduction in the number of premaxillary teeth can be related to the progressive reduction of premaxillary bones from the basal-most glyptodonts (e.g., *Propalaeohoplophorus* spp.) to the most derived forms (e.g., *Glyptodon* spp.) (Ameghino, 1889, 1895, 1898; Scott, 1903; Lydekker, 1894; Vinacci Thul, 1945; Hoffstetter, 1958).

There are several possible explanations for the presence of sMf in this specimen. One explanation that we reject is that the sMf is a retained deciduous tooth, because the existence of two generations of teeth (diphyodonty) in xenarthrans has only been demonstrated in cingulates for the extant Dasypodinae *Dasypus* spp. (Martin, 1916; Ciancio et al., 2012), a basal lineage within cingulates not closely related to glyptodonts (Engelmann, 1985; Delsuc et al., 2004; Gaudin and Wible, 2006; Billet et al., 2011). Hirschfeld and Webb (1968) noted that juvenile specimens of *Megalonyx* Harlan (Megalonychidae) and of extant tree sloths have consistently failed to yield deciduous teeth, and Gillette and Ray (1981) and Zurita et al. (2009) did not find evidence of diphyodonty in juveniles and unborn specimens of *Glyptotherium* and *Glyptodon*, respectively. Zinoviev (2010) rejects that a supernumerary molar of a wild boar corresponds to a retained deciduous tooth because its wear surface is the same as the permanent molars, the same pattern we found in *B. acostae*. Another rejected possibility is that the presence of the sMf is due to an enlargement of the skull, allowing for the development of a tooth in a different position. The lack of space in the

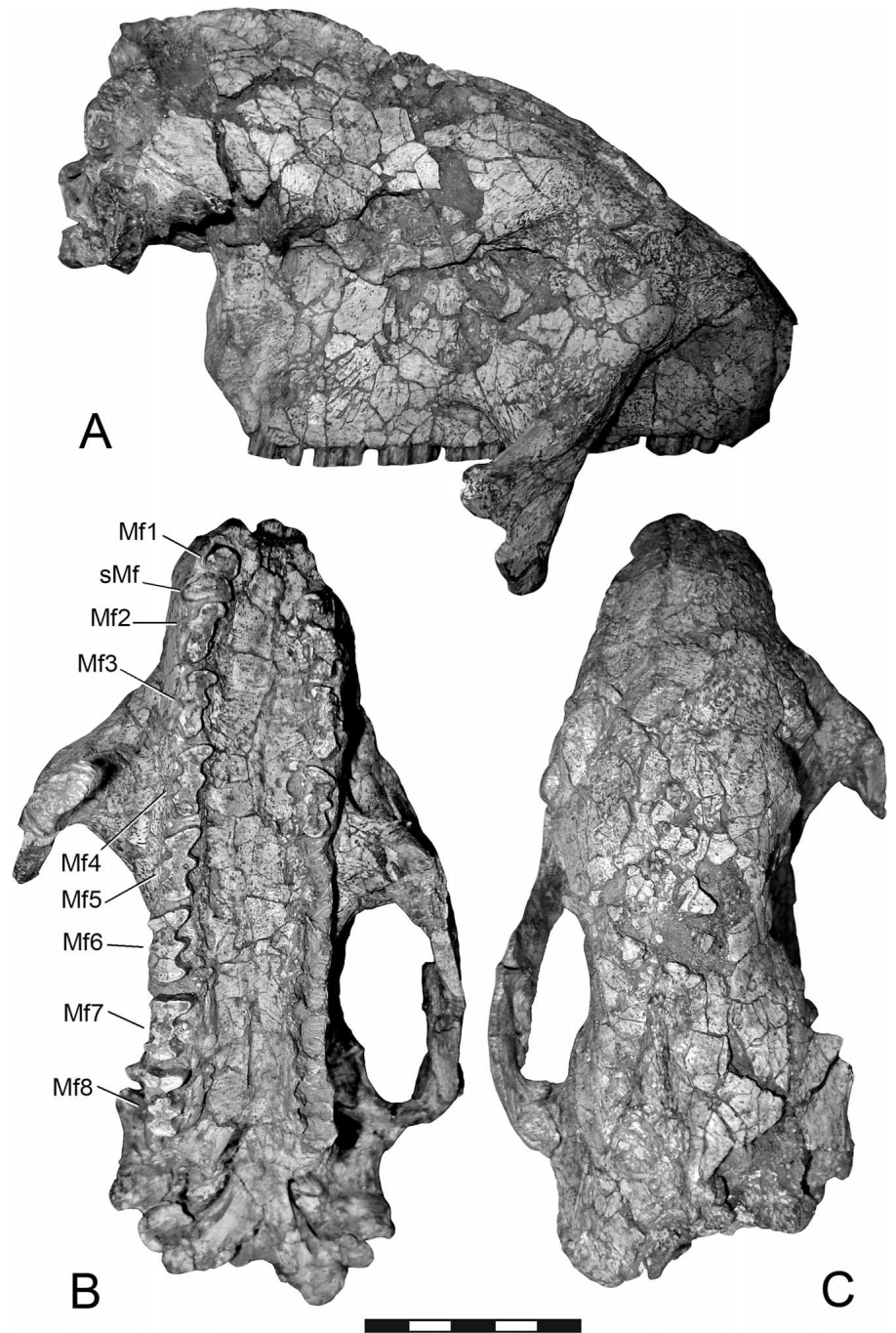


FIGURE 2. Skull of *Boreostemma acostae*, UCMP 38104. **A**, lateral view; **B**, ventral view showing the dental formula; **C**, dorsal view. Scale bar equals 5 cm.

