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Source: American Museum Novitates, 2006(3536) : 1-18

Published By: American Museum of Natural History

URL: [https://doi.org/10.1206/0003-0082\(2006\)3536\[1:PPXFCC\]2.0.CO;2](https://doi.org/10.1206/0003-0082(2006)3536[1:PPXFCC]2.0.CO;2)

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AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024

Number 3536, 18 pp., 4 figures

October 19, 2006

Paleogene Pseudoglyptodont Xenarthrans from Central Chile and Argentine Patagonia

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ABSTRACT

Herein we describe a new, large-bodied species of *Pseudoglyptodon*, a close sloth ally, from volcaniclastic deposits of the Abanico (= Coya-Machalí) Formation of the central Chilean Andean Main Range. This species, *P. chilensis*, is a rare element of the Tinguiririca Fauna, on which the recently formalized Tinguirirican South American Land Mammal “Age” is founded, being known from just two specimens. The holotype of *P. chilensis*, a partial skull and largely complete mandibles (preserving seemingly complete upper and lower dentitions), is by far the best-preserved specimen referable to *Pseudoglyptodon* known. As such, this material permits a more refined phylogenetic placement of this enigmatic xenarthran than has been possible previously, with *Pseudoglyptodon* representing the proximal outgroup to the clade including the most recent common ancestor of *Choelepus* and *Bradypus*, plus all its descendants (i.e., crown clade sloths).

A fragmentary specimen from Argentina is removed from *Glyptatelus* and referred to *Pseudoglyptodon*. Although this specimen is distinct from *P. chilensis* and other previously recognized species of *Pseudoglyptodon*, it offers too meager a basis for formally establishing a new name.

Finally, phylogenetic definitions of the names Phyllophaga and Tardigrada are proposed. Historically these terms have been used largely interchangeably, but here we advocate linking the latter to the crown clade.

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INTRODUCTION

South America continues to yield enlightening paleontological surprises. Here we describe the first-known associated skull and mandibles of *Pseudoglyptodon* Engelmann, 1987, from Eocene–Oligocene volcanoclastic sediments of the Abanico (= Coya Machali) Formation, Termas del Flaco, valley of the Tinguiririca River, central Chile. This is the first xenarthran from the Tinguiririca Fauna (Wyss et al., 1994) to be described in detail. The two Chilean specimens are referred to a new, large-bodied species of *Pseudoglyptodon*, an aberrant early sloth relative, the type species of which, *P. sallaensis*, is based on a lower jaw from Branisa Locality V-12, lower part of the Salla Beds, Deseadan South American Land Mammal “Age” (SALMA) of Salla, Bolivia (MacFadden et al., 1985). The name “*Pseudoglyptodon*” is intended to reflect the morphology of the cheek teeth of these edentates, superficially resembling the cheek teeth of glyptodontids in their trilobate external form, but lacking the central figure (an axial crest of osteodentine) typical of glyptodontids. We also refer several teeth from the Mustersan and Deseadan of Argentine Patagonia—previously interpreted as glyptateline glyptodontids—to *Pseudoglyptodon*. The new Chilean species, *P. chilensis*, is similar to *P. sallaensis* in many features but is about twice the size of the latter. A second specimen probably referable to *P. chilensis* is known from Termas del Flaco, but it yields limited useful information. A third specimen, referable on present evidence to *P. chilensis*, was described by Florentino Ameghino (1897) from the couches à *Pyrotherium* (Deseadan in current terminology) of Patagonia, being placed in the poorly known early glyptodont species *Glyptatelus tatusinus*.

The Chilean specimens described here are derived from concretionary nodules harvested in place from volcanoclastic sediments of the Abanico (= Coya Machali) Formation of the central Andean Main Range. The Tinguiririca Fauna forms the basis of the recently formalized Tinguirirican SALMA (Flynn et al., 2003); the age of the fossiliferous strata in this area is constrained by $^{40}\text{Ar}/^{39}\text{Ar}$ radioiso-

topic dates to roughly 31.5 Ma (Wyss et al., 1993; Flynn et al., 2003)—early Oligocene following the time scale of Swisher and Prothero (1990). The skull preserves much of the lower jaws and snout, but rearward from the orbit the specimen is heavily damaged. Nonetheless, both petrosal bones are in position (although “floating” in the hard matrix), as are parts of the right zygomatic arch and mandibular condyle. All of the comparatively few teeth of the animal are present, but the mandibles are clenched tightly to the skull. Separation of the mandibles from the skull has not been attempted; instead, much of the dental pattern has been elucidated through computed tomographic (CT) scanning. The depositional mechanism(s) accounting for the newly recognized prevalence of mammal remains in post-Neocomian volcanoclastic strata of the Andean Main Range remain(s) uncertain. Specimens described here may have been engulfed in a lahar or volcanic debris flow and literally cooked to death, with the thinner parts of the skull and jaws reduced to cinders and only the more massive parts remaining, more or less in their natural positions. Postcranial elements were not recovered, nor were any traces of osteoderms that might have accompanied the skull. Moreover, no obvious glyptodontid osteoderms are known from any of the localities in the Abanico Formation at Termas del Flaco, even though such durable elements would be expected to have withstood deposition. Well-preserved dasypodid osteoderms occur in moderate abundance in strata near Termas del Flaco, but these are unlikely to pertain to *Pseudoglyptodon*. This absence of glyptodontid osteoderms might be argued to reflect the general scarcity of this taxon in these deposits (with only two specimens recovered) rather than the taxon’s actual lack of osteoderms. We would point out, however, that dasypodids, which are known from equally few dental remains in these strata, are nonetheless fairly abundantly represented by osteoderms—sometimes as large, articulated portions of the carapace. In short, if *P. chilensis* possessed obviously glyptodontid dermal armor, it seems highly unlikely that these would

have gone undetected, given the extensive collecting efforts undertaken in the area to date.

The dental pattern exhibited by *Pseudoglyptodon chilensis* sheds light on a variety of issues concerning xenarthran fossils and phylogeny. It is at once apparent that the new Chilean animal is closely similar in most respects but size to Engelmann's *Pseudoglyptodon sallaensis* from the Deseadan assemblage of Salla, Bolivia, and to teeth once referred to two species of the early glyptodont *Glyptatelus* Ameghino, 1897, from the Mustersan and Deseadan of Argentina. Various features of the skull and mandible of *Pseudoglyptodon* are clearly slothlike, however, as Engelmann (1987) first appreciated. The newly revealed occlusion of the caniniform teeth, wherein the lower caniniform tooth occludes almost directly opposite the upper caniniform tooth, presages the "reversed occlusion" seen in numerous sloths including *Choloepus*, and the small number of cheek teeth recalls sloths as well.

The new material from Chile clarifies somewhat the problem of glyptateline relationships by reinforcing the disassociation of the type osteoderms from the teeth dubiously referred to this group by Ameghino and accepted by various later commentators (e.g., Hoffstetter, 1958: 573; Scillato-Yané, 1977: 250). We believe that the teeth described by Ameghino as pertaining to two species of *Glyptatelus* instead should be referred to *Pseudoglyptodon*, an aberrant animal with tardigrade affinities now known from more informative material than was available to Engelmann in 1987. *Pseudoglyptodon* may have possessed osteoderms, of course, as did many other xenarthrans (including orophodonts and mylodonts among sloths), but none is known as yet. The new cranial and dental material emphasizes the morphological diversity exhibited by sloths and their closest allies as early as the Eocene/Oligocene transition. Although the relationships of *Pseudoglyptodon* to sloths or other xenarthrans remain less than "ironclad," the new information presented here adds materially to the potential solution of this question.

