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A NEW BASAL GLYPTODONTID AND OTHER XENARTHRA OF THE EARLY MIOCENE CHUCAL FAUNA, NORTHERN CHILE

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ABSTRACT—Three cingulates from the early Miocene Chucal Fauna of northern Chile (ca. 17.0–19 Ma; Santacrucian SALMA) are described. A dasypodid, represented by isolated osteoderms, a partial rostrum, and postcranial bones, resembles *Stenotatus patagonicus* (Eutatini), but is ca. 20% smaller (similar in size to *Prozaedyus*) and may represent a new *Stenotatus* species. Two isolated peltephilid osteoderms are referred to cf. *Peltephilus* sp. A new glyptodontid, *Parapropalaeohoplorus septentrionalis*, is represented by a mandible, ca. 25% of the carapace, a femur, and other postcrania. This new species differs from other glyptodontids in its dentition (triangular n1-3 and distobuccally elongate n2-3), mandible (unexpanded angle, vertical coronoid process), osteoderms (absent/poorly defined peripheral figures, large principal figure positioned along posterior edge), and femur (highly elevated greater trochanter). A second specimen may represent *P. septentrionalis* or a closely related species. No sloths have yet been collected at Chucal. A preliminary phylogenetic analysis of glyptodontids—the first for the group—suggests that Glyptatelinae and Propalaeohoplorinae are paraphyletic and that *Parapropalaeohoplorus* is an early diverging glyptodontid, not closely related to other Santacrucian species. The revised faunal list for Chucal, which includes 18 mammals and one frog, is depauperate compared to coeval Patagonian faunas. This fauna probably occupied a relatively open, seasonal habitat. Endemism in the Chucal xenarthrans parallels that in other mammal groups, indicating significant latitudinal provinciality in South America during the early Miocene. Furthermore, the record of a glyptodontid basal to a radiation matches patterns observed in other Chucal groups (e.g., chinchilline rodents, mesotheriine notoungulates).

INTRODUCTION

Xenarthrans—sloths, armadillos, vermilinguas (‘anteaters’)—are among the most distinctive living Neotropical mammals. Despite their disparate appearance, xenarthrans possess unique accessory vertebral articulations (xenarthrae), bear a reduced dentition, and share a variety of molecular and other morphological characters clearly indicating a unique common ancestry (e.g., Engelmann, 1985; Gaudin, 2003; Springer et al., 2003; Rose et al., 2005). They have been considered an early diverging clade of extant placental mammals (e.g., Novacek and Wyss, 1986; Springer et al., 2003) and consequently have figured prominently in discussions of the geographic origin of Placentalia (Hunter and Janis, 2006). There are about 30 species of extant xenarthrans, most of which are armadillos (Wilson and Reeder, 2005). For the latter two-thirds of the Tertiary, until a mere 10,000 years ago, the group was much more diverse both taxonomically (e.g., triple the number of families) and morphologically (e.g., ground sloths, giant tortoise-like forms, etc.) than it is today (Patterson and Pascual, 1968; Marshall and Cifelli, 1990; Fariña, 1995; McDonald, 2005).

Improved temporal and geographic paleontological sampling benefit our understanding of the the clade’s evolutionary history. The fossil record of xenarthrans, like that of most South American mammals, has come primarily from the southern part of the continent. This is especially true for late Eocene – early Miocene

time, an important interval of origination and radiation of many ‘family-level’ groups in South America (Simpson, 1980; Flynn and Wyss, 1998). Although the geographic extent of South American fossil mammal localities has improved markedly in recent decades (e.g., Kay et al., 1997; Flynn et al., 2003a, b; Campbell, 2004; Linares, 2004; Sánchez-Villagra et al., 2004; Antoine et al., 2006; Cozzuol, 2006; Sánchez-Villagra and Aguilera, 2006; Shockey et al., 2006; Croft, 2007), most low and middle latitude sites are middle Miocene or younger in age, and thus are too young to record the early histories of many xenarthran clades. New specimens from Chucal and other Chilean faunas—nearly all of which predate the middle Miocene—therefore shed much needed light on this critical period of xenarthran evolution (e.g., McKenna et al., 2006).

Here we describe the xenarthrans of the late early Miocene Chucal Fauna of the Altiplano of Chile and provide an updated taxonomic list for the entire fauna. The first fossil mammal from Chucal was discovered 15 years ago (Charrier et al., 1994a) and subsequent fieldwork in 1998, 2001, and 2004 has produced more than 350 additional specimens. A preliminary overview of the fauna (Flynn et al., 2002a) and a detailed study of the ungulates (Croft et al., 2004) have highlighted significant faunal endemism in northern Chile relative to roughly contemporaneous sites in Patagonia. The three xenarthrans described herein—including one or two new species—accentuate this pattern (Croft et al., 2006). The apparent absence of sloths, a diverse and abundant group in contemporaneous early Miocene faunas of Patagonia (as well as later Miocene faunas from the Bolivian Andes, and lowland tropical faunas such as Urumaco, Venezuela and La

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Venta, Colombia), further highlights the unusual composition of the Chucal Fauna.

GEOGRAPHIC AND GEOLOGIC SETTING

The Chucal Fauna derives primarily from the Chucal Formation, a 600 m thick sequence of variegated fluvo-lacustrine strata in the Chilean Altiplano (Fig. 1; Charrier et al., 1994a, 2002, 2005; Bond and García, 2002; Flynn et al., 2002a; Croft et al., 2004). A few specimens have also been collected recently from lower levels of the overlying Quebrada Macusa Formation. Both of these formations are well exposed in the Chucal Anticline, a nearly north-south trending fold located ca. 10 km northwest of Salar de Surire (18° 43' S, 69° 10' W). On the thicker, west flank of the anticline, fossils primarily occur in lacustrine and flood plain deposits of the upper two-thirds of the Chucal Formation; on the east flank, fossils are generally found in more fluvial deposits (Charrier et al., 2002, 2005). Mammal specimens from the Quebrada Macusa Formation (which do not include any xenarthrans) derive from strata on the eastern flank. All of the specimens described below are from the Chucal Formation, most from the eastern flank of the anticline. Paleobotanical evidence suggests that the area was located at an altitude of ca. 1000 m when the formation was deposited (Charrier et al., 1994b).

An $^{40}\text{Ar}/^{39}\text{Ar}$ date of 18.79 ± 0.11 Ma from an ignimbrite near the base of the Chucal Formation (Wörner et al., 2000) indicates that the Chucal Fauna is younger than 19 Ma. This is compatible with a whole rock ^{40}K - ^{40}Ar date of 21.7 ± 0.8 Ma from the upper part of the underlying Lupica Formation at the core of the anticline (Riquelme, 1998) and with dates for the Lupica Formation elsewhere in the region that range as young as 19 Ma (Bond and García, 2002). A level low within the Quebrada Macusa Formation, directly overlying the fossiliferous Chucal Formation, has been dated at 17.5 ± 0.4 Ma ($^{40}\text{Ar}/^{39}\text{Ar}$ plateau age; García, 2001). Together, these dates constrain deposition of most of the Chucal Formation to an interval of only 1–2 million years duration (see also Charrier et al., 2005). Chucal ungulates and other mammals indicate that the fauna is referable to the late early Miocene Santacrucian South American Land Mammal 'Age' (SALMA) (Flynn et al., 2002a; Croft et al., 2004; this paper), and provide the first evidence that the previously poorly constrained lower boundary of this SALMA should be extended from 17.5 Ma (Flynn and Swisher, 1995) to ~19 Ma. Other Santacrucian localities are generally considered to be younger than 16.5 Ma

(i.e., the classic Santa Cruz Formation localities of Argentina) or 17.5 Ma (i.e., localities from the Pinturas Formation further inland) (see Kramarz and Bellosi, 2005 for a review of recent biostratigraphic and geochronologic evidence bearing on the ages of these faunas).

MATERIALS AND METHODS

Anatomical Terminology—Unless otherwise indicated, dental measurements are greatest length (mesiodistal diameter) \times greatest width (labiolingual diameter). Upper tooth loci are indicated by uppercase letters and lower tooth loci by lowercase letters. The homologies of cingulate teeth to those in other placental are unknown, and we follow the general practice of using the letter 'n' for all teeth in lieu of distinguishing among incisors, canines, premolars, and molars. Tooth positions are numbered consecutively from the mesial (anterior) end of the tooth row. All measurements were taken to the nearest 0.1 mm using digital calipers.

The cingulate exoskeleton primarily includes two layers: a mostly keratinous one derived from the epidermis and a bony one derived from the dermis (Rose et al., 2005). Keratinous components of the exoskeleton are correctly referred to as 'scales' or 'scutes' whereas bony components are properly termed 'osteoderms' (e.g., Kent and Carr, 2001; Hill, 2006). Nevertheless, 'scute' has been widely used to refer to both the keratinous and bony components of the cingulate exoskeleton (either individually or together; e.g., Scott, 1903a, b; Lawlor, 1979; Engelmann, 1985; Wetzel, 1985; Nowak, 1991; Gaudin, 2003). To avoid ambiguity, we here employ 'osteoderm' for the commonly fossilized, bony component of the cingulate exoskeleton, encouraging others to do the same. Moreover, we recommend that the term 'scute' be abandoned in reference to cingulate armor entirely, with 'scale' or 'osteoderm' being used instead, depending on the exact meaning intended.

Cingulates have both fixed osteoderms (polygonal, non-overlapping osteoderms that form immobile portions of the carapace) and mobile band osteoderms (quadrangular, overlapping osteoderms that permit movement). The armadillo (dasypodid or peltophilid) and pamapatherer (pampatheriid) carapace includes two solidly fused areas (pectoral and pelvic bucklers) separated by a variable number of transverse mobile bands. The glyptodontid carapace consists almost exclusively of fixed osteoderms, although incomplete mobile bands are found in some species (see below). Dorsal osteoderms are positioned near the dorsal midline of the carapace whereas marginal osteoderms form the edge. The cephalic shield is the portion of the carapace covering the dorsum of the skull and the caudal tube covers the tail.

We use standard terminology for describing cingulate osteoderms and generally follow Vizcaíno and colleagues (2003). The main surface features (known as sculptures) include figures, sulci, and pits. Figures are raised areas of the osteoderm. Sulci are the grooves that delineate figures. We refer to the largest figure as the principal figure; it is delineated by the principal sulcus. Peripheral figures and sulci can surround the principal figure. Pits are round indentations on the surface of the osteoderm that have historically been interpreted as being associated with hairs; they are therefore usually referred to as piliferous pits. For a detailed discussion of xenarthran osteoderm structure and histology, see Hill (2006).

