



Hyoid apparatus of *Panochthus* sp. (Xenarthra; Glyptodontidae) from the Late Pleistocene of the Pampean Region (Argentina). Comparative description and muscle reconstruction

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With 7 figures and 1 table

Abstract: The main function of the hyoid apparatus in mammals is to control the entry and exit of air in the body, provide support to the tongue, hold it in position and give it movement. In some species, it also participates in the modulation of sounds produced by vocal cords. Its preservation as fossil is exceptional and very little known. It allows proposing hypotheses about how the mentioned functions would be carried out. The finding and study of two new specimens assigned to the glyptodontid *Panochthus* sp., from Lujanian sediments (Late Pleistocene) of the Pampean Region, permitted: 1) to study the anatomy and propose a new organization of the hyoid apparatus in glyptodontids, 2) to describe in detail its elements (even the thyroid cartilage), 3) to compare it with materials already published of *Glyptodon* cf. *G. clavipes*, and 4) to analyze and compare the muscles' actions. In adult mammals, this apparatus is formed generally by ten bony elements, (1) stylohyals (paired), (2) epihyals (paired), (3) ceratohyals (paired), (4) thyrohyals (paired) and (5) basihyal (unpaired); and 2 paired cartilaginous elements, (a) tympanohyals and (b) chondrohyals. In glyptodonts, the elements (1), (2), (3) form the sigmohyals (paired), and (4) and (5) the V-bone (unpaired). The bony elements of *Panochthus* sp. are more gracile and long than those of *Glyptodon* cf. *G. clavipes*, and in the former, the musculature is more developed. The study of the new specimens suggests that *Panochthus* sp. could have more freedom of tongue movement than *Glyptodon* cf. *G. clavipes*, which possibly implied a different use of food resources.

Key words: Hyoid apparatus, Glyptodontidae, *Panochthus*, Quaternary, South America.

1. Introduction

At least in mammals, the cartilages of the second and third branchial arch are ossified early and give rise to the hyoid apparatus; it is located between the mandibular branches and, through its long bones, articulates with the skull (KÖNIG & LIEBICH 2005a). Although it participates in the modulation of the sounds produced by the vocal cords, its main function is to control the entrance and the exit of the air in the organism; also, to support the tongue, hold it in position and give it

movement. In living animals the latter is relevant, since it allows inferring how the tongue participates in the obtaining, processing and swallowing of the food. Particularly in the case of fossil mammals, these inferences are very interesting, in order to elaborate hypotheses of how the aforementioned tasks would be performed.

Xenarthra is a peculiar clade of mammals typical of the Neotropical Region, widely represented in the fossil record of South America, both for its temporal extension as by its abundance of records (SCILLATO-YANÉ 1977, 1982; PAULA COUTO 1979; SCILLATO-YANÉ & CAR-

LIN, 1995; SOIBELZON 2017). The diversity of the group is reflected in the wide ranges of diets and the ways of acquiring food (VIZCAÍNO et al. 2008; VIZCAÍNO 2009).

The first descriptions of the xenarthrans hyoid apparatus were made by RAPP (1852), HYRTL (1855), LEIDY (1855), OWEN (1856), MURIE (1874), FLOWER (1885), SCOTT (1905), ALLEN (1913) and STOCK (1925). Most of these works included fossil taxa.

BURMEISTER (1864, 1871, 1874) provided the first description and comparison of the hyoid apparatus of some glyptodonts (*Glyptodon* OWEN and *Panochthus* BURMEISTER). PÉREZ et al. (2000, 2010) reconstructed the muscles of the hyoid apparatus of *Glyptodon* and other xenarthrans.

Xenarthrans are classified in two major groups: Pilosa (Vermilingua and Tardigrada) and Cingulata (WETZEL 1985; REDFORD & EISENBERG 1992; MCKENNA & BELL 1997; GAUDIN & McDONALD 2008). Glyptodontidae constitutes the group of armored xenarthrans whose representatives reach the largest size, sometimes gigantic (SCILLATO-YANÉ & CARLINI 1998; FARIÑA 2001; ZAMORANO et al. 2014a), some taxa would exceed the 2,300 kg of body mass (SOIBELZON et al. 2012). They are registered since the middle Eocene to early Holocene (SCILLATO-YANÉ 1976; FERNICOLA 2008; ZAMORANO 2012, 2013; ZURITA et al. 2016).

Panochthus is one of the most abundant and diversified glyptodonts of the South American Pleistocene, as well as one of the largest cingulate (see FARIÑA 2001; ZAMORANO et al. 2015). The most abundant records correspond to the Pampean region (SCILLATO-YANÉ et al. 1995; CIONE et al. 1999; ZAMORANO 2012; ZAMORANO et al. 2014b). Among Glyptodontidae and together with *Glyptodon* are the most widely distributed in South America (ZURITA et al. 2009; ZAMORANO 2012; ZURITA et al. 2016).

Here we present the first undoubted and the best-preserved hyoid elements attributable to *Panochthus*. These allow us to propose a different conformation of the hyoid apparatus of glyptodontids than those proposed by previous authors (e.g., BURMEISTER 1864, 1871, 1874; PÉREZ et al. 2000, 2010), to describe in detail its elements (including the thyroid cartilage present in one of the specimens), and to rebuild its musculature.

2. The hyoid apparatus in mammals, xenarthrans and glyptodontids

The mammalian hyoid apparatus is generally composed of ten bony elements and two associated cartilaginous

elements (Fig. 1). The 10 bones are four paired (1) stylohyals -St-, (2) epihyals -Ep-, (3) ceratohyals -Ce-, (4) thyrohyals -Th-, and one unpaired (5) basihyal -Ba-, in the course of ontogeny, the left and right basihyals fuse into a cross bar called “hyoid body”-Hb-. The two cartilaginous elements are (a) tympanohyals -tym- and (b) chondrohyals -cho-, which can be ossified in some taxa (Fig. 1A) (FLOWER 1885; JAYNE 1898; TAYLOR & WEBER 1951; NAPLES 1986; SHOSHANI & MARCHANT 2001; PÉREZ et al. 2010; CASALI & PERINI 2016). According to BURMEISTER (1874), in humans, the elements (1), (2) and (3) correspond to the lesser *cornua* and the (4) and (5) to the greater *cornua* and the hyoid body.

In mammals, the hyoid apparatus is developed in the gular region. The aforementioned elements have their dorsal limit in the temporal region of the skull, ventro-anteriorly they contact with the base of the tongue and ventro-posteriorly articulate with the thyroid cartilage (laryngeal zone). The basihyal (body of the hyoid) contacts with the base of the tongue; it has a lingual process located anteriorly in the transversal bar, and from there two *cornua* arise. The upper *cornua* (lesser *cornua* in humans) is directed dorsally until it contacts, through the tympanohyal cartilage, to the base of the mastoid process. On each ramus the tympanohyal contacts ventrally with the stylohyal, that in turn contacts with the epihyal that contacts with the ceratohyal which articulates, in turn, with the basihyal. The lower ramus (greater *cornua* in humans) is formed by the thyrohyal that is related to the thyroid cartilage through the chondrohyal cartilage.