SYSTEMATICS

XENARTHRA

PHYLLOPHAGA OWEN, 1842,
AS MODIFIED BELOW

Pseudoglyptodon Engelmann, 1987: 217

TAXONOMIC NOTE: Confusingly, different taxonomic names are currently used to refer to the same minimally inclusive clade encompassing the xenarthran mammals commonly known as sloths: Tardigrada and Phyllophaga. Here we propose phylogenetic definitions (sensu de Queiroz and Gauthier, 1990) to remedy this ambiguity, tying each name to a different clade. We define Phyllophaga (a name coined by Owen, 1842, but generally disused until resurrected by McKenna and Bell, 1997) as all xenarthrans more closely related to *Bradypus* or *Choloepus* than to myrmecophagids or dasypodids. Consistent with familiar, present-day usage, we tie the name Tardigrada to the crown clade. Thus, Tardigrada is defined as the most recent common ancestor of *Bradypus* and *Choloepus* plus all of its descendants. The distinction between these names is especially relevant to the current study because—as detailed below—new specimens from Chile argue that *Pseudoglyptodon* is not a member of Tardigrada (the crown clade), but rather that it represents its nearest known outgroup (and hence is a member of Phyllophaga).

TYPE SPECIES OF PSEUDOGLYPTODON: *P. sallaensis* Engelmann, 1987: 217. Holotype of *P. sallaensis*, PU 20552, collected from Branisa's locality V-12, lower Salla beds, Salla, Bolivia.

OTHER MATERIAL: Other instances of originally described material or references to the presently described material are listed below.

Glyptatelus tatusinus: Ameghino, 1897: 507, in part. The osteoderm, not the tooth, described by Ameghino (1897: 507, 1902: 48) from the Deseadan of Argentine Patagonia is selected here as the (lecto)type specimen of *G. tatusinus*. We do this for the same reason as that given by Simpson (1948: 93) in selecting the lectotype of *G. fractus*. Association of Ameghino's two syntypes

of *G. tatusinus* is unproven and unlikely, although possible. The tooth referred to *G. tatusinus* by Ameghino (1897) is clearly related to *Pseudoglyptodon* and on present evidence refers to that taxon, whatever the relationships of *Pseudoglyptodon* to other xenarthrans might be. *Glyptatelus* was made the type of the Glyptatelinae by Castellanos (1932).

Glyptatelus fractus: Ameghino, 1902: 51 or 49, in part. The osteoderm and tooth described by Ameghino, said to be from the Mustersan (couches à *Astraponotus*) of Argentine Patagonia, were discussed by Simpson (1948: 93), who selected the osteoderm as the (lecto)type specimen of *G. fractus*. As with *G. tatusinus*, no association of the osteoderm with the tooth is evident. The (lecto)type osteoderm is that of an early glyptodont, but the referred tooth, like that of "*G. tatusinus*", is related to *Pseudoglyptodon sallaensis*, the type species of *Pseudoglyptodon*. On present evidence this tooth is distinct from other recognized species of *Pseudoglyptodon*, but the scant material presently known does not yet warrant recognition of a new species. The most complete specimen of this unnamed species of *Pseudoglyptodon* (to which Ameghino's referred specimen of *G. fractus* pertains as well) is AMNH 29483 (see below).

Undescribed glyptateline from Quebrada Fiera, Mendoza Province, Argentina (Scillato-Yané, 1988): This Deseadan taxon, represented by MLP 79-XIII-18-9, is known exclusively from osteoderms.

Pseudoglyptodon sp.: Wyss et al. (1990: fig. 4), specimen SGO PV 2995. This specimen is designated as the holotype of *Pseudoglyptodon chilensis* below.

DIAGNOSIS OF *PSEUDOGLYPTODON*: Slothlike xenarthran with a total of probably just four teeth in each tooth row; first teeth caniniform and massive, lower one with triangular base, upper one with massive oval base; caniniforms followed by just three open-rooted molariform cheek teeth, each trilobed and superficially glyptodontlike but without the central figure of glyptodont cheek teeth; skull short, with fused maxilla and premaxilla and fused nasals although the latter are still

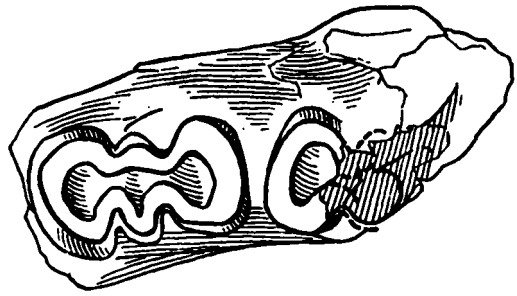


Fig. 1. AMNH 29483, mandibular fragment bearing one complete cheek tooth and part of a second, collected by G.G. Simpson from Cerro Blanco, Chubut Province, Argentina. Identified by Simpson (1948: 93) as "*Glyptodont, incertae sedis*, perhaps *Glyptatelus*", this specimen is here transferred to a new, but unnamed, species of *Pseudoglyptodon*. Reproduced from Simpson (1948: 93, fig. 23). Scale, 2×.

separate from the maxillae; lacrimal possibly fused to maxilla; large lacrimal foramen; zygomatic arch apparently deep, with weak anterior attachment to skull; lower jaw massive, ventrally everted, with anterior "spout" and underlying large foramen, fused symphysis, low coronoid process, and mandibular condyle.

Pseudoglyptodon, unnamed species

REFERRED SPECIMENS: AMNH 29483 (fig. 1), a mandibular fragment bearing one complete cheek tooth and part of a second, discussed and figured by Simpson (1948: 93, fig. 23) as "*Glyptodont, incertae sedis*, perhaps *Glyptatelus*", and also in more general terms by Hoffstetter (1958: 573, fig. 25). A cheek tooth from the Mustersan (or later; see below) of Patagonia referred by Ameghino (1902) to *Glyptatelus fractus* is here referred to *Pseudoglyptodon*, pertaining to the same unnamed species as AMNH 29483.

LOCALITY INFORMATION: Cerro Blanco, Chubut Province, Argentine Patagonia. Simpson (1948) provided no precise information about the provenance of AMNH 29483, nor is the specimen mentioned in his unpublished field notes. Nevertheless, the specimen's label reads, "Musters Formation, F5 beds, Cerro Blanco, Expedition '30." The provenance of Ameghino's specimen is uncertain.

AGE: Mustersan, according to Simpson (1948). The Mustersan, traditionally considered medial Eocene in age, has recently been suggested to be substantially younger, i.e., to postdate 35–36 Ma (Kay et al., 1999).

DIAGNOSIS: Cheek-tooth wall of hard dentine thicker than in *P. sallaensis* and lobes less angular. Differs from *P. chilensis* in smaller size (the lower tooth row being ~30% shorter anteroposteriorly).

COMMENT: These small *Pseudoglyptodon* cheek teeth are evidence of little but the presence of the taxon in Mustersan deposits, but this at least confirms other pre-Deseadan records for early phyllophagans in South America (Hoffstetter, 1958: 573).

Pseudoglyptodon chilensis, new species

Pseudoglyptodon sp.: Wyss et al. (1990: fig. 4).

TYPE SPECIMEN: SGO PV 2995, damaged skull and mandibles with seemingly complete dentition.