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; FMNH, Field Museum of Natural History, Chicago; MACN, Museo Argentino de Ciencias Naturales, "Bernardino Rivadavia," Buenos Aires; MLP, Museo de La Plata, Argentina; SGO PV, vertebrate paleontology collections, Museo Nacional de Historia Natural, Santiago, Chile; UF, Florida Museum of Natural History, University of Florida,

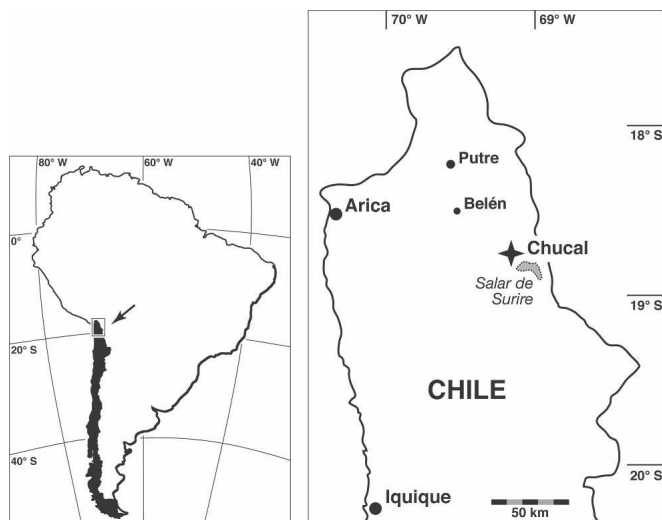


FIGURE 1. Map showing location of inset box in South America (left) and Chucal in northern Chile (right).

Gainesville; **YPM-PU**, Princeton University Collection (now housed at Yale's Peabody Museum, New Haven, Connecticut).

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
 XENARTHRA Cope, 1889
 CINGULATA Illiger, 1811
 DASYPODOIDEA Gray, 1821
 DASYPODIDAE Gray, 1821
 EUPHRACTINAE Winge, 1923
 EUTATINI Bordas, 1933

Comments—The Eutatini were first recognized as a distinct group by Bordas (1933), who considered them a subfamily (Eutatinae) of the Dasypodidae. The group has never been comprehensively revised, and thus the number of valid genera and species is uncertain. Scillato-Yané (1980) recognized 13 genera and 29 species of Eutatini plus one additional species of uncertain affinity. McKenna and Bell (1997) considered 11 of these genera valid. The group ranges from the ?late Eocene to the late Pleistocene.

Bordas (1933) cited four main character complexes as uniting the Eutatini (his Eutatinae): (1) elongate snout; (2) upper and lower dentition of 9–10 subelliptical to semicircular teeth spanning one third the length of the skull; (3) a carapace that includes two to three anterior moveable bands and a pelvic shield; and (4) enlarged pedal digits three and four and reduced pedal digit one. These characters still appear to be valid, with the exception of no. 3; eutatins typically have at least ten moveable bands (A. Carlini, pers. comm., April 2007). An additional character is the general absence of piliferous pits on the dorsal surface of each moveable osteoderm, except for a prominent row along the caudal margin (Scillato-Yané, 1977a; Scillato-Yané and Carlini, 1999).

Stenotatus Ameghino, 1891

Type Species—*Stenotatus patagonicus* (Ameghino, 1887).

Included Species—the type, *S. centralis*, *S. hesternus*, *S. ornatus*, *S. planus*.

Revised Diagnosis—Differs from *Proeutatus* in having simple oval maxillary teeth (bilobed in *Proeutatus*) and in smaller size (15%–20% smaller based on dimensions of long bones and osteoderms) (Scott, 1903a). Differs from *Meteutatus* in smaller size (ca. 30% smaller based on osteoderm dimensions) and in lacking lateral piliferous pits on the osteoderms between the central and lateral longitudinal ridges. Differs from *Pseudeutatus*, *Anteutatus*, *Eutatus*, *Doellotatus*, and *Ringueletia* in having large diastemata separating the first several maxillary teeth (the teeth are more closely positioned in these taxa) and moveable band osteoderms with three pronounced longitudinal ridges (osteoderms are differently ornamented in the other taxa) (Scott, 1903a; Bor-

das, 1933; Simpson, 1948). Further differs from *Ringueletia* in having a single caudal row of piliferous pits (two rows in *Ringueletia*; Bordas, 1933; Scillato-Yané et al., 1995). Differs from *Chasicotatus* in having an unreduced pelvic buckler and narrower (anteroposteriorly) caudal rows of piliferous pits on the osteoderms (Scillato-Yané, 1977a).

Age and Distribution—Deseado Formation, Patagonia, Argentina, late Oligocene age, Deseadan SALMA (Ameghino, 1897); Colhué-Huapí Formation, Patagonia, Argentina, early Miocene age, Colhuehuapian SALMA (Ameghino, 1902a); Santa Cruz Formation, Patagonia, Argentina, late early Miocene age, Santacrucian SALMA (Scott, 1903a); Chucal Formation, northern Chile, late early Miocene age, Santacrucian SALMA (Croft et al., 2004; this paper); Collón-Curá Formation, northwestern Patagonia, Argentina, early middle Miocene age, Collocuran SALMA (Bondesio et al., 1980; Scillato-Yané and Carlini, 1998).

Stenotatus sp. nov.
 (Figs. 2, 3)

Referred Material—SGO PV 4071, approximately ten articulated and/or isolated osteoderms (Fig. 2A), partial rostrum bearing parts of eight teeth (Fig. 3), proximal right humerus; SGO PV 5079, five partial articulated and/or isolated osteoderms (Fig. 2A), distal left tibia, three associated phalanges (one complete); SGO PV 5103, six partial osteoderms, small portion of pelvic shield (Fig. 2C), articulated left carpus; SGO PV 5144, two partial osteoderms (Fig. 2B); SGO PV 5155, four partial osteoderms (Fig. 2B); SGO PV 5168, eight partial osteoderms (Fig. 2A).

Localities—C-ALT-98-21A and C-ALT-01-12, from grey sandstone beds of Chucal Formation Member E3 (Charrier et al., 2002, 2005).

Description—No single complete osteoderm from this species has been recovered, though the incomplete pieces that have been collected provide an adequate picture of their general morphology. The osteoderms of the moveable bands vary in width from ca. 5.5–7.0 mm; the length would have been roughly 15 mm for smaller osteoderms. Osteoderms of *Stenotatus patagonicus* are slightly larger (generally 7.0–7.5 mm in width, ~20 mm in length; YPM-PU 15563, 15853). They are relatively thin, typically 2–3 mm, and have a short (5.0–5.5 mm) region of overlap between moveable band osteoderms. The most noteworthy feature of the osteoderms is the row of four large piliferous pits along the caudal margin; these pits are best illustrated by SGO PV 4071, but are also visible in SGO PV 5079 and SGO PV 5168 (Fig. 2A). As noted above, piliferous pits restricted to this region of the osteoderm is characteristic of the Eutatini. The sculpturing of the moveable band osteoderms consists of three longitudinal ridges, subequal in width, that extend caudally to the caudal row of pits (Fig. 2B). The two lateral bands often display one or two faint transverse grooves. Among dasypodids, this sculpturing most closely resembles that of *Stenotatus patagonicus*. Unlike the con-

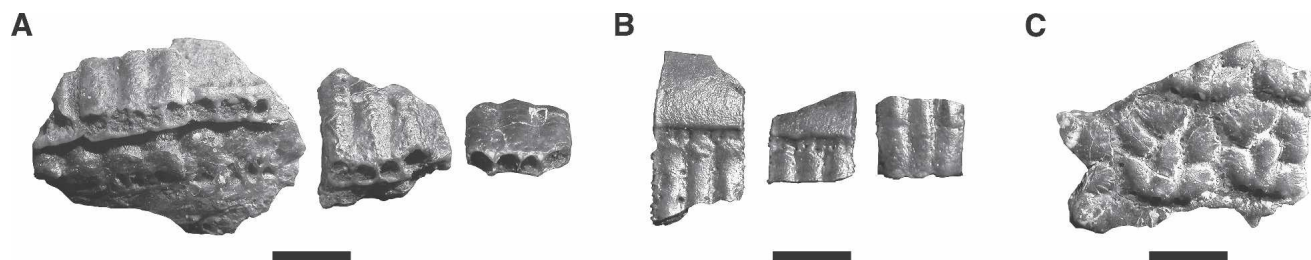


FIGURE 2. Osteoderms of *Stenotatus* sp. **A**, partial moveable band osteoderms in posterodorsal view illustrating prominent distal piliferous pits (from left to right, SGO PV 4071, SGO PV 5079, SGO PV 5168); **B**, partial moveable band osteoderms in dorsal view (from left to right SGO PV 5144, SGO PV 5155, SGO PV 5155); **C**, fused osteoderms of the pelvic shield in dorsal view (SGO PV 5103). All scale bars equal 5 mm.

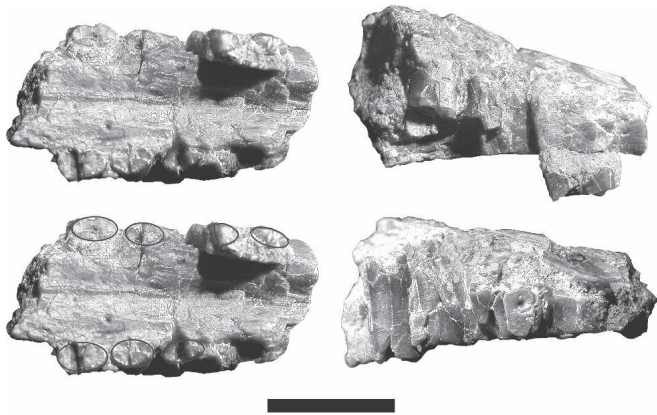


FIGURE 3. Partial rostrum of *Stenotatus* sp. (SGO PV 4071) in dorsal (top left), oclusal (bottom left), right lateral (upper right), and left lateral (reversed, lower right) views. Anterior is to the right in all views. Scale bar equals 1 cm.

dition typical of *Stenotatus*, however, the longitudinal ridges do not tend to become confluent near the caudal margin in the form from Chile. The more caudal osteoderms of the carapace are broader than those of the moveable bands and the longitudinal ridges are broken into a number of small tubercles (Fig. 2C).

The partial rostrum (SGO PV 4071; Fig. 3) is long and narrow and bears parts of eight subcylindrical teeth (four on each side). The oclusal portions of the two most mesial teeth on the right side have been displaced mesially and buccally but are still connected to the specimen by matrix. None of the oclusal surfaces is completely preserved. The rostrum has been slightly crushed (mediolaterally and dorsoventrally) but measures ca. 24 mm in length, 13.5 mm dorsoventrally at the proximal end, and ca. 7 mm dorsoventrally at the distal end. The width of the palate between the teeth is 7.5 mm posteriorly and >5 mm anteriorly. The preserved toothrow spans ca. 16 mm in length, and the teeth increase in size from 3.0 mm × 1.3 mm (most mesial tooth on right) to 3.6 mm × 2.0 mm (most distal tooth on left). The only other measurable tooth is the next most distal one on the left side (3.2 mm × 1.7 mm). These teeth fall within the range of size and morphology of *S. patagonicus* (YPM-PU 15853). Based on comparisons with *Stenotatus*, the Chucal rostrum probably preserves the middle portion of the dental series (n3-6), but this cannot be determined with certainty due to the incompleteness of the specimen. Roughly 2 mm of bone is present mesial to the first tooth on the right side, so if additional teeth were present in SGO PV 4071 anterior to ?n3, they would have been separated by a significant diastema. A large diastema is present in *Stenotatus patagonicus* between n3 and n2.