The hyoid apparatus in xenarthrans shows greater modifications than in the rest of mammals, since some of the mentioned bone elements are fused. The presence of the unpaired bone (also called V-bone), formed by the fusion of basihyal and thyrohyals, is a synapomorphy of the group (Fig. 1B, C) (NAPLES 1986; PÉREZ et al. 2010). Except for the unpaired bone, the rest of the bony elements vary in the different groups of xenarthrans, while tympanohyals and chondrohyals are, in general, constant.

Among fossil Pilosa, the hyoid apparatus is known in *Analcimorphus giganteus* AMEGHINO, *Glossotherium robustum* OWEN, *Megatherium americanum* CUVIER, *Mionothropus cartellei* DE IULIIS, GAUDIN & VICARS, *Paramylodon harlani* (OWEN), *Scelidotherium leptcephalum* OWEN, and *Thalassocnus natans* MUIZON & McDONALD (see OWEN 1856; ALLEN 1913; STOCK 1925; CARTELLE & FONSECA 1983; McDONALD & DE MUIZON 2002; PÉREZ et al. 2010; DE IULIIS et al. 2011), either complete or incomplete. Until now, the hyoid appara-

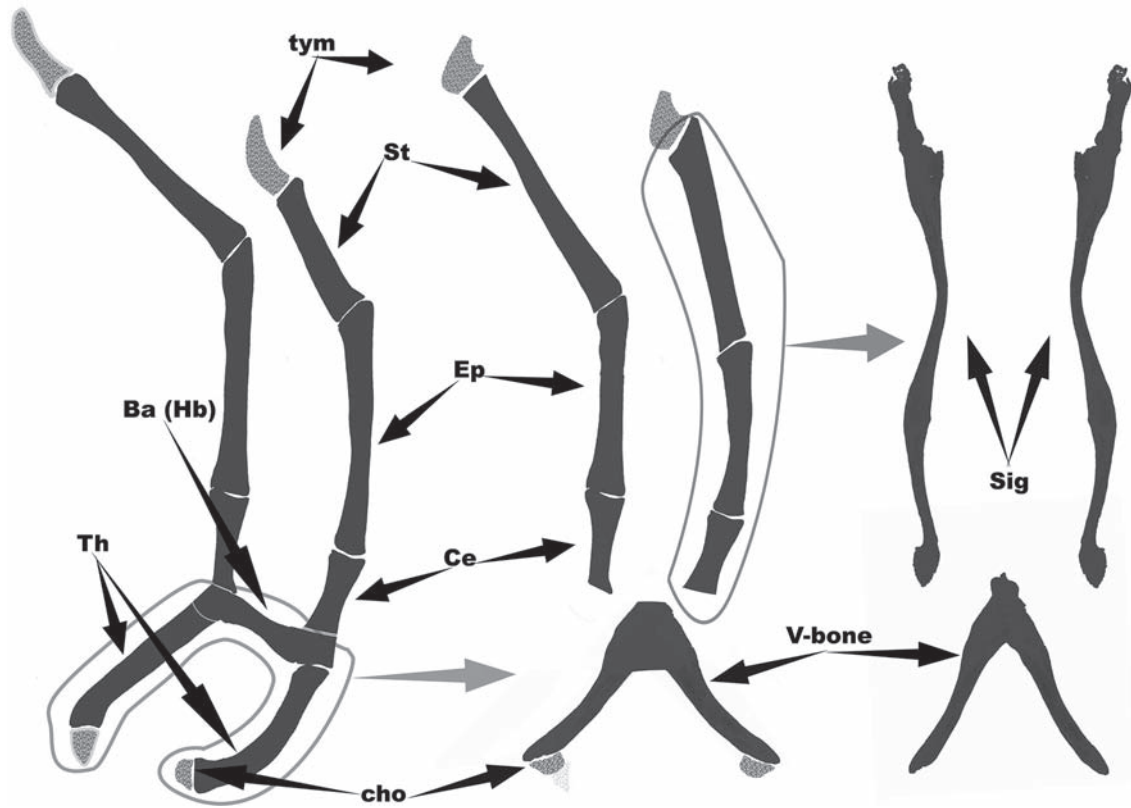


Fig. 1. The mammalian hyoid apparatus in **A** – *Felis silvestris catus* LINNAEUS (redrawing after JAYNE 1898); **B** – *Megatherium americanum* (redrawing after PÉREZ et al. 2010) and **C** – *Panochthus*. Ba, basihyal (Hb, hyoid body); cho, chondrohyals; Ce, ceratohyals; Ep, epihyals; Hi, V-bone; Sig, sigmohyals; St, stylohyals; Th, thyrohyals; tym; tympanohyal

tus of fossil *Vermilingua* remains unknown (NAPLES 1986). On the other hand, in fossil *Cingulata*, the hyoid apparatus is known for *Panochthus tuberculatus* OWEN, *Glyptodon reticulatus* OWEN, *G. clavipes* OWEN and *G. elongatus* BURMEISTER (BURMEISTER 1864, 1871, 1874; CASALI & PERIN 2016), *Glyptodon* cf. *G. clavipes* (PÉREZ et al. 2000, 2010), *Proeutatus* sp. (SCOTT 1905; PÉREZ et al. 2010) *Prozaedyus* sp. (PÉREZ et al. 2010) and *Panochthus* sp. (this contribution). At this point it is important to note that BURMEISTER (1864, 1871, 1874) never declared the collection number of the hyoid bones that he described and attributed to *Panochthus*; thus it is impossible to contrast the specimens here described with those described by BURMEISTER as well as the assignment of the specimens studied by BURMEISTER to *Panochthus*. In addition, the figures of BURMEISTER are very schematic and in some cases confusing.

In the living tardigrades (*Bradypus* LINNAEUS and *Choloepus* ILLIGER) the epihyals, and ceratohyals are

fused (NAPLES 1986) but in fossil tardigrades, stylohyals, epihyals, and ceratohyals, are independent elements. Regarding living *Vermilingua*, in *Myrmecophaga* LINNAEUS and *Cyclopes* GRAY, stylohyals, epihyals, and ceratohyals are independent; but in *Tamandua* GRAY the epihyals and ceratohyals are fused (REISS 1997; NAPLES 1999).

Inside *Cingulata*, dasypodids show unfused stylohyals, epihyals, and ceratohyals (BURMEISTER 1874; PÉREZ et al. 2000), with the exception of the fossil specimen *Proeutatus* sp. (PÉREZ et al. 2010). Instead, in glyptodonts these elements are fused (*vide infra* Discussion and Conclusions) forming the sigmohyals-Sig-, term coined by PÉREZ et al. (2000). In sum, in glyptodonts the hyoid apparatus is formed only by three bones (1) V-bone, (2) right sigmohyal, and (3) left sigmohyal (Fig. 1C).