TYPE LOCALITY: The type and referred Chilean specimens are from the Tinguiririca River valley (~35°S) in the Cordillera Principal of the Central Andes, approximately 7 km west of the Argentine border. They are derived from a steep set of exposures north of an unnamed pass (the latter of which is identified by its 2738 m elevation on the topographic sheet [Anonymous, 1985]), approximately 3 km south of the summer resort town of Termas del Flaco. *Pseudoglyptodon chilensis* and its associated fauna occur in 35–50° westward-dipping volcanoclastic deposits of various colors, dominantly brownish red, interbedded with volcanic flows and tuffs (fig. 2). Prior to discovery of fossil mammals in the region (Novacek et al., 1989) these deposits were mapped as pertaining to the Colimapu Formation of poorly constrained Aptian–Albian age (e.g., Kohn, 1960). More recent detailed mapping and associated geochronologic studies (Wyss et al., 1993; Charrier et al., 1996) indicate that the mammal-producing unit pertains to the Abanico Formation (= Coya-Machali Formation), a widespread and stratigraphically important unit in this region of the Andes. Fossils occur most abundantly in

a massive, purplish brown, volcano-sedimentary horizon, near the apparent local base of the formation. Owing to structural complexity, it has not been possible to establish the relative stratigraphic position of the fossiliferous horizon within the approximately 2-km-thick Abanico Formation. A second, substantially older fauna has been recovered from volcanoclastic sediments of the Tinguiririca Valley some 15 km west of those hosting *P. chilensis* (Flynn et al., 1991; Wyss et al., 1996), indicating that the *Pseudoglyptodon*-producing beds do not correspond to anything approaching the lowest stratigraphic levels in the formation. Still further to the west (~20 km), but still at the same latitude (35°S), thick exposures of the Abanico Formation have yielded three stratigraphically superposed fossil mammal faunas, the lowest of which also clearly predates the Tinguirirican SALMA (Wyss et al., 2004).

AGE: Tinguirirican SALMA. The diverse fauna co-occurring with *Pseudoglyptodon* at Termas del Flaco allows unambiguous correlation with the SALMA sequence. The absence of such diagnostic taxa as *Pyrotherium*, primates, mesotheres (which is problematic, because this group occurs in the Divisaderan), *Archaeohyrax*, *Plagiathrus*, hegetotheres, and *Morphippus* (Marshall et al., 1983) indicates a pre-Deseadan age for this Chilean fauna. Co-occurrence of taxa known elsewhere only from Mustersan and older deposits (notostylopids, notopithecines, and polydolopids) with taxa previously known only from younger beds (a clade of nothippids diagnosed by hypsodont incisors, interatheriine interatheres, and rodents) identifies the fauna as representing a biochronologic interval interposed between the Deseadan and Mustersan SALMAs, the Tinguirirican (Flynn et al., 2003). In this connection, the *Pseudoglyptodon*-containing fauna from Chile bears little resemblance to the problematic Divisaderan assemblage (known from a single locality some 250 km to the northeast, in western Argentina). Whatever the still uncertain relative temporal relationship of the faunas from Termas del Flaco and Divisadero Largo may be, the two are undoubtedly distinct.

That the Tinguiririca Fauna derives from a thick volcanic and volcanoclastic sequence is



Fig. 2. View east of the fossiliferous outcrop (2–3 km south of Termas del Flaco, Chile, and immediately northwest of an unnamed pass of 2738 m elevation [Anonymous, 1985]) from which the two known specimens of *Pseudoglyptodon chilensis* were recovered. The view is roughly perpendicular to the strike of the

fortuitous from the standpoint of radioisotopic dating. Multiple single-crystal laser fusion $^{40}\text{Ar}/^{39}\text{Ar}$ dates (Wyss et al., 1993) and fewer conventional $^{40}\text{K}/^{40}\text{Ar}$ analyses (Wyss et al., 1990) constrain the absolute age of *Pseudoglyptodon chilensis*. Dates from immediately above the fossiliferous horizon indicate *P. chilensis* to be minimally ~ 31.5 Ma (early Oligocene) in age (Flynn et al., 2003). Levels immediately below the fossiliferous horizon (but within the same stratigraphic unit) have been dated (Flynn et al., 2003) at a locality producing a fauna indistinguishable from the one associated with *P. chilensis*, but this second locality has not yet produced *P. chilensis* itself. Present evidence suggests, albeit indirectly, that the Tinguirirican SALMA likely extends no further back in time than an additional 1–2 Ma (Flynn et al., 2003), i.e., very near the Eo-Oligocene transition.

REFERRED SPECIMENS: A second specimen from Termas del Flaco, SGO PV 2999, consists of a badly damaged anterior end of a right mandibular ramus and part of the fused symphysis. Only alveoli and fragmentary tooth bases remain. One alveolus suggests a trilobed cheek tooth like that of the type specimen of *P. chilensis*. Unfortunately, the referred specimen from Termas del Flaco provides little useful information. A Deseadan cheek tooth from Patagonia referred by Florentino Ameghino (1897: 507) to *Glyptatelus tatusinus*, not demonstrably associated with the (lecto)type specimen and not a glyptodont in any case, may belong here as well. It provides limited information but is less certainly conspecific with *P. chilensis* than is SGO PV 2999.

DIAGNOSIS: *Pseudoglyptodon chilensis* differs from *P. sallaensis* and the unnamed species discussed above in the former's much larger size, thinner cheek-tooth wall of hard dentine, and more sharply angular cheek-tooth lobes.

DESCRIPTION: Skull: The skull of *Pseudoglyptodon chilensis* (fig. 3) is evidently short, as suggested by the small number of teeth, the position of the jaw articulation, and the position in the matrix of the two petrosal bones. The distance between the front of the skull and the anterior edge of the orbit (as judged by the position of the lacrimal foramen) is truncated, a condition generally seen in sloths but even more marked in glyptodonts. The little of the orbit that may be discerned occurs not far above the roots of the upper cheek teeth, which, although almost certainly hypselodont (no evidence of closed roots is seen on the CT scans—which are frontal sections), are not highly elongate prisms requiring a deep maxilla. Because all upper teeth appear to originate in the maxilla and no suture is evident at the anterior end of the maxillary wall of the rostrum, the premaxilla was either lost postmortem or is completely fused to the maxilla in the specimen at hand. The two nasal bones are fused to each other but not to the maxilla. They extend posteriorly to at least a position over the posterior end of the first molariform upper cheek tooth, but damage obscures their full posterior extent and whether they widened in the rear. The nasals are thus quite long and thin, contrasting with the short wide nasal judged to be typical—and ambiguously synapomorphic—of tardigrades (Gaudin, 2004—his character 100); foreshortened nasals are also typical of glyptodonts. In SGO PV 2995 the right nasal is ~ 5 mm wide at the midpoint of its preserved portion, while the element was at least 30 mm long and quite likely reached twice that length originally. Striking features of the otherwise already bizarre dentition of *P. chilensis* are the massive upper and lower “canines.” The oval, upper caniniform tooth base is housed in a prominent bulge in the maxillary bone on the side of the snout. The snout is too damaged to provide information about the anterior end of the palate, housing

←

west-dipping strata. Fossil mammal localities occur in the dark band of volcanoclastic sediments of the Abanico (= Coya Machalí) Formation in the mid-foreground (straddled by the top half of the circle). A cluster of tents in the circle gives a sense of scale. The light-colored strata in the middle distance are of the Baños del Flaco Formation (Neocomian), with the snow-covered rocks in the distance belonging to the Río Damas Formation (Kimmeridgian). The horizon approximates the border with Argentina.