Several parts of the appendicular skeleton are preserved, including a proximal right humerus, an articulated left carpus, three partial phalanges, and a distal left tibia. The preserved portion of the humerus (SGO PV 4071) is only 9.4 mm in length; the head is 6.6 mm in width and the maximum breadth of the proximal end is 12.8 mm. It more closely resembles *Stenotatus patagonicus* than *Prozaedyus exilis* but is ca. 20% smaller than the former, similar in size to the latter; corresponding breadths of the head and proximal humerus are 8.3 mm and 15.8 mm for *Stenotatus* (YPM-PU 15863) and 6.5–6.6 mm and 12.2 mm for *Prozaedyus* (YPM-PU 15579, 15604). The left carpus (SGO PV 5103) includes seven carpals (all elements except the pisiform), metacarpal (MC) IV, and portions of MC II and MC III. It is ca. 13 mm in breadth across the proximal row of carpals. MC IV is ca. 9 mm long (the same as MC IV of *S. patagonicus* figured by Scott, 1903a) and 4.8 mm wide at its distal end. The three pha-

langes (SGO PV 5079) include one complete phalanx (the middle) and two partial phalanges. The complete phalanx is 10.4 mm long and measures 5.5 mm × 5.0 mm at its proximal end (dorsoventral × mediolateral diameter). It has a prominent dorsal process that overhangs the proximal articulation, and a well developed digital extensor fossa on the dorsal surface of the shaft. Based on the morphologies and relative lengths of the phalanges, they appear to represent proximal phalanges II–IV of the left manus. The distal tibia (SGO PV 5079) measures 11.4 mm in breadth and 6.2 mm anteroposteriorly. It bears a prominent distal process on the posterior surface, as in most armadillos, and two prominent tendonal sulci are present between it and the medial malleolus. The distal fibula was apparently fused to the tibia but is not preserved.

Comments—The available material of this armadillo provides sufficient information to determine its taxonomic affinities, but does not permit a definitive species-level identification. It is clearly a eutatin closely related to *Stenotatus patagonicus*, but differs from this species at least in its smaller size. Other currently recognized *Stenotatus* species are less well known but the Chucal species does not appear to pertain to any of these. The Chucal form differs from *S. hesternus* in lacking large and conspicuous piliferous pits in the longitudinal grooves of the moveable osteoderms (Ameghino, 1889), from both *S. ornatus* and *S. centralis* in lacking enlarged piliferous pits (relative to *S. patagonicus*) along the posterior margins of moveable osteoderms (Ameghino, 1897, 1902a), and from *S. planus* in having relatively prominently sculptured osteoderms (Scillato-Yané and Carlini, 1998). The moveable osteoderms may also be shorter (anteroposteriorly) than in currently recognized *Stenotatus* species, but this cannot be demonstrated conclusively with available material. An undescribed eutatin (probably *Stenotatus*) from the Deseadan fauna of Salla, Bolivia (YPM-PU 22165) also has relatively short moveable band osteoderms, a feature that may be common to middle latitude species of *Stenotatus*. Until more complete material is collected from the Chucal Fauna, the Chucal eutatin is provisionally regarded as a new species of *Stenotatus*, albeit one that is too poorly known to permit adequate diagnosis or to merit formal naming.

PELTEPHILIDAE Ameghino, 1894

Comments—Peltephilids are one of the most easily recognized groups of xenarthrans. They are perhaps best known for possessing a pair of horn-like nasal osteoderms (e.g., Scott, 1932; Dixon et al., 1988), although the robust architecture of the skull and mandibles is equally unusual relative to other dasypodoids (Vizcaíno and Fariña, 1997). The shape and surface texture of peltephilid osteoderms also are diagnostic; they are relatively wider than those of other dasypodoids, have a very small area of overlap with other osteoderms, are often rough in texture, and exhibit two to four very conspicuous dorsal piliferous pits (which may have been associated with large glandular cisterns; A. Carlini, pers. comm., April, 2007).

Recent paleobiological studies have suggested that *Peltephilus* (and peltephilids in general) were likely fossorial herbivores that fed on plant roots and possibly invertebrates (Vizcaíno and Fariña, 1997). This contrasts with earlier interpretations of peltephilids as above-ground, cursorial carnivores (e.g., Ameghino, 1910; Scillato-Yané, 1977a).

Peltephilids range from the ?Paleocene (Riochican SALMA) to late Miocene (Chasicoan SALMA), but specimens at either end of this span are fragmentary and have not been identified below the family level (Scillato-Yané, 1980; Marshall et al., 1983; McKenna and Bell, 1997; Carlini et al., pers. comm., April, 2007). The group has previously been recorded only from Argentina and Bolivia; the specimens from Chucal thus extend the range of the family westward into Chile.

Twelve peltephilid species are currently recognized, distributed among five genera: *Peltephilus*, *Peltecoelus*, *Parapeltecoelus*, *Anantiosodon*, and *Epipeltephilus* (Scillato-Yané, 1980; McKenna and Bell, 1997). The first four of these are known exclusively from the late Oligocene through early Miocene, with most species occurring in the late early Miocene Santa Cruz Formation of Argentina; *Epipeltephilus* is known from the middle or late Miocene of Laguna Blanca, Argentina (Ameghino, 1904).

Scott (1903a) suggested that *Anantiosodon rarus* (the type species of *Anantiosodon*) might be referable to *Peltephilus*, perhaps even to *P. nanus*, but believed the holotype to be too fragmentary for a more definitive taxonomic assignment. Bordas (1936) recognized *Anantiosodon* as a new genus based on apparent differences from other peltephilids in the mandibular dental formula, referring *nanus* to this genus; this taxonomy has been followed by subsequent authors (e.g., Scillato-Yané, 1980; McKenna and Bell, 1997). Studies by Bordas (1936, 1938) are the most recent detailed revisions of the family, although additional systematic revisions are currently underway (Vizcaíno et al., 2006).

Peltephilus Ameghino, 1887

Type Species—*Peltephilus strepens* Ameghino, 1887.

Included Species—the type, *P. pumilus*, *P. ferox*, *P. depressus*, *P. granosus*.

Diagnosis—Differs from *Anantiosodon* in much larger size (osteoderms of *A. nanus* are ca. half the size of *Peltephilus*) and in dental formula (apparently four mandibular teeth in *A. rarus*, six in all other peltephilids) (Bordas, 1936, 1938). Differs from *Peltecoelus* in rougher osteoderm architecture (osteoderms are smooth in *P. praelucens*; Ameghino, 1902a) and/or smaller size (osteoderms are about 2/3 the size those of *P. grandis* and *P. protervus*). Differs from *Parapeltecoelus* in smaller size (about 85% the size of *Parapeltecoelus*, based on condylobasal length) and a variety of characteristics of the skull, including a much smaller cranial capacity (Bordas, 1938). Differs also from *Epipeltephilus* in many craniodental characters, including a higher and narrower posterior skull, anteriorly inclined upper molariforms (vertically implanted in *Epipeltephilus*), and reduced upper and lower last molariforms (Ameghino, 1904).

Age and Distribution—Deseado Formation, Patagonia, Argentina, late Oligocene age, Deseadan SALMA (Ameghino, 1887; Marshall et al., 1986); Salla Beds, Bolivia, late Oligocene age, Deseadan SALMA (Hoffstetter, 1968; MacFadden et al., 1985); Colhué-Huapí Formation, Patagonia, Argentina, early Miocene age, Colhuehuapian SALMA (Ameghino, 1902a); Santa Cruz Formation, Patagonia, Argentina, late early Miocene age, Santacrucian SALMA (Scott, 1903a); Chucal Formation, northern Chile, late early Miocene age, Santacrucian SALMA (Croft et al., 2004; this paper); Nazareno Formation, southern Bolivia, ?middle Miocene age, ?Colloncuran SALMA (Oiso, 1991).

cf. *Peltephilus* sp.
(Fig. 4)

Referred Material—SGO PV 4111 and SGO PV 5150, two isolated osteoderms.

Localities—C-ALT-98-21A, grey sandstone beds of Chucal Formation Member E3; C-A-01-30, brownish-grey mudstones of Chucal Formation Member W4 (Charrier et al., 2002, 2005).

Description—The two peltephilid osteoderms from Chucal are similar in overall size and morphology (Fig. 4). SGO PV 4111 measures 16.6 mm × 15.3 mm (length × width); SGO PV 5150 measures 16.4 mm × 13.5 mm (length × width). The most conspicuous morphological features include: (1) a rough dorsal surface perforated by many vascular pits; (2) a series of three raised

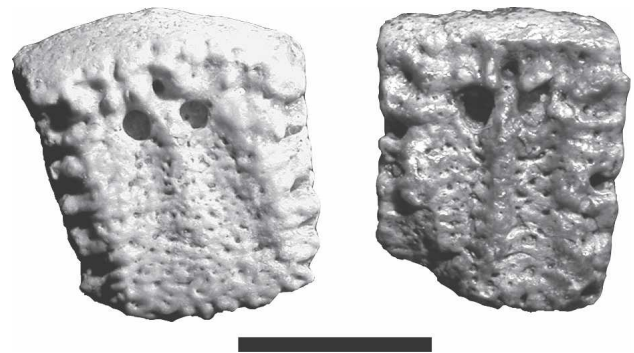


FIGURE 4. Osteoderms of cf. *Peltephilus* sp. (SGO PV 4111, left; SGO PV 5150, right) in dorsal view. Scale bar equals 1 cm.

longitudinal ridges, one in the middle and one along each side; (3) a pair of large piliferous pits near the cranial end; and (4) a smooth transverse strip along the cranial edge.

The distribution of vascular pits is similar in the two specimens; small pits are present over most of the dorsal surface of the osteoderm whereas larger pits occur along the lateral edges. Pits are nearly absent from the longitudinal ridges. The lateral longitudinal ridges are pronounced in both specimens, but the medial ridge is much more conspicuous in SGO PV 5150 than in SGO PV 4111. Large piliferous pits are located on either side of the median longitudinal ridge near its cranial end. They are slightly larger in SGO PV 5150 (2.0 mm diameter) than in SGO PV 4111 (1.4 mm diameter). A third piliferous pit is present in both specimens, but it is smaller and shallower than the other two; it is located along the midline of the osteoderm between the cranial termination of the median longitudinal ridge and the smooth transverse strip. The smooth transverse strip is larger (craniocaudally) in SGO PV 4111 than in SGO PV 5150 suggesting that this osteoderm was overlapped to a greater degree by more cranial osteoderms. The ventral surface of both osteoderms is smooth. In lateral view, the osteoderms are thickest (4.5–4.6 mm) near the middle; they thin slightly (3.8–4.0 mm) toward the cranial end, and thin much more dramatically (1.6–2.0 mm) toward the caudal end.