BURMEISTER (1864, 1874) interpreted this reduction of bony elements as loss of elements, while PÉREZ et al.

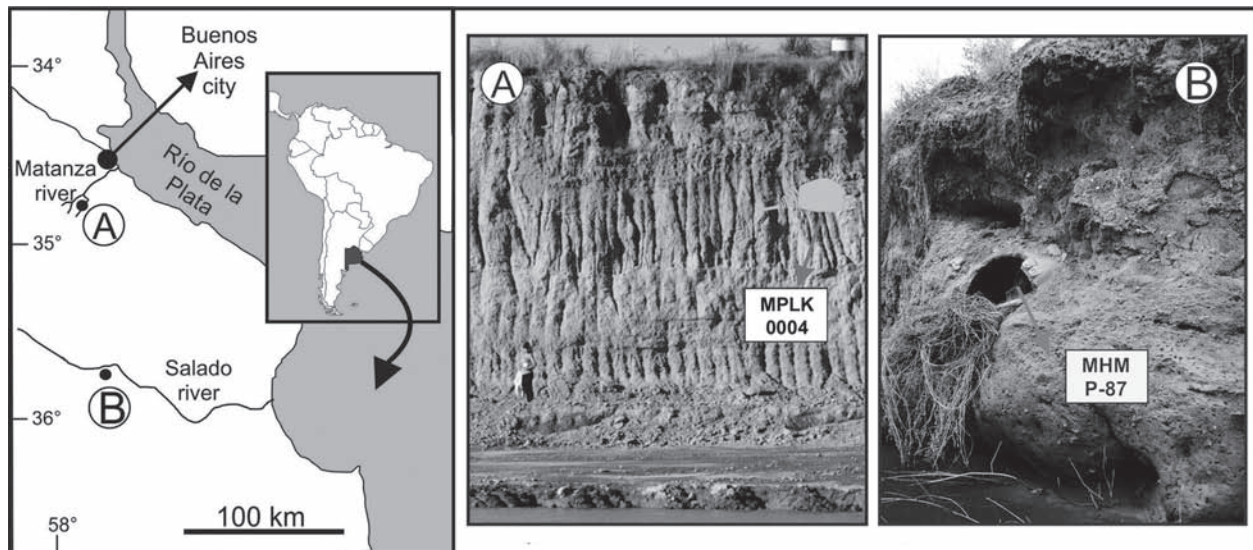


Fig. 2. Geographic location of the sites where the studied specimens were found. A, “Cantera Nicolás Vignogna III”, Marcos Paz city, Buenos Aires Province; B, Salado River margins, General Belgrano city, Buenos Aires Province.

(2000, 2010) proposed that this reduction is produced by the merger of elements. Although PÉREZ et al. (2000: 295) mentioned, for the specimen MHM P-34, that “the tympanohyal cartilage could participate” in a coossification between the mastoid process and the sigmoidals, we consider that with the available information, this hypothesis cannot be tested. Consequently, the tympanohyal and chondrohyal cartilages are not mentioned in this study.

3. Material and methods

Here we study two recently exhumed specimens assigned to *Panochthus* sp. (*vide infra* Comments on the taxonomic assignment) found in two localities of the Buenos Aires Province, Argentina (Fig. 2). We followed the anatomical terminology of PÉREZ et al. (2000, 2010), ZAMORANO (2012) and CASALI & PERINI (2016); the systematic classification of ZURITA et al. (2017); and the chronostratigraphic scheme of CIONE & TONNI (1999, 2005). A manual caliper and measuring tape were used to measure the specimens (see Fig. 3). All values included in Table 1 are expressed in millimeters (mm), with an error range of 0.5 mm.

Institutional abbreviations: AMNH, American Museum of Natural History, New York, USA; MHM-P, Museo Histórico Municipal Alfredo Múlgura, General Belgrano, Buenos Aires, Argentina; MLP: Museo de la Plata, División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Buenos Aires, Argentina. MNRJ: Museo Nacional, Rio de Janeiro, Brazil;

MPLK, Museo Paleontológico “Lucas Kraglievich”, Marcos Paz, Buenos Aires, Argentina.

3.1. Fossil provenance, localities and age

MPLK 0004: This specimen was collected at ‘Cantera Nicolás Vignogna III’ (34°54’51” S – 58°42’28” W (Fig. 2) from sediments assigned to the Late Pleistocene. It is temporarily housed at the Museo de La Plata collection, while the Museo de Ciencias Naturales “Lucas Kraglievich” (conditions both building and catalogues of its “Carlos Rusconi” paleontological repository, as was established by the National Law of archaeological and paleontological heritage protection.

MPLK 0004 it is composed of a complete skull, mandibles, cephalic shield, complete hyoid apparatus with all elements paired and unpaired and the ossified thyroid cartilage. All remains belong to the same individual and were found in the upper levels of the studied section, which is composed of continental facies. This facies is very rich in fossils vertebrates as *Megatherium americanum*, *Lagostomus* sp., *Equus* (A.) *neogaeus* LUND, *Notiomastodon platensis* (AMEGHINO), *Tayassu pecari* (LINK), *Glyptodon* sp., *Chaetophractus* sp., *Macrauchenia patachonica* OWEN, *Toxodon platensis* OWEN, among others. The faunal assemblage is typical of the Lujanian Age in the Pampean region, which temporally extends from the Late Pleistocene to Early Holocene (CIONE et al. 2015), but our radiocarbon dates indicates an age *ca.* 30 kyBP (Late Pleistocene) for the FA 4 (GASPARINI et al. 2016).

MHM-P 87: This specimen was found in the margins of the Salado River, near “Estancia La Invernada” (35°45’5.52” S – 58°37’35.96” W downstream La Chumbiada Village, General Belgrano, Buenos Aires Province) (Fig. 2) in sediments