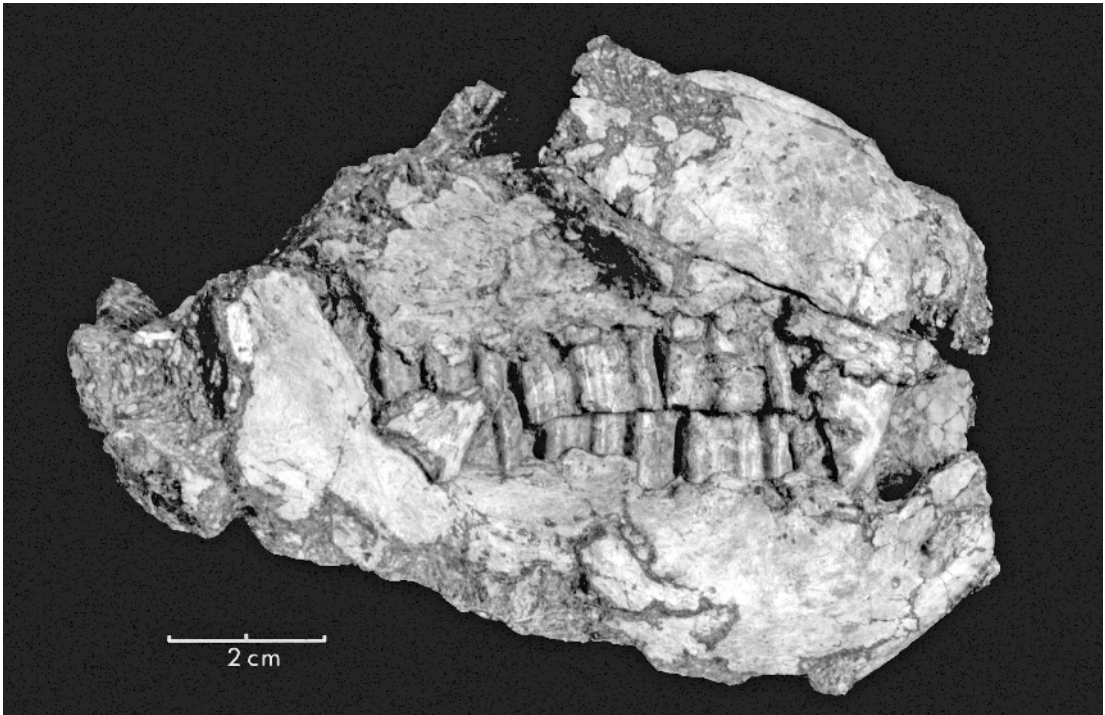


Fig. 3. Lateral view of the holotype of *Pseudoglyptodon chilensis*, SGO PV 2995. Visible near the base the coronoid process, appressed against the ventrolateral margin the mandibular ramus, is a thin fragment of bone interpreted as a remnant the descending process of the jugal. Wedges of the anterior and posterior parts of the base of the lower caniniform are visible immediately lingual of the upper caniniform, reflecting the unusual side-to-side occlusion of these enlarged anterior teeth.

for the organ of Jacobson, septomaxillary bone if any, or other anterior structures. The narial opening was large, but apparently little flared. Details of the orbit are lacking due to damage, but the orbit was probably not large. An apparent lacrimal bone occurs on the right side, where it appears to be fused to the maxilla. Its large lacrimal foramen lies anterior to the orbital rim. The anterior end of a possibly deep, posteroventrally descending wing of the anterior part of the zygomatic arch arises between the lacrimal foramen and the anterior end of the second of the three molariform upper cheek teeth. Although the maxillary part of the arch does not appear to have been especially strong (judged from its broken cross section), there is circumstantial evidence of a strong descending process of the jugal. A thin, triangular fragment of bone is appressed against the dorsoexterior border of the right mandibular ramus near the base of

the coronoid process, and outboard of the last upper and lower cheek teeth. This element (obviously not part of the mandible) sits at a considerable distance from broken base of the anterior root of the zygomatic arch. Nevertheless, if this element is in anything close to its life position, it can only represent a distal portion of an elongated ventral process of the jugal. The leading edge of this element is seemingly smooth and unbroken, its orientation consistent with that expected for a descending process of the jugal, as seen in many sloths. The possibility that this element represents a displaced element from the skull roof or orbit cannot be completely excluded, however. If this element is indeed a portion of the zygomatic arch, it resembles much more the condition seen in tardigrades than in glyptodontids (wherein the descending process is much more anteriorly situated).

The zygomatic arch was probably not continuous with the squamosal, but evidence is weak. We have not seen the infraorbital foramen, but it may be obscured by breakage and unremoved matrix. No traces of the frontals remain, unless one of several fragments of bone above the right lacrimal foramen represents the anterolateral corner of the right frontal. The parietals, squamosals, occipitals, alisphenoids, basisphenoid, basioccipital, vomer, pterygoids, and certainly any possible mesethmoid are all now absent, but the rear of the palate, presumably involving the palatine bones, extends to the rear past and around the posterior lobe of the last upper molariform cheek tooth, forming an indented torus of sorts that may incorporate a part of the palatine as well as the maxilla. The palate is unusually narrow between the cheek-tooth rows (best seen on CT scan images). At the gumline the two upper tooth rows are nearly parallel centrally but diverge slightly anteriorly (particularly from the first molariform tooth forward) as well as posteriorly (particularly m3).

The lower jaw is massive, especially in the symphyseal area, which is fused but shows traces of the suture on SGO PV 2995 but not on SGO PV 2999. The horizontal rami bulge laterally beginning below the second molariform tooth, extending and becoming more pronounced posteriorly. This results in a ~5-mm-wide shelflike area lateral to the third molariform tooth. The anterior end of the jaw supports a short upturned “spout,” below which lie one large and several smaller mental foramina on each ramus. Immediately behind the “spout” is the massive base of the lower caniniform tooth, which is followed by the three molariform lower cheek teeth (which are set off from each other by short diastemata). The lower cheek-tooth rows diverge posteriorly, especially deep within the alveoli. However, their occlusal surfaces meet those of the upper cheek-tooth row with less posterior divergence.

The ascending process of the mandible arises from the side of the horizontal ramus lateral to the last lower molariform cheek tooth, slanting up at an angle of about 135° to the plane of occlusion. The junction of the ascending and horizontal rami of the mandible

occurs near the midpoint of the third lower molariform tooth; this, coupled with the slow rate of climb of the ascending process, results in the cheek teeth being exposed in lateral view (i.e., not covered by the ascending process), save for the posterior third of the last lower teeth and the posteroventral corner of last upper teeth. Importantly, there is no evidence of an external opening of the posterior mandibular canal near the horizontal–ascending ramus junction. Although the inferior portion of the horizontal ramus is broken on the right side of SGO PV 2995, enough is preserved to demonstrate that no such foramen was present. The occurrence of a foramen in this region uniquely characterizes tardigrades among xenarthrans (Gaudin, 2004).

Owing to the shelf of bone lateral to the third lower molariform mentioned previously, the ascending process occupies a plane substantially lateral to the cheek-tooth row. The ascending process appears to be small, unexcavated either laterally or medially, evidently not projecting upward or rearward very far. Breakage of the dorsal, posterior, and ventral borders of the process, however, obscures its original size and shape. A small, detached knob of bone floating in the matrix near the posteroventral corner of the preserved part of the ascending ramus may be a remnant of the right mandibular condyle. If so, the condyle is positioned low, near the plane of occlusion, just in front of and lateral to the right petrosal. This contrasts with the primitive condition seen in most sloths (except mylodontids and *Choloepus*) and dasypodids (glyptodontids included), wherein the condyle is positioned well dorsal to the tooth row (Gaudin, 2004). Nothing can be said of the posteroventral parts of the mandible. A trace of a robust hyoid bone may possibly be represented by a bone fragment in the matrix at the appropriate position anterior to the right petrosal and medial to the presumptive mandibular condyle.