TABLE 1. Dental measurements (mm) of upper molariforms and dental series for comparison.

Molariform	Measurement	<i>Propalaehoplophorus australis</i> MLP 16-15	<i>Boreostemma acostae</i> UCMP 38104	<i>Glyptodon munizi</i> GCF 10
Mf1	Tl	4.6	5.1	22.11
sMf	Tl	—	9.6	—
Mf2	Tl	5.6	12.8	25.21
Mf3	Tl	10.3	14.0	28.02
Mf4	Tl	12.2	14.7	29.34
Mf5	Tl	14.2	15.4	29.09
Mf6	Tl	14.6	15.1	28.77
Mf7	Tl	13.6	13.3	29.56
Mf8	Tl	12.6	13.1	27.50
	Tlds	97.8	117.9	219.6

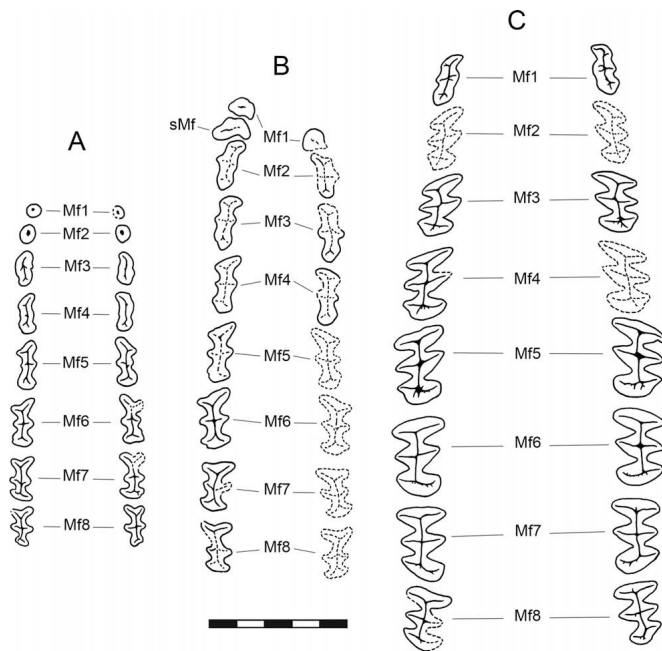


FIGURE 3. Drawing of the occlusal dental morphology and the dental series of glyptodonts. **A**, *Propalaeohoplorus australis*, MLP 16-15; **B**, *Boreostemma acostae*, UCMP 38104; **C**, *Glyptodon munizi*, GCF 10. Scale bar equals 5 cm.

maxilla of this specimen to accommodate the sMf is evident. Its longitudinal axis is transverse to the dental series, likely resulting from an absence of space during its development (Fig. 2B).

The presence of a supernumerary molariform in *Boreostemma acostae* might be explained by a mutation producing a new tooth germ or by a division of an existing tooth germ. According to Wood and Wood (1933:39), "If the presence of an extra tooth were due to a splitting of the tooth germ, one would assume, both a priori, and from experiments in splitting the anlagen of other organs, that in such a case either the two teeth would have the same pattern, that they would be mirror images of each other, or that the two together would approximate the pattern of the original tooth." In this context, we cannot reject the origin of the sMf by division of the tooth germ corresponding to Mf2, given its greater similarity to this tooth. Also, the lack of space for the development of the new tooth germ may lead to its distortion and generation of a morphologically different tooth (Archer, 1975; Natsume et al., 2005). Tooth germ division has been cited for homodont armadillos, and it has been proposed that their teeth originated by division of dental germs (Wood and Wood, 1933).

An alternate explanation would be that this specimen shows a return to a lost primitive condition (atavism). If this were the case, the resulting dental formula should correspond to the ancestral xenarthran dental formula and the extra tooth should have the serial size and form continuing along the tooth row (Natsume et al., 2005). This sMf is within the serial size and form of the dental series, and two armadillo genera (i.e., *Eutatus* spp. and *Proeutatus* spp.), sometimes recovered as basal to glyptodonts (Gaudin and Wible, 2006; Billet et al., 2011), have nine Mfs in the maxilla, making this a possible explanation. Despite this, the basal position of these genera to glyptodonts is unsupported by other phylogenetic analyses (Engelmann, 1985; Abrantes and Bergqvist, 2006; Ciancio, 2010). Also, other armadillo groups considered basal within cingulates (e.g., *Dasybus* spp., *Peltephilus* spp.)

and even the sister group to glyptodonts (i.e., Pamphtheriidae) have typically eight or seven Mfs in the maxilla (Gaudin and Wible, 2006; Fericola, 2008; Billet et al., 2011), providing no support for an atavism as the explanation for the extra Mf described herein.

Finally, after reviewing almost all North and South American collections where glyptodont skulls are housed (as well as the existing literature), this is the first record of a supernumerary tooth in Glyptodontidae, indicating that this phenomenon is very rare in this lineage.

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