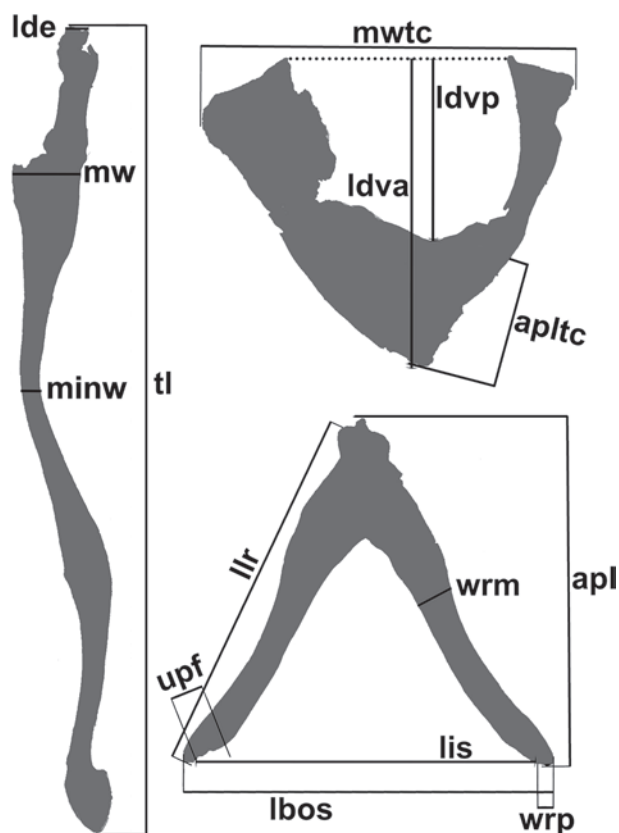


Fig. 3. Measurements of the hyoid apparatus in glyptodontids. apl, antero-posterior length; apltc, antero-posterior length; lbos, length between the outer sides of the posterior end of the branches; lde, length of the distal end; ldva, dorso-ventral length at the anterior margin; ldvp, dorso-ventral length at the posterior margin; lis, length of the inner sides of the back end of the cornua; llc, length of the lateral cornua; wrm, ramus width at the middle of its length; mw, maximum width; Mw, maximum width; Mwtc, maximum width; stl, sigmoidal total length; wrpe, width of the ramus at the posterior end; upf, ulnar posterior facet.

of the Luján Formation dated between 12 to 14 ky BP (latest Pleistocene, Fucks et al. 2015).

MHN-P 87 is composed of a V-bone and fragments of bones of the hyoid apparatus, remains of pharyngeal rings, fragments of right mandible, cervical ribs, fragments of pelvis, humerus, femurs and an almost complete dorsal carapace. All remains belong to the same individual. From the same unit were exhumed remains of *Hippidion principale* OWEN, *Smilodon populator* LUND, *Doedicurus clavicaudatus* (OWEN) and *Megatherium americanum*, among others (see SCANFERLA et al. 2013). The faunal assemblage is typical of the Lujánian Age in the Pampean Region.

4. Systematic paleontology

Xenarthra COPE, 1889
 Cingulata ILLIGER, 1811
 Glyptodontia AMEGHINO, 1889
 Glyptodontoidea GRAY, 1869
 Glyptodontidae GRAY, 1869
 Genus *Panochthus* BURMEISTER, 1866

Type species: *Glyptodon tuberculatus* OWEN, 1845.

Panochthus sp.
 Figs. 4, 5, Table 1

Referred specimens: MPLK 0004 (Late Pleistocene of 'Cantera Nicolás Vignogna III', Buenos Aires, Argentina) and MHN-P 87 (Late Pleistocene of the Salado River, Buenos Aires, Argentina).

Comments on the taxonomic assignment: The specimens described here (MPLK 0004 and MHN-P 87), are certainly attributable to *Panochthus*, since they share all diagnostic characters of the genus. MPLK 0004 is assigned to *Panochthus* because: nasal area heavily inclined antero-ventrally, the palatal and rostral areal planes conform a $\approx 45^\circ$ angle; skull length is less than a $1\frac{1}{2}$ its height, (regardless the descending processes of the zygomatic arch); the external nasal openings are antero-ventral orientated; molariforms 2 to 8 are trilobulated; cephalic shield subcircular and convex, presenting osteoderms where the central figure is large and surrounded by one to seven rows of peripheral figures. MHN-P 87 is assigned to *Panochthus* because: the dorsal carapace presents thick polygonal osteoderms with small polygonal tubers similar in size distributed over the whole surface of the osteoderm or with a central figure (flat or slightly depressed) surrounded by tubers. Concerning the postcranial bones (humerus and femur), the humeral head of *Panochthus* is not circumscribed by a defined neck and the bicipital groove is well marked, although it is not as deep as in *Glyptodon*; in the proximal epiphysis of the femur of *Panochthus*, the articular surface of the femoral head is subcircular, and in the external sector of this epiphysis is the greater trochanter, in a plane slightly higher than the femoral head, unlike *Neosclerocalyptus* PAULA COUTO and *Propalaehoplophorus* AMEGHINO (ZAMORANO et al. 2014a).

In the Lujánian (Late Pleistocene-Early Holocene) of the Pampean Region three species of *Panochthus* are recognized: *P. tuberculatus* (OWEN), *P. frenzelianus* AMEGHINO and *P. greslebini* CASTELLANOS (ZAMORANO 2012; ZAMORANO et al. 2014a). They are differentiated by some characters of the skull, and from the general morphology of their carapace. MPLK 0004 could not be assigned to *P. frenzelianus* (material described by AMEGHINO 1889; housed in the AMNH, but see FERNICOLA et al. 2014), since in this species the postorbital process is incomplete, but in MPLK 0004 this process is complete. The specimen MHN-P 87 could not be assigned to *P. frenzelianus* either, since its dorsal carapace is anteriorly elevated and laterally compressed, and in *P. frenzelianus* its profile is uniformly convex. It is unlikely that MPLK 0004