Comments—Although two isolated osteoderms do not provide sufficient information for a definitive identification, nothing in the morphology of these specimens suggests that they pertain to a taxon other than *Peltephilus*. The presence of a small, midline accessory piliferous pit in each specimen may be an autapomorphy, but normal intraspecific variation cannot be ruled out as an explanation; differentiating between these alternatives requires recovery of additional material. The dimensions of both specimens fall within the range. *Peltephilus* osteoderms from Santa Cruz, Argentina (Scott, 1903a), supporting referral to this taxon.

GLYPTODONTIDAE Gray, 1869

Diagnosis—Large to giant xenarthrans with extensive, thick dermal armor composed mostly of pentagonal to hexagonal fixed osteoderms. Teeth are complex and lobed (glyptodont means ‘carved teeth’) and include a central region of osteodentine in addition to the orthodentine and cementum typical of xenarthrans (Ferigolo, 1985). Many other craniodental, postcranial, and exoskeletal characters also distinguish glyptodontids from other xenarthrans (see Hoffstetter, 1958).

Comments—Five subfamilies of glyptodontids (including some 65 genera) are currently recognized: Glyptatelinae, Propalaeohoplorinae, Hoplophorinae (= Sclerocalyptinae), Doedicurinae, and Glyptodontinae (Castellanos, 1932; McKenna and

Bell, 1997; Vizcaíno et al., 2003). The phylogenetic relationships within and among these groups have not been resolved, however, and are hampered by a plethora of poorly founded species and a lack of understanding of intra- and interspecific variation (Perea, 2005).

The Glyptatelinae include the earliest known glyptodontids; until recently they were thought to be restricted to late Eocene and Oligocene faunas, but they are apparently also present in the middle Miocene of Colombia and the late Miocene of Uruguay (Castellanos, 1932; McKenna and Bell, 1997; Carlini et al., 1997; Vizcaíno et al., 2003; Villarroel and Clavijo, 2005). They are the least diverse and most poorly known subfamily of glyptodontids; three genera are currently recognized (*Glyptatelus*, *Clypeotherium*, and *Neoglyptatelus*), all represented primarily by isolated osteoderms or partial carapaces. Simpson (1948) questionably referred a partial mandible (AMNH 29483) to *Glyptatelus*, but this specimen more likely pertains to (or is closely related to) *Pseudoglyptodon*, an unusual phyllophagan (sloth) with glyptodont-like teeth (Wyss et al., 1994; McKenna et al., 2006). The same is probably also true of various specimens referred by Ameghino (1897, 1902b) to *Glyptatelus* (McKenna et al., 2006). A small maxilla and mandible were included, with doubt, in the hypodigm of *Neoglyptatelus originalis* because there was no clear association between these specimens and a diagnostic osteoderm, but these specimens were not described (Carlini et al., 1997). A poorly known species from the Pleistocene of Florida, *Pachyarmatherium*, may also be a glyptateline, but the affinities of this cingulate are unresolved (Downing and White, 1995; McKenna and Bell, 1997; Vizcaíno et al., 2003).

Propalaeohoplorines include early to late Miocene forms (and possibly a late Oligocene species; Scillato-Yané, 1977b) that are more derived than glyptatelines in many features, but that lack the diagnostic character states of hoplophorines, doedicurines, and glyptodontines. They are best represented in the classic late early Miocene Santa Cruz Fauna of Argentina (Scott, 1903b; Marshall, 1976) where five genera are present: *Propalaeohoplorus*, *Eucinepeltus*, *Cochlops*, *Metopotoxus*, and *Asterostemma*. *Propalaeohoplorus* is the most abundant of these and virtually all parts of the skeleton are represented in museum collections. *Eucinepeltus*, *Cochlops*, and *Metopotoxus* also are known from both craniodental and exoskeletal material. *Cochlops* was considered a junior synonym of *Peltephilus* by McKenna and Bell (1997), but in fact only some of Ameghino's (1889) syntypes are peltephilid (Scillato-Yané, 1980); the remaining syntypes are glyptodontid, and are distinct from other propalaeohoplorines (Scott, 1903b). *Asterostemma* is only represented by sparse exoskeletal material from Argentina (some craniodental material also may pertain to it; Simpson, 1947), but more complete specimens from Venezuela and Colombia have been questionably referred to this genus (Simpson, 1947; Carlini et al., 1997). The tropical South American '*Asterostemma*' may represent a new genus more closely related to hoplophorines (= sclerocalyptines) than propalaeohoplorines (Scillato-Yané and Carlini, 1999). Prior to the present report, species from the Santa Cruz Fm. were the earliest (and possibly most basal) glyptodontids represented by good craniodental and exoskeletal material.

The Chucal glyptodontid described below shares features with both glyptatelines and propalaeohoplorines, and therefore cannot unequivocally be referred to any currently recognized subfamily (see Phylogenetic Analysis, below).

Glyptodontidae incertae sedis

Parapropalaeohoplorus septentrionalis, gen. et sp. nov.
(Figs. 5–10)

Holotype—SGO PV 4165, partial skeleton including: nearly complete left mandible bearing n1–7 and base of n8 (field no.

C-ALT-8-21-04-160); portion of left lateral carapace (field no. C-ALT-8-21-04-163); portion of right anterolateral carapace (field no. C-ALT-8-21-04-164); nearly complete left femur (field no. C-ALT-8-21-04-159); partial right femur and articulated partial right tarsus including partial ?fibula, astragalus, calcaneus, and several other bones (unprepared; field no. C-ALT-8-20-04-158); chevron (field no. C-ALT-8-20-04-155); ca. nine articulated vertebrae (unprepared; field no. C-ALT-8-20-04-157); proximal portion of left tibiofibula, ?middle phalanx, many bone fragments, many fixed carapace osteoderms (mostly isolated; field no. C-ALT-8-21-04-161); one fixed carapace portion and one moveable band osteoderm and some osteoderm pieces (field no. C-ALT-8-21-04-165; associated with C-ALT-8-21-04-163). The various parts of this specimen were given separate field numbers to facilitate tracking of individual parts during field collection; none duplicate elements and they all clearly pertain to a single individual.

Type Locality—Loc. C-A-53, upper part of Chucal Formation Member E2 (Charrier et al., 2002, 2005).

Age and Distribution—Chucal Formation, northern Chile, late early Miocene age, Santacrucian SALMA (this paper).

Etymology—*Para*, near, and *Propalaeohoplorus*, the best known early Miocene glyptodontid, in reference to the temporal and phylogenetic position of the new Chucal glyptodontid; *septentrionalis*, northern, in reference to the geographic location of Chucal within Chile and relative to classic Santacrucian localities in Patagonia. The specific epithet also parallels that of the type species of *Propalaeohoplorus*, *P. australis* (southern).

Diagnosis—The dentition of *Parapropalaeohoplorus* differs from that of all glyptodontids for which the lower dentition is known except propalaeohoplorines in having n1-5 simplified relative to n6-8; it differs from propalaeohoplorines in having triangular n1-3 with n2-3 extended distobuccally (n1-3 are reniform to slightly lobed in most propalaeohoplorines). The mandible of *Parapropalaeohoplorus* apparently is closer to the ancestral glyptodontid morphology than is any other species for which this element is known; the posterior edge of the ascending process is less extended and the condylar and coronoid processes are less inclined anteriorly than in *Propalaeohoplorus* and later glyptodontids. Fixed dorsal osteoderms of the carapace differ from those of all other glyptodontids in the unique combination of: a relatively large, round, principal figure; principal figure positioned along the posterior edge of each osteoderm; few to no medial and lateral peripheral figures; faint sculpturing; no conspicuous piliferous pits. Osteoderms of propalaeohoplorines are similar to those of *Parapropalaeohoplorus* but have peripheral figures completely surrounding the principal figure; in *Parapropalaeohoplorus*, the central figure abuts the posterior margin and lies close to the medial and lateral margins. Some propalaeohoplorines also have a convex principal figure (e.g., *Propalaeohoplorus*, *Cochlops*) whereas the principal figure is flat to concave in *Parapropalaeohoplorus*. Osteoderms of glyptatelines have prominent piliferous pits and some have a flat-sided principal figure (*Neoglyptatelus* and *Clypeotherium*). The femur of *Parapropalaeohoplorus* differs from that of other glyptodontids in having a higher, straighter greater trochanter, likely also a primitive condition.

Description—SGO PV 4165 includes a nearly complete mandible; it lacks only the occlusal surface of n8, a portion of the medial side of its alveolus, and a small portion of the ascending ramus near the middle of the posterior border (Fig. 5). It is typically glyptodontid in form, with a short, deep horizontal ramus (152 mm in greatest length; 48 mm deep below n6), a well-developed angle, and a tall, anteroposteriorly broad ascending ramus (131.5 mm from tip of coronoid process to base of horizontal ramus; ca. 60 mm in breadth at tooththrow). The angle of the mandible does not extend as far posteriorly as in *Propalaeohoplorus* (or later glyptodontids) and the articular condyle

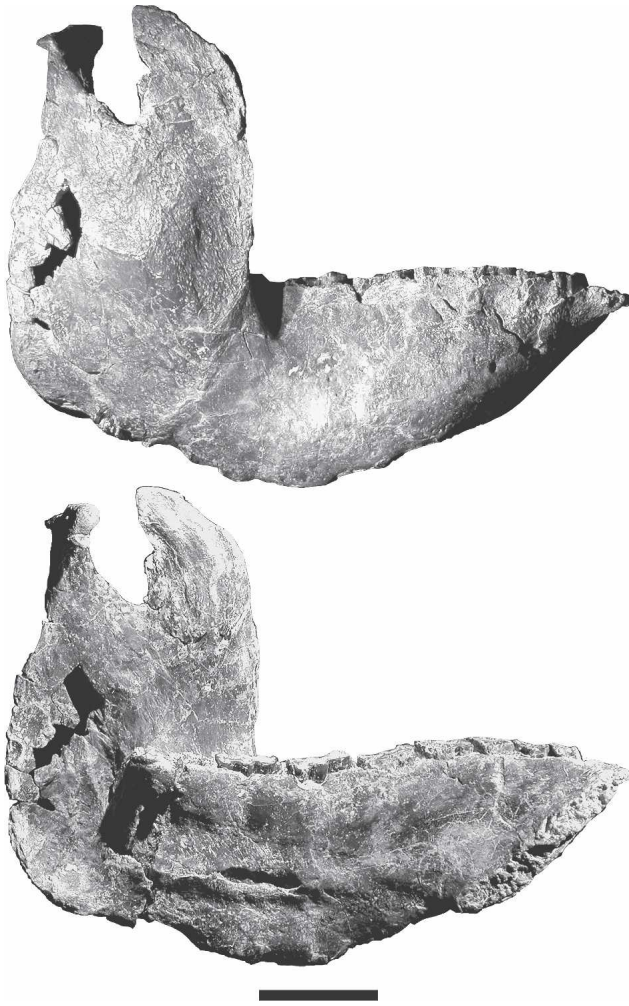


FIGURE 5. Left mandible of *Parapropalaeohoplophorus* in buccal (reversed, above) and lingual (below) views (SGO PV 4165). Scale bar equals 2 cm.