Dentition: The significance of SGO PV 2995 was revealed on the outcrop when its melon-sized encasing nodule was delicately cleaved with a sledge hammer; just the surface of the anterior end of the left mandible was visible initially. Mechanical preparation revealed the labial faces of the teeth. Because the mandibles

are tightly clenched, however, it has not been possible to disengage the upper and lower dentitions. Computerized tomography was used to more fully elucidate the dental morphology of SGO PV 2995. Twenty CT cross sections, taken as parallel to the occlusal plane as possible (CT scan nos. 563-11 through 563-30) were generated by Scientific Measurement Systems, Inc., (Austin, Texas) using a 420-kV 3-mA X-ray source. This stack of slices ranges from the bases of the lower cheek teeth to above the roots of the upper molariform cheek teeth. Distance in the x direction is 128.8 mm (i.e., preserved skull length), and distance in the y direction is 61.8 mm (i.e., preserved skull width). Each slice is 0.25 mm thick. Separation of the slices is 2.5 mm. The following description is based largely on this CT imagery. It must be cautioned that although the CT scans roughly parallel the occlusal plane, because the vertical axes of the high-crowned teeth are not consistently normal to this plane, the tooth outlines seen on the scans are distorted by the progressively more oblique angle at which they were sectioned (fig. 4). This is particularly true for sections taken the greatest distance from the occlusal plane, especially for the posterior postcanines, whose apparent buccolingual dimensions are exaggerated near the tooth bases owing to canted and slightly bowed vertical axes of these teeth.

The number of teeth in *Pseudoglyptodon* is unusual, probably just four above and four below on each side, all fairly closely spaced with only short gaps between them. A more substantial gap behind the upper caniniform tooth on the specimen's left side is likely artifactual, as a large crack disrupts the specimen in this region. Additionally, the degree to which the upper and lower left caniniforms are compressed into each other anteroposteriorly suggests a small degree of postmortem distortion in this region of the specimen. It is uncertain whether teeth occurred anterior of the upper caniniforms, because that region of the rostrum is missing.

The caniniform teeth of *Pseudoglyptodon* may or may not be true canines. Grassé (1955) regarded the anterior teeth in sloths to represent the true canine of the upper tooth row and the first premolar of the lower.

Nevertheless, as with other xenarthrans, until detailed embryological work is carried out, the homology of these teeth remains uncertain. It seems plausible, however, that either the upper or the lower caniniform tooth in *Pseudoglyptodon* is not a true canine, because the occlusion of these teeth, as in sloths, differs from that seen in other mammals. This conclusion assumes that an anterior premolar can be more readily transformed into a canine imposter, than the position of true canines can be shifted anteriorly or posteriorly relative to the opposing tooth. Regardless of whether phyllophagan "canines" are C1/p1, C1/c1, or some other permutation, tardigrades are unique among xenarthrans in having upper tooth rows extend anterior to the lower tooth rows. On the damaged left side of SGO PV 2995 the lower caniniform appears to occlude behind the upper, but on the better preserved right side the upper and lower caniniforms sit side by side. Thus, the upper and lower tooth rows of *Pseudoglyptodon* terminate at nearly the same level anteriorly. *Pseudoglyptodon* is therefore alone among xenarthrans in this regard, bearing an apomorphic resemblance to the condition seen in tardigrades (where the upper tooth row extends anterior to the lower). Some artiodactyls convert an anterior lower premolar into a caniniform tooth that occludes behind the upper canine, but the resemblance to sloths is not as close as that seen in *Pseudoglyptodon*.

The lower caniniform tooth of *Pseudoglyptodon* occludes with the sloping postero-medial wear facet of the upper caniniform tooth, much as in *Choloepus* except that, in *Pseudoglyptodon*, the lower tooth is more medially placed relative to the upper. The occlusal relationship of these teeth is best exhibited on the right side of SGO PV 2995 (fig. 3), because postmortem deformation has damaged the left pair of caniniforms. On the right side, the upper and lower caniniforms sit in a more normal orientation, directly side by side, the medial surface of the upper tooth occluding against the lateral side of the lower.

Judged from the CT scans, the tip of the lower caniniform tooth was not accommodated by an excavation in the palate. The three molariform cheek teeth following the caniniform tooth on both the upper and lower tooth