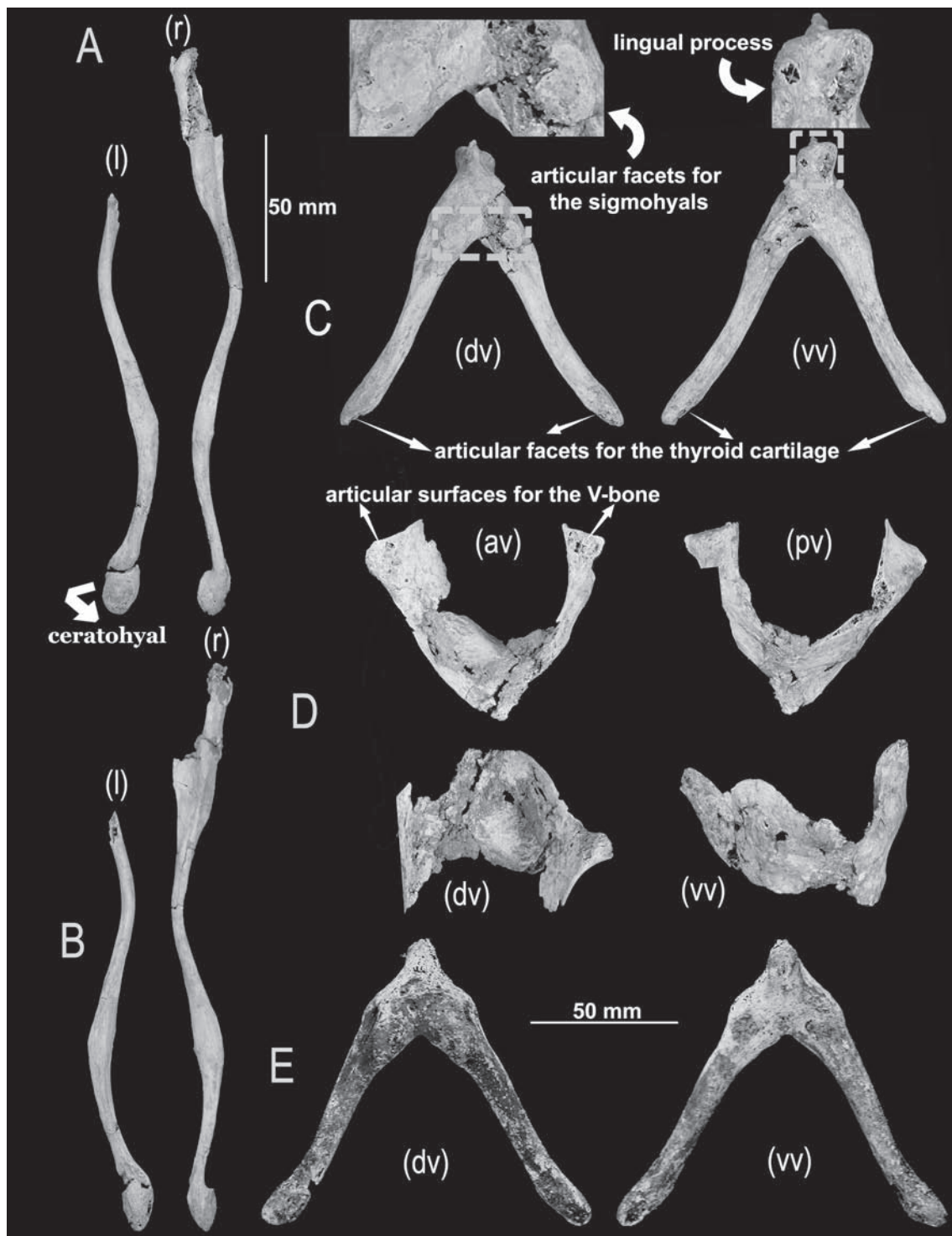


Fig. 4. Described materials. MPLK 0004: A, B, sigmohyals; C, V-bone; D, thyroid cartilage. MHM-P 87: E, V-bone. (av) anterior view; (dv), dorsal view; (l), left; (pv), posterior view; (r), right; (vv), ventral view.

belongs to *P. greslebini*, a species known from some bones of the postcranial skeleton (both femurs and a fragment of tibia-fibula), a fragment of dorsal carapace and several cau-

dal tubes; unfortunately the specimens described here have not preserved those elements. On the other hand, MHN-P 87 has an almost complete dorsal carapace; unfortunately



Fig. 5. Disposition of the hyoid apparatus (MPLK 0004). A, anterior view; B, posterior view; C, dorsal view; D, ventral view; E, in position in the skull, posterior view; F, in position in mandible, dorsal view.

the fragmentary nature of the carapace of the referred material of *P. greslebini* (*i.e.*, MNRJ 2760/5V, see BERGQVIST 1993) prevents us to assign this specimen to *P. greslebini*.

The specimens here described cannot be assigned to *P. tuberculatus* (*i.e.*, MLP 16-29, see ZAMORANO *et al.* 2012, but see CRUZ *et al.* 2013). The skull of MPLK 0004 is similar to

that of *P. tuberculatus*, but that of *P. greslebini* is unknown. In turn, MHN-P 87 could not be identified as *P. tuberculatus* through its carapace and postcranial bones; however, it could be assigned to *P. greslebini*, since the fragment of carapace and postcranial bones of *P. greslebini* have no significant differences with those of *P. tuberculatus*. Due to the absence of anatomical characters that allows undoubted assignment of MPLK 0004 and MHM-P 87 to some of the known species of *Panochthus*, we considered that the most parsimonious decision is to attribute them to *Panochthus* sp.

Comparative description (for measurements see Table 1)

Sigmothyal: Sigmothyal total length (stl) of MPLK 0004 (only the right *cornua* is complete) is ca. 10% greater than that of *Glyptodon* cf. *G. clavipes* (MHM-P 34, *sensu* PÉREZ et al. 2000). In the latter, the whole bone is significantly more robust. The region of the maximum width (Mw) is almost circular in section, with only one posterior flange and the remainder rounded. In MPLK 0004 this area is triangular in section, very compressed laterally, with the antero-interior edge sharper than the other two. Dorsally, the epiphysis is tuned toward the distal end. In the specimens described here the epiphysis width is 29.4% of the maximum width, while in *Glyptodon* cf. *G. clavipes* it is 66.7% of the maximum width. Between the distal end and the mastoid process, the tympanohyals cartilage is present in most mammals, but it is absent in glyptodonts (see chapter on hyoid apparatus in mammals, xenarthrans and glyptodontids). The shortest width of the sigmothyal of MPLK 0004 is approximately half of that of *Glyptodon* cf. *G. clavipes*. The maximum width of the sigmothyal of MPLK 0004 is three times its minimum width, while in *Glyptodon* cf. *G. clavipes* it is approximate twice. The length of the distal end (lde) in MPLK 0004 is approximately half the one observed in *Glyptodon* cf. *G. clavipes*, and in this latter, it is much closer to the most robust region of the bone. The proximal end of MPLK 0004 also differs greatly from that of *Glyptodon* cf. *G. clavipes* (see Discussion and Conclusions). In MPLK 0004 the area in which it contacts with the articular facets of the impair bone is sub-circular in section. Although this bone is sigmoidal in both specimens, in MPLK 0004 it has two large curves; instead in *Glyptodon* cf. *G. clavipes*, one curve is much larger than the other.

V-bone: The unpaired bone is V-shaped; it lies horizontally between the mandibular rami, with the tip of the V anteriorly directed. The antero-posterior length of the V-bone (apl) is longer in *Glyptodon* cf. *G. clavipes* than in MPLK 0004 and MHM-P 87, being in the former slightly shorter.

The distance between the outer sides of the posterior end of the branches (lbos) is shorter in MPLK 0004 than in MHM-P 87, being smaller than in *Glyptodon* cf. *G. clavipes*. In contrast, the distance between the inner sides of the back end of the *cornua* (lis) is longer in MPLK 0004 than MHM-P 87, being in *Glyptodon* cf. *G. clavipes* even shorter.

The lateral *cornua* (llc) is in MPLK 0004 shorter than in MHM-P 87 and *Glyptodon* cf. *G. clavipes*. This length is similar in the last two specimens. The V-bone of *Glyptodon* cf. *G. clavipes* is more robust than that of both specimens described here, which is reflected mainly in the width of the ramus at the middle portion (rwm). The *cornua* of MPLK 0004 are narrower than those of MHM-P 87, and both are

Table 1. Linear measurements of the hyoid apparatus. apl, antero-posterior length; apltc, antero-posterior length of thyroid cartilage; lbos, length between the outer sides of the posterior end of the branches; lde, length of the distal end; ldva, dorso-ventral length at the anterior margin; ldvp, dorso-ventral length at the posterior margin; lis, length of the inner sides of the back end of the *cornua*; llc, length of the lateral *cornua*; rwm, ramus width at the middle of its length; minw, minimum width; mw, maximum width; mwtc, maximum width of thyroid cartilage; stl, sigmothyal total length; wrpe, width of the ramus at the posterior end; upf, ulnar posterior facet.