therefore lies much closer to the mandible's posterior edge (ca. 15 mm). The coronoid process is short (26.5 mm above the base of mandibular notch), arches posteriorly, and its tip rises slightly above the level of the articular condyle (9.5 mm). The coronoid process appears to be larger in *Propalaeohoplophorus* owing to the greater depth of the mandibular notch, but its tip is at a similar height relative to the articular condyle, as in *Parapropalaeohoplophorus*. The midpoint of the articular surface of the condyle is 57 mm above the level of the toothrow in *Parapropalaeohoplophorus*; in posterior view, it is inclined ca. 15–20° dorso-medially relative to the vertical axis of the ascending ramus. On the inferior surface of the medial side of the condyle, two small spurs are present along the anterior edge; a small pit is located between these spurs and the posterior edge of the inferior surface. Together, these structures may represent the attachment point of a particularly well-developed ligament or tendon. No deep fossa is present on the external surface of the ascending ramus as has been noted in *Eucinepeltus* (Ameghino, 1898).

The mandibular angle is well developed, but the bone is thin and is partly missing. The medial face of the angle is roughly textured and raised ridges indicate attachments for well developed pterygoid muscles. An open, 3.3 mm wide groove, runs nearly vertically along the lingual junction of the angle and the horizontal ramus, just behind n8. Based on its position, this

groove likely represents (or is an earlier stage in the development of) the “postdental canal” described in later glyptodontids (Holmes and Simpson, 1931; Gillette and Ray, 1981). It likely conveyed the inferior alveolar neurovascular bundle prior to this bundle entering the mandibular foramen proper (Lundelius, 1972). An elongate defect (19.4 mm x 3.6 mm) in the lingual face of the horizontal ramus of SGO PV 4165 appears to be the result of breakage along the path of this bundle within the ramus (i.e., in the mandibular/dental canal).

The entire lateral surface of the ascending ramus is roughly textured, indicating a large masseter complex and temporalis muscle. The inferior border of the horizontal ramus is gently convex but to an even greater degree than is seen in *Propalaeohoplophorus*. The medial symphyseal spout does not appear to be damaged to any appreciable degree in SGO PV 4165, but still only extends 12.5 mm anterior to n1. In this regard, *Parapropalaeohoplophorus* more closely resembles *Eucinepeltus* than *Propalaeohoplophorus* (Scott, 1903b). A series of swellings along the inferior border of the ramus evidently correlates with the positions of the bases of n4-8; the posteriormost of these swellings is cracked and the base of the root of n8 is clearly visible ventrally. An irregular depression is present on the external surface of the horizontal ramus ca. 2 cm below the alveolar border between n5 and n6. This may represent a fossa for the descending process of the zygomatic arch as occurs in *Propalaeohoplophorus* and some specimens of *Cochlops* (Ameghino, 1895; Scott, 1903b). Four mental foramina are present on the anterolateral surface of the horizontal ramus. The posteriormost lies 21.5 mm below the midpoint of n3 and measures just over 1.2 mm in diameter. The largest (3.2 mm in diameter) lies at this same level, but is situated along the anterior face of the ramus. A third foramen lies between these two, closer to the larger; it is about the same size as the first and is positioned slightly more dorsally. A very small fourth foramen is situated ca. 7 mm below the third. The mandibular symphysis is long (53 mm) and the two mandibles were evidently unfused; this is likely the ancestral condition for glyptodontids (Fariña and Vizcaino, 2001). The horizontal ramus is fairly thick (16–17 mm) throughout its length.

Seven complete teeth and the base of an eighth are preserved in SGO PV 4165; the first three are subtriangular in occlusal outline, the last three are trilobed, and the middle two are partially lobed, intermediate in morphology between the anterior and posterior teeth (Fig. 6). The first tooth, n1, approximates a right triangle with a lingual leg (5.9 mm), a distal leg (5.6 mm), and a mesiobuccal hypotenuse (7.7 mm). No distinct occlusal morphology is visible. The second tooth is similar to the first except that the distobuccal corner is greatly extended and the distal face is more concave; the lingual, distal, and mesiobuccal faces measure 5.5, 7.4, and 9.6 mm, respectively. A barely visible midline region of osteodentine runs along the main axis of the tooth. The third tooth continues the trend seen in the first two but is also larger, oriented more mesiodistally (as opposed to having the mesial end angled medially), and has more concave distal and mesiobuccal faces; the corresponding measurements are 8.0 mm, 7.8 mm, and 12.1 mm, respectively. A central region of osteodentine along the main axis of the tooth is clearly visible. The three anterior teeth of *Parapropalaeohoplophorus* differ significantly from n1-3 of typical Santacrucian glyptodontids (Fig. 7). Although n1-3 of *Propalaeohoplophorus australis* differ in shape, they are generally subcircular or longitudinally elliptical in outline (Fig. 7C; Scott, 1903b). This is also true of later species of *Propalaeohoplophorus* (Fig. 7E). In *Eucinepeltus petestatus*, n1-3 are more or less reniform and buccally concave (Fig. 7A; Ameghino, 1898; Scott, 1903b). In *Cochlops*, n1 is small and peglike, n2 is simple and elongate, and n3 is trilobed (Ameghino, 1898:fig. 75). The lower dentition of *Metopotoxus* is unknown. No lower dentition is definitely known for *Asterostemma depressa*, but Simpson (1947) suggested that the holotype of *Pro-*



FIGURE 6. Left lower dentition of *Parapropalaehoplophorus* in occlusal view, anterior to the right (SGO PV 4165). Both photos are of the same specimen, but tooth outlines and osteodentine tracts have been highlighted in the lower photo. Scale bar equals 1 cm.

palaehoplophorus minus (MACN A-4757; Fig. 7D) may be referable to *A. depressa*. The anterior teeth of *Parapropalaehoplophorus* do not resemble the corresponding teeth of that specimen, although n4 of SGO PV 4165 does resemble n3 of MACN A-4757. The first two teeth of *Parapropalaehoplophorus* most closely resemble n1-2 of *Asterostemma venezolensis* in overall shape, but nevertheless differ in details; n1 is less triangular in *Parapropalaehoplophorus* and the distobuccal corner of n2 is much broader in *A. venezolensis* than in the Chucal species (Fig. 7F; Simpson, 1947).

The third and fourth molariforms are quite different in *Parapropalaehoplophorus*; n4 vaguely resembles a tribosphenic tooth, with a shorter trigonid and a longer talonid. It measures 13.7 mm × 6.4 mm. The mesial face is flat and angled ca. 30° relative to the long axis of the tooththrow. Two sulci on the buccal face form three lobes, the distalmost being largest. The lingual face, in contrast, is characterized by a single groove located closer to the mesial end than to the distal. There is no distinct distal face, but rather a long, gently curving distolingual surface. The central osteodentine figure of n4 is aligned along the main axis of the tooth, but bifurcates at its mesial end. The next tooth (n5) is damaged lingually, but appears to be generally similar to n4. Obvious differences in n5 (relative to n4) include: more pronounced buccal lobes; the presence of a second, very slight lingual sulcus; and a more complex central figure that adds transverse extensions and potentially a distal bifurcation (the occlusal surface is damaged there). Additionally, the flat face of the anterior lobe is more angled relative to the axis of the tooththrow. The tooth measures 14.4 mm × ca. 5.5 mm. Compared to other glyptodontids, n4-5 of *Parapropalaehoplophorus* most closely resemble the corresponding teeth of *Eucinepeltus* (Fig. 7A).

The three most distal teeth are variations on a similar theme (though the last is missing the occlusal surface): each is trilobed on both buccal and lingual faces; the mesial lobe is rounded; the width across the mesial lobes is similar to that across the distal lobes; the distal lobe is flat; and the central figure resembles that of n5 (and the same teeth in glyptodontids in general). The greatest differences among n6-8 are in the orientation of their distal

faces; this portion of the tooth is angled from mesiolingual to distobuccal in n6, roughly transverse in n7, and angled from distolingual to mesibuccal in n8. The maximum dimensions of n6, n7, and n8 are 15.5 mm × 7.4 mm, 14.5 mm × 7.6 mm, and ca. 15 mm × ca. 7 mm, respectively. The total length of the tooththrow is 104.5 mm, shorter than that of *Eucinepeltus petestatus* (ca. 113 mm; MACN A 4760) and longer than that of *Propalaehoplophorus australis* (ca. 90 mm; MLP 16-15).

Much of the lateral and dorsolateral portions of the carapace of *Parapropalaehoplophorus* are preserved, primarily in two large pieces (Fig. 8); the anteriormost, dorsalmost, and posteriormost portions are missing. The left carapace section of SGO PV 4165 includes parts of 15 transverse bands (each with 1-8 osteoderms) and 84 osteoderms in total; the right carapace section includes parts of 12 transverse bands (each with 7-11 osteoderms) and 110 osteoderms in total. Each section appears to include only a single moveable band; it is the anteriormost band in the left portion of the carapace and the fourth band from the front in the right portion of the carapace. Assuming these bands were directly opposite each other, the two large chunks of carapace share portions of nine bands, the left one including portions of six more posterior bands and the right one including portions of three more anterior bands. Eighteen bands thus appear to be represented, with the right piece overlapping with, but offset anteriorly relative to, the left. The carapace of *Propalaehoplophorus* includes ca. 27 bands along the ventral margin (Scott, 1903b) and that of *Asterostemma venezolensis* includes 22-25 bands (Simpson, 1947); thus, ca. 65-85% of the transverse bands are likely represented in SGO PV 4165. We estimate that 25-30% of the carapace is preserved in the two large pieces. The left piece measures ca. 45 cm × 20 cm. The right piece approximates a right triangle with legs of 24 cm and 33 cm and a hypotenuse of 41 cm. The presence of moveable bands is characteristic of propalaehoplophorines (Simpson, 1947) but their number is of uncertain taxonomic utility; for example, band number can vary between conspecific individuals and even differ on opposite sides of a single carapace (Scott, 1903b).