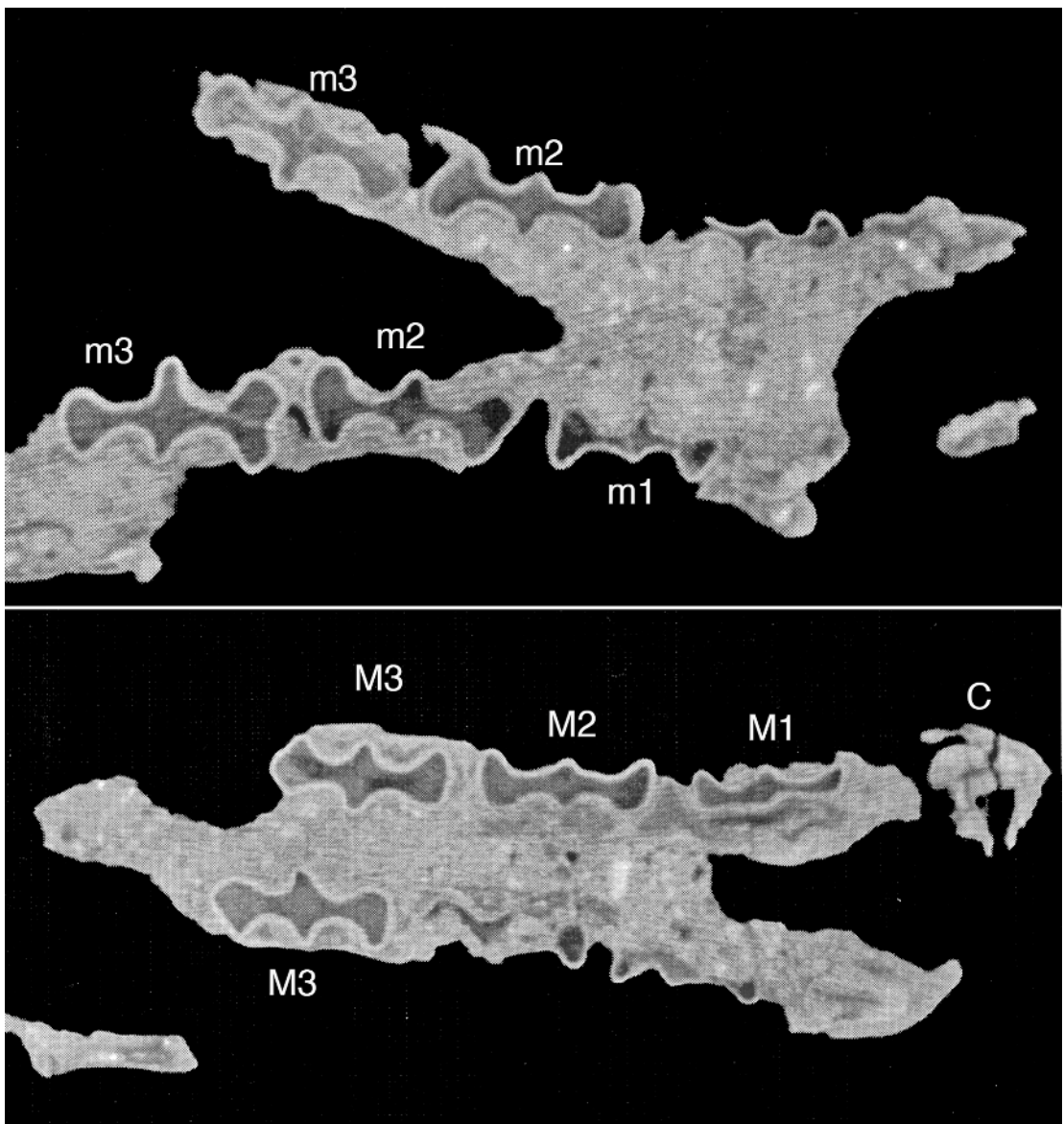


Fig. 4. CT scans of the holotype of *Pseudoglyptodon chilensis*, SGO PV 2995, revealing aspects of this taxon's dental morphology (dorsal plane). **Upper scan**, no. 563.18, showing molariform 2 and molariform 3 near the gumline. **Lower scan**, no. 563.24, illustrating cross sections of the upper canine roots and the upper postcanine dentition, also above the gumline. "M" and "m" signify upper and lower molariform teeth, respectively, as the true positions of these teeth are unknown.

rows are anteroposteriorly elongate and trilobed, being about as high as they are long. It cannot be established whether any of the teeth is deciduous, or had replaced a precursor.

The upper caniniform tooth is enormous and is supported by a large oval base (not

really a root in the usual sense) that extends high into the maxilla. At its dorsal extremity the base of the upper caniniform tooth opens widely rather than closing to a blunt tip. CT sections of the unworn parts of the tooth are narrower at the front than the rear, and the

labial wall of the tooth is relatively convex, whereas the lingual wall is flatter. A rather flat transverse wear facet has been created by action with the lower caniniform tooth, from the recurved anterior tip of the upper caniniform tooth diagonally upward until the facet reaches the broad rear of the tooth's base at the gum line.

The lower caniniform tooth differs in shape from its upper counterpart. CT scans show that its massive open base is wide in front and nearly flat on the anterior face within the alveolus. It then narrows, followed by a narrower rear-projecting lobe. The cross sections within the alveolus thus have a "pinched," triangular shape. Near the gum line, the broad anterior face of the lower caniniform tooth becomes more rounded, and the posterior lobe becomes even narrower. Above the gum line, the anterior face is transversely worn by the action of the upper caniniform tooth. The diagonal (anteroventral–posterodorsal) slope of the transverse wear facet is guaranteed by the initial wear that would have occurred when these curiously shaped teeth first made contact.

As with the caniniforms, the homologies of the molariform teeth in *Pseudoglyptodon* are uncertain. All three molariform cheek teeth in both the upper and lower dentition have essentially the same trilobed external shape of glyptodont teeth, in outline reminiscent of a bat in flight seen from directly below. The long axes of these teeth parallel the long axis of the tooth row. As in glyptodontids, the crowns of these teeth are worn nearly flat except for the anterolabial lobe of the right third lower molariform cheek tooth, which projects somewhat between the second and third upper molariform cheek teeth labially in a manner reminiscent of the anterior ends of the crowns of rear lower molariform cheek teeth of *Orophodon* and *Octodontotherium* (Hoffstetter, 1958: fig. 42). The various molariform cheek teeth change slightly in shape with wear, as seen in their various cross sections, but they do not change significantly in dimensions throughout the various levels of each tooth. The base of each molariform cheek tooth is open, as in most tooth-bearing xenarthrans. Unlike glyptodont molariform cheek teeth, there is no central figure in the dentine of teeth of *Pseudoglyptodon*.

The first of the three upper molariform cheek teeth is the smallest of the upper postcaniniform series and is the narrowest transversely. Its anterior lobe is flattened and oriented normal to the tooth's anteroposterior axis deep within the alveolus. Near the occlusal surface the flat anterior surface faces more lingual. The isthmus between the anterior and medial lobes is narrower than in the two more posterior upper cheek teeth. The medial lobe is blunter and projects less than those of the succeeding teeth, and the posterior wall of the posterior lobe is more flattened. The indentations demarcating the lobes of the molariform teeth are less pronounced on the lingual walls of the teeth than they are labially. Both the anterior and posterior labial lobes diverge from one another strongly, in contrast to those of the succeeding teeth.

The second of the molariform upper cheek teeth is more symmetric about its medial lobes than the first, although the labial reentrant between the anterior and medial lobes seems to have a small secondary fold high above the present occlusal surface (at least on the specimen's right side). The anterior wall of the anterior lobe and the posterior wall of the posterior lobe are gently convex. The medial lobe is smaller and less acute than that of the third molariform tooth. As on the first molariform tooth, the anterior and posterior lobes of the second diverge labially more than lingually, contrasting with the orientation of the lobes of the posterior tooth.

The third (and last) upper molariform cheek tooth is the largest of the upper series. The anterior wall of its anterior lobe is gently convex and is not subdivided by an anterior indentation, as is its lower counterpart. The posterior lobe is broad, with a flattened, posterolabially facing wall that is indented slightly on the animal's left tooth but not on the right one. Both the anterior and posterior lobes are more acute labially than lingually, but the prominent medial lobe is acute both lingually and labially, forming the widest part of the tooth. Breakage of the maxilla posterior to the last left molariform reveals that this tooth is implanted such that its vertical axis slopes labially from top to bottom.

The symphysis of SGO PV 2995 is well enough preserved that the presence of any

lower teeth anterior of the caniniforms seems unlikely. Confoundingly, SGO PV 2999 exhibits the broken stubs of two small teeth floating in matrix above the symphyseal region. Both consist of little more than broken, ovoid cross sections 2–3 mm in diameter. Nevertheless, these tooth remnants are positioned symmetrically (one on either side of the symphysis, and about 1 cm apart from one another), so it must be assumed that they are preserved in life position. What are these teeth? Two explanations seem credible. The bone–matrix interface on SGO PV 2999 is indistinct anteriorly, making it difficult to determine what these teeth were originally attached to. Nevertheless, there is a distinct rim of bone immediately lateral of the right tooth—this rim is clearly the medial margin of an alveolous for an enlarged anterior lower tooth, probably the caniniform. The medial position of this tooth relative to the mandibular alveolus suggests that both tooth remnants are likely the tips of the upper caniniforms (which were clenched), the remainder of the upper dentition having been broken away. Alternatively (but less likely), these tooth remnants could represent small anterior teeth of the lower dentition, elements which simply are not preserved in SGO PV 2995.

The first lower molariform is the smallest cheek tooth, and has the narrowest isthmuses between lobes. The anterior lobe lies mainly anterolabial to its isthmus, with the result that there is little or no anteroposterior curvature of the lingual wall of the tooth anterior to the medial lobe. The medial lobe projects slightly labially, but forms a larger and more acute projection on the lingual side, limiting the anterior end of a deep reentrant behind it. The posterior lobe is more symmetrical than the offset anterior one, and it is slightly indented at the rear. It is the widest and most massive lobe.