		<i>Panochthus</i> sp. RPCR 1021 MHM-P 87		<i>Glyptodon</i> cf. <i>G. clavipes</i> MHM-P 34
Sigmothyal	Mw	16	---	19
	mw	4	---	9
	stl	194	---	180
	lde	5	---	12
V-bone	llc	117	118	118
	lbos	103	111	114
	apl	101	99	114
	rwm	9	10	13
	wrpe	4	5	8
	lis	93	91	90
	upf	12	14	11
Thyroid cartilage	apltc	39	---	---
	Mwtc	84	---	---
	ldva	68	---	---
	ldvp	41	---	---

smaller than those of *Glyptodon* cf. *G. clavipes*. This is more evident when considering the width of the ramus at the posterior end (wrpe), which is twice wider in *Glyptodon* cf. *G. clavipes* than in MPLK 0004; in MHM-P 87 it is a little longer than in MPLK 0004. In turn, the ulnar posterior facet (upf) of MPLK 0004 and MHM-P 87 is longer than that of *Glyptodon* cf. *G. clavipes*.

The V-bone has articular facets for the sigmothyls on its dorsal side, near the lingual process but posteriorly. In MPLK 0004 and MHM-P 87 the articular surfaces are oval in dorsal view, while in *Glyptodon* cf. *G. clavipes* they are subcircular. In *Glyptodon*, there is an oval foramen (arterial foramen, according to PÉREZ et al. 2000) between the articular facets and the lingual process, while in MPLK 0004 and MHM-P 87 this region is completely smooth.

The lingual process is developed at the anterior end of the V-bone. This process is in *Glyptodon* cf. *G. clavipes* triangular in dorsal view and dorso-ventrally compressed, with marked roughness, corresponding to muscular insertions (PÉREZ et al. 2000). In MPLK 0004 and MHM-P 87 it is not compressed. In the specimens of *Panochthus* under study, the surface is smooth.

On the ventral side and at the base of the V-bone, BURMEISTER (1874) observed a marked "tuberosity", for articulation of a bone or cartilage of the larynx (see below Discussion and Conclusions). In MPLK 0004 and MHM-P 877 a

potential contact surface can be distinguished at the same position. Although this area in MPLK 0004 is slightly damaged, a small depression is observed; on MHM-P 87 this depression is more conspicuous. On the other hand, in *Glyptodon* cf. *G. clavipes*, this depression is larger and sub-oval, its transverse major diameter comprises almost the entire base of the V-bone. In addition, MPLK 0004 and MHM-P 87 have two depressed areas (one on each ramus) on the ventral surface just under the articular facets.

Thyroid cartilage: At the posterior end of V-bone there are articular facets for the thyroid cartilage. Due to the exceptional preservation of MPLK 0004 and *Glyptodon* cf. *G. clavipes*, this ossified and extremely fragile cartilage could be studied. The thyroid cartilage is similar in morphology but more gracile (PÉREZ et al. 2000). Unfortunately, we could not compare it with the thyroid cartilage studied by PÉREZ et al. (2000) because it is currently lost.

This cartilage is U-shaped in section. The dorso-ventral length is 39.7% greater at the anterior margin (ldva) than at the posterior margin (ldvp). The antero-posterior length (apltc) occupies 42.43% of the maximum width (mwtc). The articular surfaces for the V-bone could be distinguished in front view.

5. Reconstruction of the musculature of the hyoid apparatus in glyptodonts

The musculature of the hyoid apparatus of glyptodonts was first described by PÉREZ et al. (2000, 2010) on one specimen attributed to *Glyptodon* cf. *G. clavipes*. In PÉREZ et al. (2000) they compared it with *Bos primigenius taurus* LINNAEUS. Their descriptions were used to reconstruct the muscles of the hyoid apparatus of MPLK 0004 and MHM-P 87 attributed to *Panochthus* sp.

The muscles involved in the mammalian hyoid apparatus are typically eight: mylohyoid, geniohyoid, stylohyoid, ceratohyoid, occipitohyoid, styloglossus, hyoglossus and transverse hyoid; this last one is unpaired while the other seven are paired (Fig. 6).

The mylohyoid muscle is responsible for elevating the hyoid apparatus, the tongue and the floor of the oral cavity. This muscle in mammals usually extends over a medial-ventral longitudinal ridge and is mainly inserted into the middle fibrous fossa of the mandibular symphysis and lingual process. In glyptodonts it is ventrally inserted in the lingual process and, by analogy with the living ruminants, this muscle would develop the functions mentioned above.

The geniohyoid muscle is the responsible for rostrally moving the tongue in mammals. It is located ventrally to the tongue and dorsally to the mylohyoid. In glyptodonts, the marked chin-spine, located at the post-ventral end of the mandibular symphysis, and the great

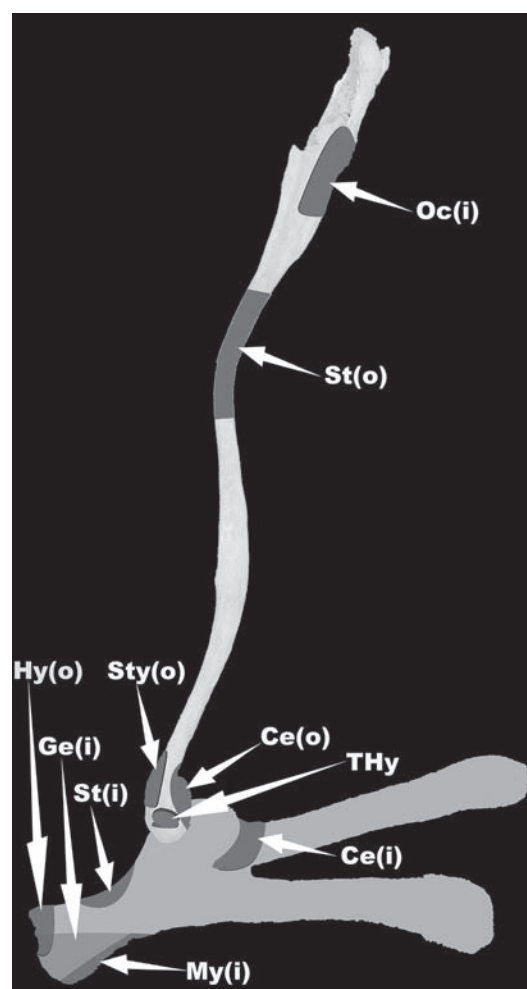


Fig. 6. Muscles involved in the hyoid apparatus of glyptodontids. Ce, ceratohyoid; Ge, geniohyoid; My, mylohyoid; Oc, occipitohyoid; St, stylohyoid; Sty, styloglossus; Hy, hyoglossus; THy, transverse hyoid; (i) insertion; (o), origin.

development of the ventral region of the lingual process of the V-bone, indicates that this muscle is robust. In *Panochthus* sp. the lingual process is more voluminous than that of *Glyptodon* cf. *G. clavipes*; therefore, it can be assumed that the geniohyoid muscle would also be more voluminous.