The left piece of carapace includes three marginal osteoderms

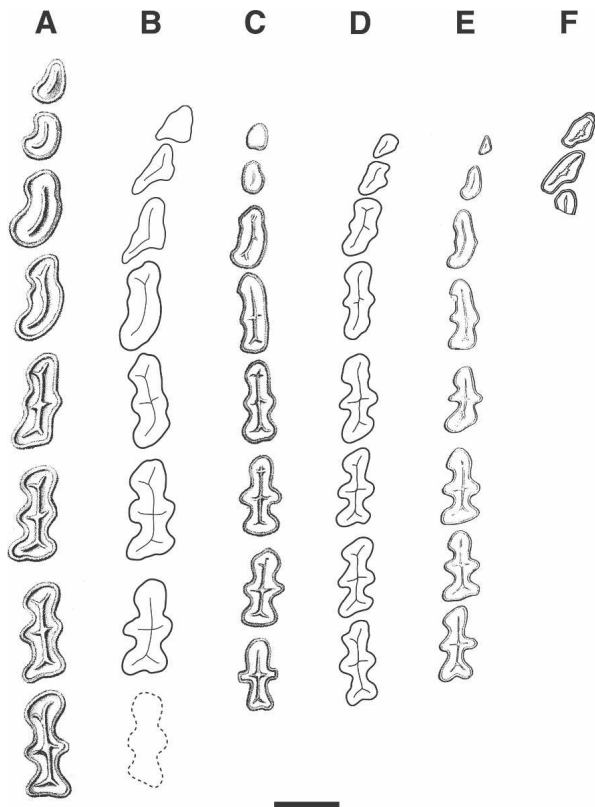


FIGURE 7. Left lower dentitions of propalaeohoplorine glyptodontids and *Parapropalaeohoplorus*. **A**, *Eucinepelus petestatus*, MACN A-4760 (from Scott, 1903b); **B**, *Parapropalaeohoplorus*, SGO PV 4165 (dashed line approximates shape of n8); **C**, *Propalaeohoplorus australis*, MLP 16-15 (from Scott, 1903b, reversed); **D**, *Propalaeohoplorus minus* holotype, MACN A-4757 (reversed); **E**, *Propalaeohoplorus andinus* holotype, UF 26677 (from Frailey, 1988); **F**, *Asterostemma venezolensis* holotype, unnumbered specimen in the collections of the Ministerio de Fomento, Venezuela at time of description (from Simpson, 1947). All illustrations are at the same scale (scale bar equals 1 cm), mesial is toward the top of the figure, and the specimens are aligned along the middle lobe of n5.

(one of which is from the moveable band) and therefore forms part of the ventral edge of the carapace. The right piece includes no marginal osteoderms but has a similar number of osteoderms in the moveable band as the left piece (4–5; it cannot be determined precisely where the moveable osteoderms transition to fixed osteoderms in the right carapace piece). It seems likely that at least the anterior portion of the right piece (i.e., near the moveable band) is also close to the ventral edge of the carapace. The dorsalmost osteoderms of the right piece likely lie roughly 60–75% of the distance from the ventral edge of the carapace to the dorsal midline.

Osteoderm shape varies by position in the carapace and includes subtriangular (marginal osteoderms, indicating a serrate marginal border); rectangular or quadrangular (those of the moveable band and near the ventral edge of the carapace); pentagonal (those slightly more dorsal on the carapace); and hexagonal (the most dorsal osteoderms). Osteoderm size also varies. The smallest osteoderms are those of the moveable band; on the right side, these are ca. 28–30 mm long by ca. 16–17 mm wide. Two isolated moveable band osteoderms (which might be from the tail sheath) measure 30.5 mm × 21.0 mm and 29.5 mm × 20.0 mm. The dorsalmost osteoderms are the largest; the largest of these (from the second most posterior band of the right side) measures 42 mm long × 34 mm wide. Approximate widths (in

mm) of osteoderms in this band from ventral margin to dorsal are: 19, 19, 21, 24, 25, 29, 31, 34, 34. The osteoderms of *Parapropalaeohoplorus* are larger than those of *Asterostemma venezolensis* (which range from 18–26 mm in width; Simpson, 1947) and are smaller than those of *A. gigantea* (maximum size 44–48 mm long and 35–48 mm wide; Carlini et al., 1997). The largest single osteoderm from *Parapropalaeohoplorus* is comparable in size to the largest of an indeterminate propalaeohoplorine from the Deseadan of El Parajito, Chubut, Argentina described by Scillato-Yané (1977b). The osteoderms of *Parapropalaeohoplorus* vary in thickness from ca. 9 mm (the dorsalmost osteoderms and those of the moveable bands) to ca. 15 mm (the posteriormost). An isolated posterior fixed osteoderm measures 17.2 mm in maximum thickness.

Osteoderm sculpturing is quite faint in *Parapropalaeohoplorus*, although it is more pronounced in the posteriormost osteoderms (i.e., part of the left carapace and in some isolated osteoderms); this is typical of both glyptatelines and propalaeohoplorines. In each osteoderm, a large principal figure is located along the posterior edge and occupies ca. 50–75% of the surface area; the principal figure is concave and sometimes has a very slight convexity in the middle that does not seem to vary regularly with osteoderm position. The principal figure is surrounded by a faint principal sulcus, from which radiate a varying number of radial sulci; usually only three sulci are conspicuous, although portions of up to two more can be present. Very small piliferous pits can occur at the intersections of the principal and radial sulci. Anterior peripheral figures are present in nearly all osteoderms. Medial and lateral peripheral figures are always much smaller and more poorly distinguished than the anterior figures; the lateral (ventral) peripheral figures are larger than the medial (dorsal) ones toward the anterior end of the carapace whereas the converse is true toward the posterior end. Because the principal figure lies close to the posterior margin in all osteoderms, posterior peripheral figures are almost totally absent, occurring only in some of the most dorsal osteoderms. In the marginal osteoderms, the principal figure is located along the ventral edge. In the moveable bands, the principal figure occupies nearly the entire surface of the exposed (i.e., non-overlapping) portion of the osteoderm. The osteoderm pattern in *Parapropalaeohoplorus* does not resemble that of any Santacrucian glyptodontid. Although a large, posteriorly positioned principal figure sometimes is present in the ventral osteoderms of *Propalaeohoplorus* and *Cochlops*, in no propalaeohoplorine does it characterize all osteoderms. In overall form, the osteoderms of *Parapropalaeohoplorus* most closely resemble those of *Glyptatelus*, a poorly known glyptodontid from the late Oligocene (Deseadan SALMA) of Argentina (Ameghino, 1897). The osteoderms differ from this taxon, however, in their very faint sculpturing; in their lack of conspicuous piliferous pits; and in their flat to slightly concave principal figures (the corresponding figures in *Glyptatelus* being smoothly convex). Given the many primitive character states evident in the osteoderms of *Parapropalaeohoplorus*, the osteoderm morphology of this species may closely approximate the ancestral glyptodontid condition (Fig. 9).

No detailed vertebral morphology can be discerned in SGO PV 4165 since these elements remain unprepared; even their position within the spinal column cannot be determined precisely. The relatively large size of the neural canal visible in some vertebrae indicates they likely pertain to the cervical and/or thoracic regions. The chevron (from the caudal region) has not been completely prepared but resembles the corresponding element of *Propalaeohoplorus* as far as can be determined. It measures ca. 51 mm in length, ca. 45 mm across the proximal end (incompletely preserved), and 27.5 mm across the distal end.

The left femur is essentially complete, although the neck is crushed and small portions of bone are missing near the base of

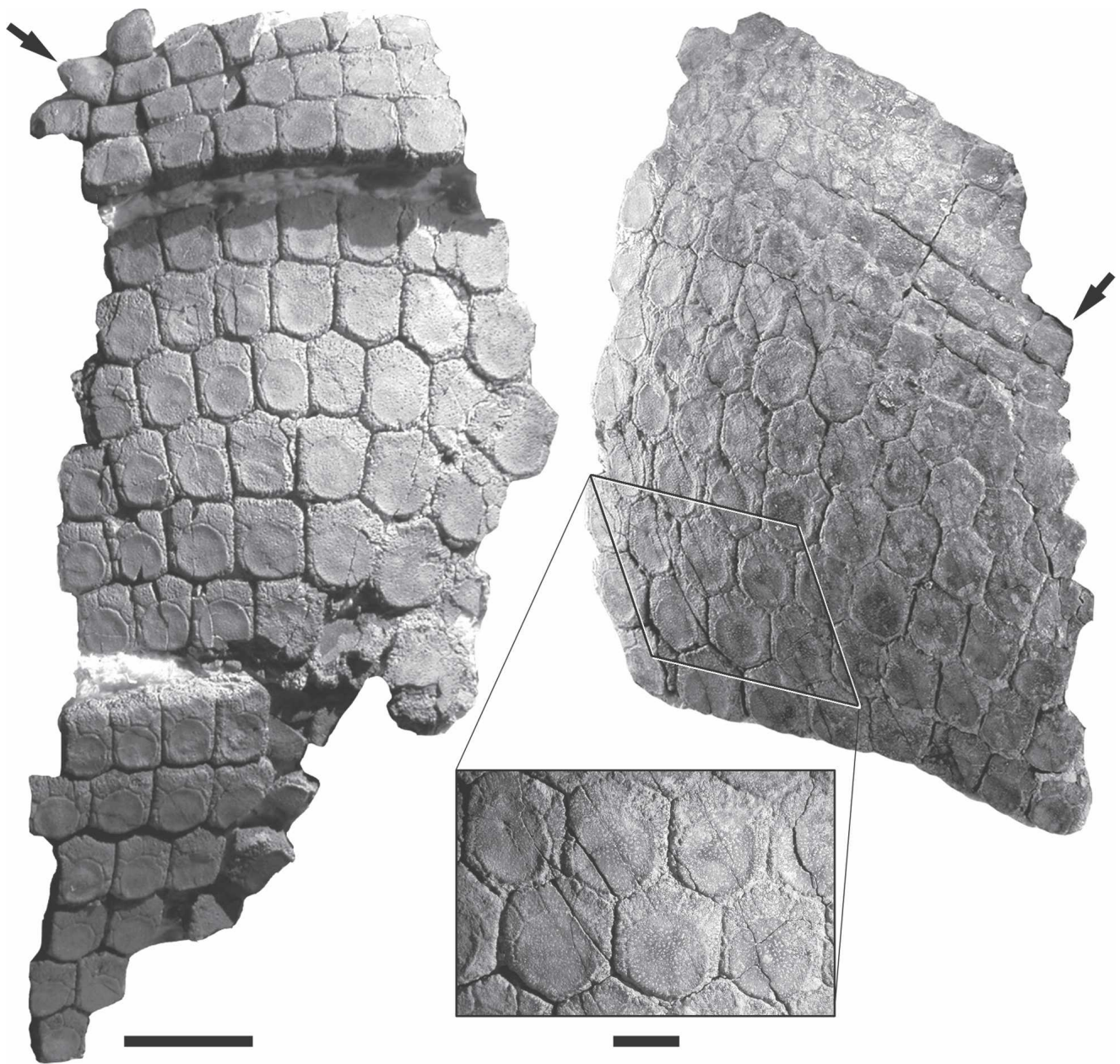


FIGURE 8. Portions of left (left) and right (right) sides of carapace of *Parapropalaeohoplophorus* in dorsal view (SGO PV 4165). Both pieces are at the same scale (scale bar equals 5 cm) and anterior is toward the top of the figure. The moveable band of each piece is indicated by an arrow. Six dorsal osteoderms from the right side are shown in the inset box (scale bar equals 2 cm).