The second lower molariform tooth is larger than the first and bears a large posterolabially–anterolingually oriented anterior lobe, the anterolabial wall of which is nearly flat. The lingual part of the lobe is larger and less acute than the labial part. The posterior lobe is even larger than the anterior one but is oriented somewhat posterolingually–anterolabially. It too is larger and less acute lingually

than labially. The medial lobe is smaller and, like the other lobes, more pronounced lingually than labially.

The third molariform, the largest lower cheek tooth, is distinguished by a very large and transverse anterior lobe that is markedly indented anteriorly, resulting in a large, rounded lingual sublobe and a smaller, somewhat more acute labial one. The medial lobe is also very large, transverse, and acute on both sides of the tooth, but it is especially prominent lingually. The posterior lobe is somewhat asymmetrically placed, lying mainly posterolabially, somewhat the mirror image of the anterior lobe of the first molariform tooth. As in the other lower molariform cheek teeth, it is more acute labially than lingually. Breakage of the dentary posterior to molariform 3 on the left side of SGO PV 2995 shows this tooth to be inclined lingually. It also shows clearly that the root of this tooth is quite short compared with the second molariform of *P. sallensis*. In the latter, the second molariform reaches the base of the mandible, and the tooth is nearly 3 cm high (i.e., the height is triple the length). In the Chilean form the molariforms are subequal in height and width.

Petrosals: Although both petrosals are preserved (indeed, they constitute nearly the entirety of the preserved portion of the skull posterior to the upper dentition), neither reveals much anatomical or phylogenetically informative data. The left petrosal consists of a badly damaged, featureless lump. The right petrosal preserves perfectly ordinary-looking oval and round windows, and an unremarkable promontorium.

PSEUDOGLYPTODON PHYLOGENETICS

Is *Pseudoglyptodon* a sloth? This of course depends on one's definition of "sloth". *Pseudoglyptodon* clearly falls phylogenetically outside the minimally inclusive clade of which *Bradypus* and *Choloepus* are a part, i.e., it is the nearest outgroup to what has traditionally been termed sloths. Is it preferable to amend the definition of "sloth" such that it is applicable to *Pseudoglyptodon* as well, or should a different name be defined for the minimally inclusive clade of xenarthrans of

which *Pseudoglyptodon* is a member? As mentioned earlier, the recognition of two new species of *Pseudoglyptodon* herein presents an excellent opportunity to rectify a long-standing nomenclatural problem, the existence of two names (Tardigrada and Phyllophaga) that have been employed nearly interchangeably in xenarthran systematics in reference to the same group. We have opted to attach the former to the crown clade, using the name Phyllophaga to refer to all xenarthrans more closely related to sloths (Tardigrada) than to anteaters or armadillos. Following this usage, we are confident that *Pseudoglyptodon* is a member of the Phyllophaga, but it is almost certainly not a tardigrade.

A number of features argue for the out-group placement of *Pseudoglyptodon* relative to Tardigrada. In common with tardigrades, *Pseudoglyptodon* apomorphically possesses a short, deep skull and robust mandibles. Anteriorly the mandibles of *Pseudoglyptodon* bear a spoutlike structure and a large foramen like that of tardigrades. There is no posterior opening of the mandibular canal in *Pseudoglyptodon*, contrasting with the condition in tardigrades. There are likely only four upper and four lower teeth on each side in *Pseudoglyptodon*, of which the most anterior are caniniform. This represents a reduction of the dental formula from the five upper teeth/four lower teeth considered ancestral for tardigrades (Gaudin, 2004). The enlarged caniniform teeth of *Pseudoglyptodon* occlude in a manner approaching the condition seen in some tardigrades; in sloths having caniniform teeth, the upper one occludes anterior to the lower one (the reverse of the situation seen in most mammals). By contrast, in *Pseudoglyptodon* the caniniforms occlude nearly side by side. The cheek teeth of *Pseudoglyptodon* are hypselodont and trilobed, reminiscent of glyptodont teeth in these respects, but lacking the central dentine figure of glyptodontids. In our estimation, the closest approach to the dental pattern of *Pseudoglyptodon* among tardigrades is seen in various mylodonts, a group generally recognized as having diverged early in the history of sloths. Among these, orophodontids may be singled out. The bilobed cheek teeth of *Octodontobradys puruensis* from the Mio-

Pliocene of western Brazil (Santos et al., 1993), may hint that this pattern was primitive for sloths. This had been suggested earlier by incomplete orophodont dentitions containing several sequential bilobed teeth. Thus, the cheek-tooth outline exhibited by *Pseudoglyptodon* may represent: (1) a still more primitive condition (wherein sloths may have been characterized ancestrally by trilobed cheek teeth behind simpler caniniforms); (2) an autapomorphic modification to three lobes from the bilobed condition seen in some early, *Octodontobradys*-like orophodonts; or (3) a completely independent derivation from an unlobed ancestral condition.

Beyond the unusual outline of the cheek teeth in *Pseudoglyptodon*, the departure of this taxon's dental formula (4/4) from the pattern typical of tardigrades (5/4) should also be emphasized. *Pseudoglyptodon* retains fully functional caniniforms, meaning that the reduction of the upper dental count was likely achieved through the loss of the first or the last molariform. Thus, it seems inescapable that this and potentially other aspects of *Pseudoglyptodon*'s dental anatomy do not typify phyllophagans ancestrally (nor any other group of xenarthrans to which this taxon is potentially related). Given the early age of *Pseudoglyptodon*, its high degree of aberrant dental specialization is unexpected.

In a superb recent assessment of tardigrade relationships, Gaudin (2004) identified 22 nonauditory cranial features as unambiguously diagnostic of the group. Of these, currently available specimens of *Pseudoglyptodon* permit scoring of only the following (using Gaudin's character/character state numbering scheme). Gaudin's analysis did not include glyptodonts, however, so we caution that several of these features are not unique among xenarthrans.

37(3): Depth of mandible $>22.5\%$, $\leq 25\%$ of maximum mandibular length. This number is difficult to estimate in *Pseudoglyptodon* due to breakage, but the maximum mandibular length is ~ 10 cm. The mandible of *P. chilensis* is 2.5 cm deep at a minimum, and probably approached 3 cm in life. Thus, mandibular depth in *Pseudoglyptodon* meets

or exceeds the primitive sloth condition, potentially matching the most extreme deepening seen among tardigrades, e.g., *Acratocnus*, *Megatherium*, and *Octomylodon* (Gaudin, 2004). Glyptodont mandibles are also deep, which is interpreted here as homoplasy.

- 61(1): Fused mandibular symphysis. Fusion of the symphysis in *Pseudoglyptodon* argues that this feature is diagnostic of Phyllophaga. A fused symphysis occurs also in glyptodonts, presumably homoplastically.
- 74(1): Posterior external opening of mandibular canal. Absent in *Pseudoglyptodon*.
- 85(3): Length of snout (preorbital length measured to tip of nasal) $<25\%$, $\geq 15\%$ of basonasal length. In *Pseudoglyptodon* the basonasal length is ~ 12 cm. The preorbital length is less securely known given breakage of the anterior rostral region in SGO PV 2995; we estimate it to be between 3 and 4 cm. Although there is considerable variability in the length of the snout in tardigrades, the condition in *Pseudoglyptodon* clearly more closely resembles the rostral form typically seen in that group than it does the form in cingulates (except glyptodonts) or myrmecophagids.
- 142(2): Lacrimal foramen large, diameter $\geq 2.5\%$, $< 3\%$ of basonasal length (BNL). The diameter of the lacrimal foramen in *Pseudoglyptodon* is ~ 3 mm, i.e., roughly 2.5% of BNL.
- 145(2): Jugal with large ascending and descending processes. Although the ascending process is not preserved in *Pseudoglyptodon*, this taxon appears to have been marked by a strong descending process.