The muscle with the ability to depress and retract the tongue is the stylohyoid, which in glyptodonts is originated in the most dorsal angular region of the sigmoidal bone and traverses this bone until it is inserted into the antero-dorsal region of the unpaired bone. This muscle is very poorly developed [according to PÉREZ et al. (2000), could even be reduced], since its point of origin and insertion are in the same plane. The fusion

of elements and the vertical arrangement of the sigmoidohyals, in *Glyptodon* cf. *G. clavipes*, limited the action of the stylohyoid muscle to the stabilization of the joint with the unpaired bone, and secondarily to collaborate in the tongue depression by pulling the posterior region of the unpaired bone upwards (PÉREZ et al. 2000). In *Panochthus* sp. this muscle would be more developed since the angular region, where it originates, exhibits a more pronounced curve than in *Glyptodon* cf. *G. clavipes*. However, the ceratohyoid muscle mainly fulfills the antagonistic function of the geniohyoid muscle.

The function performed by the ceratohyoid muscle is to ascend the posterior end of the V-bone and direct the larynx – and indirectly the tongue – rostrally. This muscle in glyptodonts originates at the posterior margin of the ceratohyals and is inserted into the base of the V-bone (posteriorly to the articular surfaces for sigmoidohyals). The contraction of this muscle pulls the V-bone dorsally and moving ventro-posteriorly the lingual process, depressing and retracting the tongue (PÉREZ et al. 2000) and acting as antagonist of the geniohyoid muscle.

The muscle that indirectly descends the tongue and larynx is the occipitohyoid. It is originated in the lateral region of the jugular process of the occiput and is inserted into the posterior border of the distal region of the sigmoidohyals. The vertical arrangement of the sigmoidohyals would only allow caudal movements of its proximal end. PÉREZ et al. (2000) also suggested poor mobility of the distal end of sigmoidohyals, due to an observed co-ossification between this bone and the skull. We observed that in *Panochthus* sp. the occipitohyoid is inserted in the wider region of sigmoidohyals. This region presents (below the distal end) a very compressed laterally isosceles triangular section (in *Glyptodon* this region is almost rounded), with a very sharp and protruding anterior edge (see above comparative description) that would provide greater support for anchorage to the occipitohyoid muscle, giving indirectly greater mobility to the tongue compared to *Glyptodon* cf. *G. clavipes*.

The styloglossus originates in the proximal region of the sigmoidohyals, while the hyoglossus originates in the anterior region of the lingual apophysis. The contraction of these muscles retracts and depresses the tongue.

The only unpaired muscle of the hyoid apparatus is the transverse hyoid (KÖNIG & LIEBICH 2005b). This muscle is responsible for joining the sigmoidohyals. It extends transversely over the proximal base of the sigmoidohyals (at the level where the ceratohyals were present before the fusion). In glyptodontids the transverse hyoid

should have an insignificant functional value since the distance between the proximal ends of the paired bones of the hyoid apparatus is very short (less than 25 mm in *Panochthus* sp. and *Glyptodon* cf. *G. clavipes*).

6. Discussion and conclusions

BURMEISTER (1874: 37, pl. 1, fig. 4) described in detail the hyoid apparatus of *Panochthus*. At the ventral side of the V-bone, posterior to the lingual process, this author described and figured a quadrangular tuberosity, assuming that it would be attached to a bone or cartilage, contacting the V-bone with the larynx (including the thyroid cartilage). In the specimens of *Panochthus* sp. described here there are signs (see Comparative Description) that allow inferring that when the thyroid cartilage oscillates, on its articulation with the V-bone, it makes contact with the ventro-anterior region of the V-bone.

In *Glyptodon* cf. *G. clavipes*, could be observed a depression at the ventro-anterior area of V-bone (see above Comparative description) interpreted by PÉREZ et al. (2000: 295, fig. 3B) as muscular insertion. Whereas BURMEISTER (1864: 228) described a “quite high tuberosity” in *Glyptodon*; then in 1874 (BURMEISTER 1874: 283) he added that *Panochthus* and *Glyptodon* could be differentiated by the size of this tuber, indicating that in *Glyptodon* the tuberosity is smaller.

BURMEISTER (1874: 39, pl. 1, fig. 4), compared the apparatus of *Panochthus* with that of some living dasypodids (*Chaetophractus* FITZINGER = *Dasyopus* BURMEISTER and *Praopus* BURMEISTER = *Dasyopus* LINNAEUS). He noted that in living dasypodids there is a third bone (ceratohyal) between the stylohyal and epihyal and the V-bone, and that it is not present in *Panochthus*. He also concluded that this bone (ceratohyal) could have been lost during the preparation process; that is why he included this bone in the mentioned figure. Later, BURMEISTER (1874: 284, pl. 30, figs. 3, 4) discussed this again and decided to figure out the hyoid apparatus of *Glyptodon* and *Panochthus* without including the small bone that was found between the sigmoidohyal and the V-bone. It should be noted that the proximal end of the sigmoidohyal figured by BURMEISTER resembles notably the right sigmoidohyal of *Panochthus* sp. (MPLK 0004), in which the ceratohyal is fused to the sigmoidohyal. According to PÉREZ et al. (2000) and CASALI & PERINI (2016), the sigmoidohyal is formed by the fusion of stylohyal, epihyal and probably also the ceratohyal. On the other hand, PÉREZ et al. (2010) comparing the sigmoidohyal of glyptodontids with the stylohyal and epihyal of *Pilosa*,