the greater trochanter and along the posterodistal surface (Fig. 10). It measures 24 cm in greatest length and is similar in size to that of *Propalaeohoplophorus* (YPM-PU 15212 measures ca. 22 cm). It resembles the femur of *Propalaeohoplophorus* in overall form, but differs in details. Like *Propalaeohoplophorus*, the articular surface of the head (ca. 30.5 mm in width) is oriented mostly proximally; it extends slightly further posteriorly than anteriorly, and the pit marking the attachment of the ligament of the head is positioned posteromedially. The greater trochanter extends well above the head (ca. 30 mm) and is capped by a large (47.4 mm × 29.0 mm), elliptical, flat, rugose surface, which is oriented dorsolaterally and slightly anteriorly. The more anterior orientation of this surface differs from that of *Propalaeohoplophorus*, as does the lesser degree of lateral flexure of the process as a whole; the lateral margin of the greater trochanter is

angled only 10–15° relative to the long axis of the bone in *Parapropalaeohoplophorus* whereas it approaches 45° in *Propalaeohoplophorus*. Moreover, the trochanter extends only about half as far above the head in *Propalaeohoplophorus* as in *Parapropalaeohoplophorus* (ca. 15 mm in YPM-PU 15212). The lesser trochanter is small (ca. 9 mm × 12 mm) and located immediately distal to the head; a flat, narrow (ca. 10 mm), rugose area extends distally from the lesser trochanter ca. 50 mm along the medial face. At midshaft, the femur measures 27.4 mm (anteroposterior) × 34.1 mm (mediolateral), ca. 20% larger than that of *Propalaeohoplophorus* (YPM-PU 15212 measures 21.1 mm × 29.6 mm). The prominent third trochanter is located just below midshaft and includes a large (28.8 mm × 17.5 mm), elliptical, flat, rugose surface that is oriented almost directly laterally. Such a position is typical for propalaeohoplophorines and resembles the condition

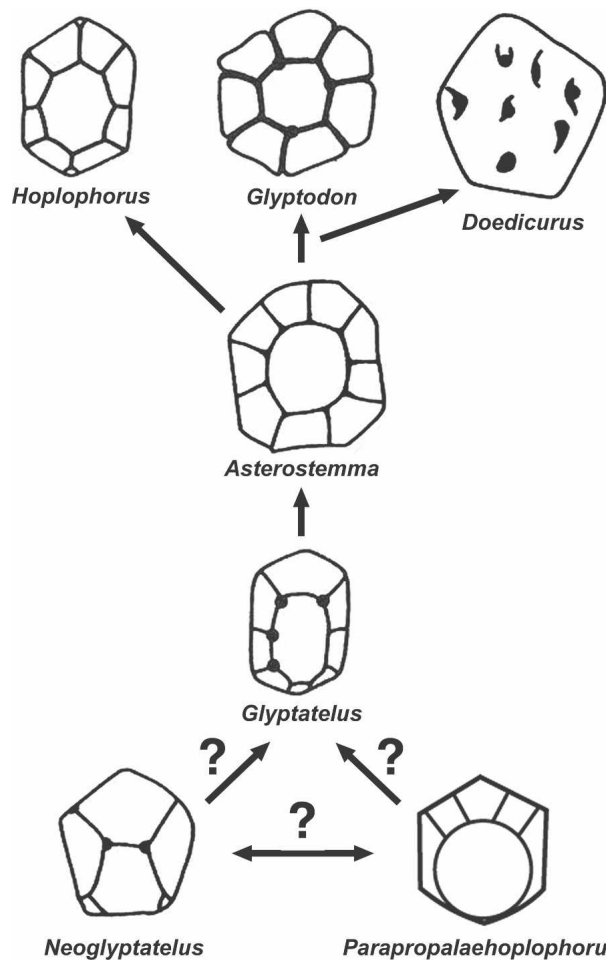


FIGURE 9. Hypothetical evolution of osteoderm morphology in glyptodontids based on the phylogenetic analysis in this study (modified from Carlini et al., 1997). The many primitive character states present in the osteoderms of *Parapropalaeohoplophorus* suggest that this species may more closely approximate the ancestral glyptodontid condition than *Neoglyptatelus*.

in armadillos (Ameghino, 1895). The distal margin of the third trochanter blends gradually into the lateral supracondylar ridge in *Parapropalaeohoplophorus*, whereas in *Propalaeohoplophorus* it forms a more pronounced angle, creating a distinct notch between it and the lateral condyle. The patellar groove is highly asymmetric, as in *Propalaeohoplophorus*; the medial face is raised and oriented distolaterally whereas the lateral face is oriented almost directly anteriorly. Pronounced muscle scars occur proximal to the lateral condyle on the lateral, posterolateral, and posterior surfaces. The femur measures 53.0 mm across the distal condyles. The medial condyle is much larger than the lateral.

SGO PV 4165 includes other elements of the appendicular skeleton or portions thereof, but most have not been sufficiently prepared to permit description. For example, an isolated ?intermediate phalanx is short and stout, measuring 15.2 mm (mediolateral) \times 11.7 mm (proximodistal) \times 9.9 mm (dorsoventral).

Comments—*Parapropalaeohoplophorus* is a relatively large early Miocene glyptodont, similar in size to *Eucinepeltus*, the largest Santacrucian form. As is evident above, the distinctiveness of *Parapropalaeohoplophorus* is manifest in nearly all parts of the skeleton including the mandible and lower dentition, the carapace, and the femur. It exhibits a mix of primitive and derived features (see Phylogenetic Analysis) that clearly distinguish it from all previously recognized species.



FIGURE 10. Left femur of *Parapropalaeohoplophorus* in anterior (left) and posterior (right) views (SGO PV 4165). Scale bar equals 5 cm.

Gen. et sp. indet.
(Fig. 11)

Referred Material—SGO PV 5097, two complete caudal osteoderms, one complete fixed marginal osteoderm, one partial moveable band osteoderm, 15 osteoderm fragments.

Locality—C-ALT-98-8, brownish-grey mudstones of Chucal Formation Member W4 (Charrier et al., 2002, 2005).

Description—Most of the osteoderms of SGO PV 5097 preserve little or no useful morphology save for four; two caudal osteoderms, one fixed marginal osteoderm, and one partial moveable band osteoderm, possibly from the tail (Fig 11). The two caudal osteoderms (Fig. 11A-B) measure 20.8 mm \times 16.3 mm (8.6 mm thick) and 16.3 mm \times 9.2 mm (6.0 mm thick). The larger is nearly oval in outline and the smaller is rectangular. The dorsal surface of each is nearly filled by a large, smooth, convex, oval principal figure positioned along the posterior edge. The principal figure of the larger osteoderm bears a raised ridge along the midline of its posterior half. The small area anterior to the principal figure is not divided into any obvious peripheral figures on either osteoderm and no piliferous pits are evident. These two osteoderms do not differ significantly from caudal osteoderms of typical propalaeohoplophorines. They could potentially pertain to *Parapropalaeohoplophorus*, but the few caudal osteoderms known of that taxon do not bear the raised ridge on the principal figure.

The fixed marginal osteoderm (Fig. 11C) is irregularly pentagonal and measures 19.1 mm \times 13.9 mm \times 7.6 mm thick. No principal or peripheral figures are present. It does not resemble the few available marginal osteoderms of *Parapropalaeohoplophorus*, which are larger, thicker, and more triangular. It is possible, however, that this marginal pertains to a part of the

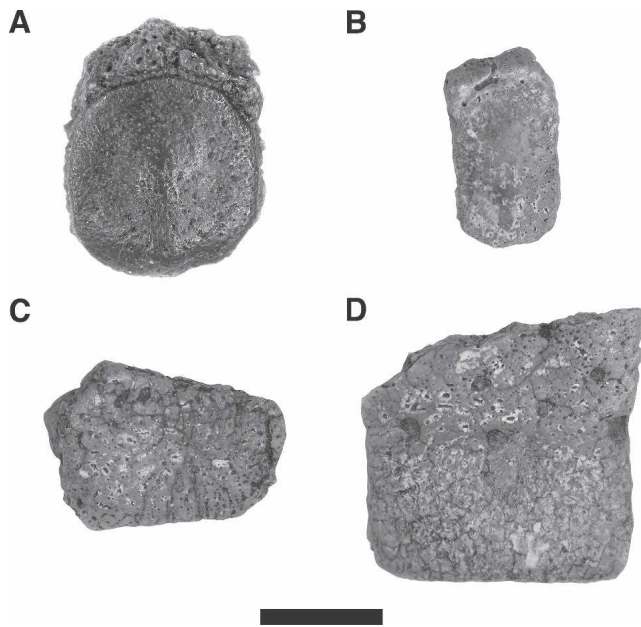


FIGURE 11. Isolated osteoderms from an indeterminate glyptodontid (SGO PV 5097). **A**, caudal; **B**, caudal; **C**, fixed marginal; **D**, moveable band. Scale bar equals 1 cm.

carapace (or the caudal armor) not preserved in the holotype of *Parapropalaeohoplophorus* rather than to a different taxon.

The moveable band osteoderm (Fig. 11D) is the most unusual of the group and differs dramatically from carapace moveable band osteoderms of *Parapropalaeohoplophorus*. It is 22.3 mm wide, roughly similar in size to moveable band osteoderms of *Parapropalaeohoplophorus*, but the dorsal surface bears seven large, conspicuous, evenly distributed piliferous pits, and it lacks principal or peripheral figures. The lack of such large pits in any available osteoderm of *Parapropalaeohoplophorus*, and the prominence of the principal figure in nearly all osteoderms, suggest this specimen may pertain to a species different than *P. septentrionalis*. It most resembles a caudal ring osteoderm of the glyptateline *Clypeotherium* figured by Scillato-Yané (1977:pl. 1) although the piliferous pits are more evenly distributed in SGO PV 5097 than in *Clypeotherium*. Alternatively, it is possible that the morphology of this specimen is typical of caudal ring osteoderms of *Parapropalaeohoplophorus*, which are probably unrepresented in the type specimen.

Comments—Although the large moveable band osteoderm of this specimen resembles a caudal ring osteoderm of *Clypeotherium*, the other osteoderms do not compare closely to this taxon. Because the morphology of the caudal armature of *Parapropalaeohoplophorus* is unknown, we cannot rule out the possibility that it pertains to this taxon. If the material pertains to a second Chucal glyptodontid species, nothing more can be said of its affinities based on this limited material.