In addition, there are a number of derived features seen in *Pseudoglyptodon* that are optimized as ambiguously synapomorphic for Tardigrada by Gaudin (2004, his node 6).

- 2(2): Dental formula: 5 upper teeth, 4 lower teeth. *Pseudoglyptodon* should actually be scored with Gaudin's character state 3 (i.e., 4 uppers, 4 lowers), a condition occurring elsewhere among xenarthrans only in

Myiodon. Nevertheless, the dental formula seen in *Pseudoglyptodon* (4 uppers, 4 lowers) closely approaches that typical of tardigrades ancestrally.

- 7(1): Hypsodont cheek teeth. *Pseudoglyptodon* is clearly high crowned, and moreover is hypselodont. *P. chilensis* shows that early members of *Pseudoglyptodon* are substantially less hypsodont than the slightly younger *P. sallaensis*. Glyptodonts also have hypso- and hypselodont cheek teeth, presumably independently derived.
- 9(2): Modified orthodontine core of teeth, large, typically well vascularized. Although the degree of vascularization has not been assessed in *Pseudoglyptodon*, the teeth are nonetheless quite large for a xenarthran.
- 11(2): Outer layer of cementum forms thick layer around outside of teeth. There is no obvious evidence of cementum on the teeth in *Pseudoglyptodon*.
- 18(1): Upper tooth row extends anterior to lower. This condition is just barely met in *Pseudoglyptodon*, judging from the less distorted right side of SGO PV 2995.
- 20(1): Wear surface on C1/c1 oblique.
- 36(6): Trilobate m3. Among xenarthrans, *Pseudoglyptodon* is remotely comparable only to glyptodonts in this respect.
- 100(0): Length and width of nasals. Tardigrades are typified (ambiguously) by short wide nasals, the ratio of maximum length to width measured at midpoint < 3 . In *Pseudoglyptodon* this ratio is > 6 , probably approaching 12, being difficult to estimate due to anterior and posterior damage to the nasals. Slightly less elongated nasals (length:width ratio > 4) uniquely (and apomorphically) typifies Scelidotheriinae among tardigrades. *Pseudoglyptodon* is quite unusual in this respect, probably reflecting the condition marking pilosans primitively. Glyptodonts are also characterized by short wide nasals.
- 153(1): Descending process of jugal present and hooking posteriorly. The bone fragment floating in isolation just lateral to the

base of the coronoid process in SGO PV 2995 (see description) indicates that a descending process with this orientation was likely present in *Pseudoglyptodon*.

CONCLUSIONS

New material referable to *Pseudoglyptodon* from the Andean Main Range of Chile offers tantalizing new evidence about character evolution in the early history of Phyllophaga. The Chilean taxon exhibits several diagnostic features previously seen only in sloths; nevertheless, its retention of at least one primitive attribute argues for its divergence prior to the appearance of the common ancestor that gave rise to *Bradypus* and *Choloepus* plus all its descendants. SGO PV 2995, the holotype of *P. chilensis*, is regrettable for all the phylogenetically important information it might have revealed were it not for the violent, and likely hot, conditions prevailing during the skull's volcanically associated deposition. The thinner areas of the specimen (most of the back end of the skull and basicranium, posteroventral region of the mandible, and zygomatic arch) were likely incinerated during burial.

The remains of pseudoglyptodontids are extremely rare: of the hundreds of mammal specimens collected at Tinguiririca, only two are referable to *Pseudoglyptodon*. Furthermore, we have recovered no specimens referable to the group from the dozens of other Cenozoic mammal localities recently uncovered across a ~500-km-long swath of the Andean Main Range. Given the scarcity of reported specimens, the group was uncommon in higher (Patagonia, Argentina) and lower (Salla, Bolivia) latitudes as well.

Pseudoglyptodontids complicate what would otherwise be a fairly straightforward picture of dental evolution in the early diversification of xenarthrans (teeth reduced to simple, peglike structures in early xenarthrans, with the number of these primitively simple teeth greatly reduced in phyllophagans). Inasmuch as the nearest known outgroup to tardigrades is characterized by trilobed cheek teeth, a number of more complex scenarios must now be entertained. Was, as Engelmann (1987) suggested, the ancestral tardigrade dentition marked by lobate postcanines? If

it was, given the trilobate cheek teeth of glyptodontids, are such teeth primitive for dasypodids and/or xenarthrans as a whole, with subsequent loss several times independently? Given the poorly resolved phylogenetic placement of glyptodontids relative to other cingulates, the possible transformation history of the dentition in early xenarthrans is currently not readily optimized. Unless glyptodontids can convincingly be shown to diverge basal to all other cingulates, the trilobed cheek teeth in *Pseudoglyptodon* are likely convergent upon those in glyptodontids (which lack the reduced number of teeth characterizing phyllophagans). Thus, it is also possible that simple ovoid teeth characterized phyllophagans (and tardigrades) ancestrally, with *Pseudoglyptodon*, orophodonts, and glyptodontids each developing more complex cheek teeth independently.

Finally, in view of the many derived resemblances between *Pseudoglyptodon* and glyptodonts, a word about the possible relationship of these two groups is in order. Might *Pseudoglyptodon* be an early-diverging, peculiarly specialized glyptodont, rather than a phyllophagan? It is conceivable, after all, that the resemblances noted between *Pseudoglyptodon* and glyptodonts reflect a unique common ancestry—in which case there is either a great deal of convergence between this glyptodontoid clade and tardigrades, or the unusual features common to *Pseudoglyptodon*, glyptodontids, and tardigrades represent ancestral conditions for Xenarthra. Acceptance of an exclusive *Pseudoglyptodon*–glyptodont relationship would imply that *Pseudoglyptodon* diverged from other members of the clade prior to the origin of the central dentine figure, and potentially before the appearance of osteoderms (assuming *Pseudoglyptodon* truly lacked them). While intriguing, pending a clearer understanding of the phylogenetic placement of glyptodonts relative to other cingulates, we regard this alternative as currently less viable than the hypothesized tardigrade affinities of *Pseudoglyptodon* favored above.

ABBREVIATIONS

AMNH	American Museum of Natural History
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MLP Museo de La Plata
 PU Princeton University
 SGO PV Museo Nacional de Historia Natural,
 Santiago, Chile, vertebrate paleontology
 collections

ACKNOWLEDGMENTS

We thank the National Geographic Society for support of the initial field season, the National Science Foundation, and the Eppley Foundation. Reynaldo Charrier freely shared his geologic expertise and has enthusiastically embraced mammal fossils for deciphering Andean geochronology. We thank the reverse fault in the upper reaches of the Río Tinguiririca, for without it there would be no Termas del Flaco, without which there would have been no economic rationale for a road so deep into the Andean Main Range, without which the paleontological riches of the Abanico Formation might not have come to light for another century. Our work has had the long-term backing of the Museo Nacional de Historia Natural and the Consejo de Monumentos Nacionales, Santiago, Chile. Daniel Frassinetti and María Eliana Ramírez have been pivotal in this regard. Gastón Mancilla provided access to land producing part of the Tinguiririca Fauna. Susan Bell provided invaluable assistance with locality and specimen data. Chester Tarka produced the photograph making up figure 3. Timothy Rowe was generous beyond the call of duty in facilitating the CT scanning, without which our description would be far less complete. The comments of George Engelmann and those of a highly insightful anonymous reviewer improved the manuscript substantially.

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