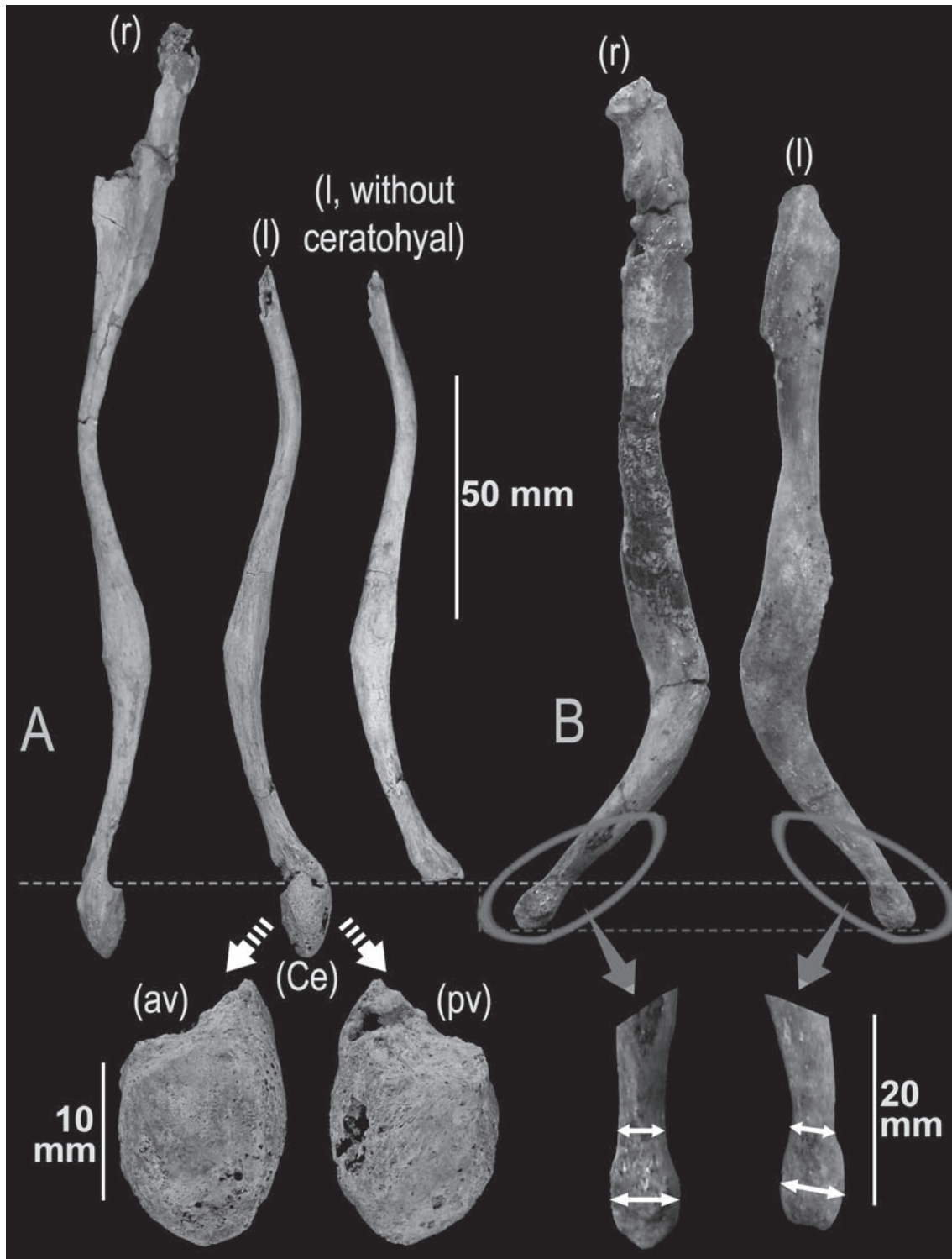


Fig. 7. Presence of the ceratohyal. A, sigmohyals, MPLK 0004; B, sigmohyals, MHM-P 34. (av), anterior view; (Ce), ceratohyal; (l), left; (pv), posterior view; (r), right.

they concluded that the sigmohyal is conformed only by the fusion of stylohyal and epihyal; they considered

as well that the ceratohyal is in an unknown position or, simply, it has been lost in the glyptodontids.

In MPLK 0004 (*Panochthus* sp.) the proximal epiphysis of left sigmoidhyal is the detached one. Here it is interpreted as corresponding to the ceratohyal not yet completely fused. Although this is an adult specimen, it is well known that in some groups of Xenarthra (e.g., dasypodids) some bones can be completely fused at different stages of development, even surpassed adulthood (CIANCIO et al. 2017). On the other hand, in the proximal region of the sigmoidhyal of *Glyptodon* cf. *G. clavipes* (1 cm far from the tip), it can be observed a narrowing at the same level, where the ceratohyal is fused to the sigmoidhyal in *Panochthus* sp.; then the bone is considerably widened proximally. So, it could be assumed that the ceratohyal is fused to the sigmoidhyal. However, the possibility that the ceratohyals in *Glyptodon* cf. *G. clavipes* have been detached during taphonomic processes or that they were never fused, as in the left sigmoidhyoid of MPLK 0004, cannot be discarded (Fig. 7).

According to our results, the ceratohyal would be present in glyptodontids, as well as in tardigrades (STOCK 1925; NAPLES 1986; PÉREZ et al. 2010), vermilinguans (NAPLES 1999; CASALI & PERINI 2016) and dasypodids (BURMEISTER 1874; PÉREZ et al. 2000; PÉREZ et al. 2010).

SCOTT (1905: 45) described the hyoid apparatus of *Proeutatus robustus* SCOTT and pointed out that the upper ramus is composed by two elements, being the distal much longer than the proximal. The proximal could be identified with the ceratohyal, which is subcylindrical and articulates laxly with the V-bone. PÉREZ et al. (2010: 1126, fig.7) described and figured a specimen assigned to *Proeutatus* sp., in which the hyoid apparatus consists on a single elongated element (that was found articulating with the base of the skull) and they identified it with the sigmoidhyal. PÉREZ et al. (2010: 1130) suggested that the presence of the sigmoidhyal (they considered that the sigmoidhyal is formed by the stylohyal and the epihyal) could be an exclusive feature that closely relates eutatines and glyptodontids. This phylogenetic relation was postulated also by previous authors (see ENGELMANN 1985; VIZCAÍNO & BARGO 1998; GAUDIN & WIBLE 2006). In this work, it is proposed that the sigmoidhyal of glyptodontids is formed by 3 elements: stylohyal, epihyal and ceratohyal; while that of *Proeutatus* sp. has only 2 elements: stylohyal and epihyal.

The fusion of stylohyal, epihyal and ceratohyal forming the sigmoidhyal, and the basihyal and tyrohyal forming the V-bone, results in only three bones of the hyoid apparatus being recognizable in the glyptodontids. Moreover, the fused conformation of the sigmoidhyal

prevents the motion between elements, verified in other taxa. In turn, the sigmoidhyal has a disposition almost perpendicular to that of the V-bone since the structure of the hyoid apparatus in glyptodontids is affected (along with the rest of the skull) by the telescoping process in which the masticatory apparatus moves beneath the neurocranium (FARIÑA & PARIETTI 1983; PÉREZ et al. 2000, 2010; FARIÑA & VIZCAÍNO 2001). Thus, the sigmoidhyal swings only in the antero-posterior plane. In the case of *Glyptodon* cf. *G. clavipes*, PÉREZ et al. (2000: 299, 2010: 1131) stated that this movement occurs because the action of two antagonistic muscles, geniohyoid and ceratohyoid. We propose that in *Panochthus* sp. the stylohyoid and occipitohyoid collaborate significantly to perform this movement. Therefore, *Panochthus* sp. could have more freedom of tongue movement than *Glyptodon* cf. *G. clavipes*, which possibly implied a different use of food resources.

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