PRELIMINARY PHYLOGENY OF GLYPTODONTIDAE

Parapropalaeohoplophorus, like propalaeohoplophorines and glyptatelines, retains many character states that appear to be primitive for glyptodontids and lacks many presumably derived character states shared by later diverging clades (e.g., Hoplophorinae, Doedicurinae, Glyptodontinae). It thus appears to be a relatively basally diverging member of the glyptodontid radiation. To test this proposition we performed a cladistic analysis of Glyptodontidae focused on resolving interrelationships of taxa that might lie near the base of the glyptodontid tree. Because a

comprehensive analysis of glyptodontid relationships has never been carried out—a task well beyond the scope of the present study—and because our concern is chiefly the position of *Parapropalaeohoplophorus* relative to other glyptodontids, the analysis primarily incorporated characters preserved in *Parapropalaeohoplophorus*. Besides *Parapropalaeohoplophorus*, the analysis included ten OTUs (genera): two glyptatelines, five propalaeohoplophorines, and one representative from each of the three later-occurring subfamilies (i.e., Hoplophorinae [*Hoplophorus*], Doedicurinae [*Doedicurus*], Glyptodontinae [*Glyptodon*]). *Pampatheriidae* was used as the outgroup (following Carlini and Scillato-Yané, 1993, and the classification of McKenna and Bell, 1997). A list of 26 phylogenetic characters was compiled from direct specimen observations and surveys of the literature (Appendix 1). The character-taxon matrix (Appendix 2) was analyzed via a heuristic search using PAUP 4.0b (Swofford, 1998) with multiple character states observed within the species of particular genera coded as polymorphisms. This analysis excluded many glyptodontids (especially hoplophorines) and some character complexes (e.g., the skull), making the results preliminary, but nonetheless informative for resolving interrelationships of basal glyptodontids.

The analysis produced four most-parsimonious trees of 46 steps; the strict consensus is presented in Figure 12. Aside from one large polytomy, resolution of the tree is reasonably good. Bootstrap values from 1,000 replicates range from low to high at various nodes, but decay indices are generally low; adding one step results in a near complete loss of resolution and adding three steps collapses the tree entirely. The lack of resolution stems not only from the comparatively small number of characters relative to taxa (a ratio of 2.6:1) and homoplasy, but also from the large amount of missing data; more than half of the characters could not be scored for *Neoglyptatelus*, *Glyptatelus*, and *Metopotoxus* and ca. 25% could not be coded for *Eucinepeltus*, *Asterostemma*, and *Parapropalaeohoplophorus*. In total, nearly 30% of ingroup character states were coded as unknown. Consequently, much of the resolution in the tree is based on osteoderm characters, the only traits that could be scored for all taxa. Because all of the less complete taxa are likely to be basal

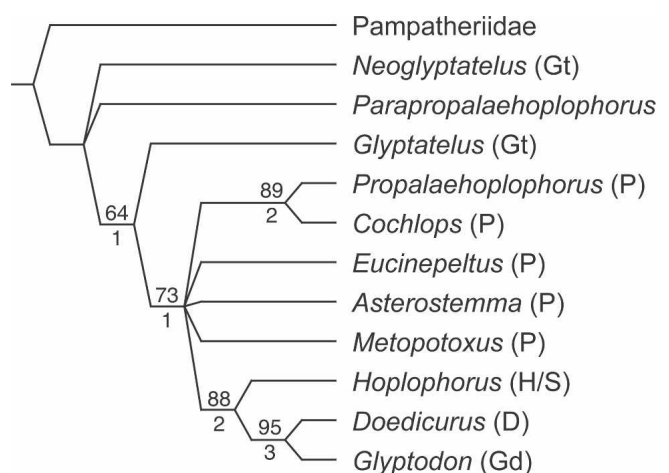


FIGURE 12. Phylogenetic relationships among representative basal glyptodontids. Strict consensus of four equally most-parsimonious trees based on the phylogenetic analysis in the present study; consistency index (CI) = 0.86; retention index (RI) = 0.86; rescaled consistency index (RC) = 0.74. Nodal support: bootstrap values > 50% are noted above branches and decay indices are noted below branches. Traditional subfamilial designations are noted in parentheses: **D**, Doedicurinae; **Gd**, Glyptodontinae; **Gt**, Glyptatelinae; **H/S**, Hoplophorinae (Sclerocalypitinae); **P**, Propalaeohoplophorinae.

glyptodontids, however, excluding any of them due to lack of scoreable characters would have resulted in an inadequate test of the position of *Parapropalaeohoplophorus*.

The two earliest diverging glyptodontids are *Parapropalaeohoplophorus* and *Neoglyptatelus*, which form a polytomy with a clade including the other glyptodontids. These two taxa are excluded from this latter clade based on their posteriorly positioned principal figure (it is more anteriorly positioned in other glyptodontids; no. 4:1–2). The lack of resolution in the positions of the two most basal taxa stems from homoplasy in character no. 5 (development of medial and lateral peripheral figures; derived in *Neoglyptatelus* and primitive in *Parapropalaeohoplophorus*) or character no. 9 (shape of the principal figure; primitive in *Neoglyptatelus* and derived in *Parapropalaeohoplophorus*), such that the basal glyptodontid polytomy cannot be resolved based on the present data set. Within the clade of remaining glyptodontids, *Glyptatelus* diverges first, and is excluded from the clade of typical Santacrucian glyptodontids (i.e., propalaeohoplophorines) and later forms based on the position of its principal figure (intermediate between the posterior edge and the middle, no. 4:1; centrally located in the remaining taxa, no. 4:2).

Propalaeohoplophorines are of uncertain monophyly, as those five taxa form a polytomy with a clade of the three Pleistocene glyptodontid genera. Among propalaeohoplophorines, only *Propalaeohoplophorus* and *Cochlops* share a relationship exclusive of other taxa, forming a clade characterized by a principal figure with a small elevation (no. 8:1) as opposed to the generally flat principal figure in other taxa (no. 8:0). This character state appears to be independently derived in *Glyptodon*. *Propalaeohoplophorus* and *Cochlops* also share a serrate carapace margin (no. 10:1), a feature also occurring in *Parapropalaeohoplophorus* and *Glyptodon*, and a fused mandibular symphysis (no. 15:1), also present in Pleistocene glyptodontids.

Monophyly of the clade consisting of Pleistocene glyptodontids (i.e., *Hoplophorus*, *Doedicurus*, *Glyptodon*) is more strongly supported than the other glyptodontid subgroups, and is characterized by the unique presence of deep osteoderm sculpturing (no. 3:1), the absence of moveable bands in the adult carapace (no. 11:1), and roughly symmetrical n5-8 (no. 23:1). This clade also shares the presence of a fused mandibular symphysis (no. 15:1), a feature that appears to be independently derived in the clade consisting of *Propalaeohoplophorus* and *Cochlops*. Among the three Pleistocene glyptodontids analyzed, *Doedicurus* and *Glyptodon* are nearest relatives, sharing fusion of carapace osteoderms (no. 7:1), relatively complex n2-3 (no. 20:1), spiked tail sheath osteoderms (no. 13:1), and a similar femur morphology (no. 25:1 and no. 26:1).

Overall, this analysis suggests that both glyptatelines and propalaeohoplophorines are best regarded as paraphyletic ‘grades’ rather than monophyletic clades. Although subsets of taxa within these two groups may be monophyletic (e.g., *Propalaeohoplophorus* plus *Cochlops*), there are presently few characters supporting such nodes. Sampling additional character complexes (e.g., skull) would likely improve the resolution of this tree, as would recovering additional dental and postcranial material of Oligocene and early Miocene glyptodontids. *Parapropalaeohoplophorus* appears to be one of the earliest diverging glyptodontids, and clearly is not closely related to other Santacrucian species. The monophyly of each of the later-occurring glyptodontid subfamilies was not tested in this study, because only a single species of each was included; their status must await more detailed analyses focused on this portion of the tree. Nevertheless, the basal character state transformations examined in this study should facilitate future analyses of the relationships of these later forms.

DISCUSSION AND CONCLUSIONS

The relatively few xenarthran specimens thus far collected from the Chucal Fauna of the Altiplano of Chile pertain to at

least three distantly related species. The Dasypodidae, nearly ubiquitous in South American Neogene faunas, are represented by a single species of *Stenotatus*. This taxon may be distinct from all previously described species of *Stenotatus*, but this cannot be demonstrated unequivocally based on the available material. All *Stenotatus* specimens from Chucal were collected from two localities, and therefore may represent the remains of only two individuals. Similarly, the two osteoderms referred to cf. *Peltephilus* sp. come from two widely separated localities and thus likely represent the remains of just two individuals. The glyptodontid *Parapropalaeohoplophorus* is the most complete and most important xenarthran from Chucal; not only does it represent a new taxon, it is the oldest and earliest diverging glyptodontid represented by good exoskeletal, craniodental, and postcranial material, thus helping to clarify character transformations near the base of the glyptodontid phylogeny. A second glyptodontid specimen also may pertain to *Parapropalaeohoplophorus*. In total, the minimum number of individual xenarthran specimens collected at Chucal is six.

Among xenarthrans, sloths are conspicuously absent from the Chucal Fauna. In contrast, they are both diverse and abundant in classic Santacrucian localities in Patagonian Argentina (Scott, 1903b, 1932). They also occur in the Santacrucian of southern Chile, but are rarer than cingulates (Flynn et al., 2002b). We do not know whether the non-recovery of sloths reflects their true absence from northern Chile at the time of deposition or particular taphonomic and/or ecological factors limiting their preservation and recovery. Regardless, sloths seem to have played a much less prominent role in late early Miocene communities of northern Chile than in those of southern Argentina. Anteaters (myrmecophagids) are also absent from Chucal, but given their general scarcity in the South American fossil record, this is not surprising.

The revised faunal list for the Chucal Fauna includes a minimum of 18 species of mammals and one anuran (Table 1). This total assumes that the poorly preserved toxodontid described by Bond and García (2002) does not pertain to *Nesodon*, a proposition difficult to test owing to the fragmentary nature of the

TABLE 1. Revised taxon list for the Chucal Fauna.

Mammalia		
Marsupialia (Ameridelphia)	Caenolestidae	*?Pichipilinae sp. indet. (incl. Tiny Undescribed Taxon 2 of Croft et al., 2004)
Xenarthra	Dasypodidae	* <i>Stenotatus</i> sp. nov.? (Euphractini sp. indet. of Croft et al., 2004)
	Peltephilidae	cf. <i>Peltephilus</i> sp.
	Glyptodontidae	* <i>Parapropalaeohoplophorus</i> <i>septentrionalis</i>
Rodentia	Chinchillidae	Undescribed Chinchillinae 1 *Undescribed Chinchillinae 2
	Dasyproctidae	<i>Neoreomys</i> sp.
	Octodontidae	* <i>Acarechimys</i> sp.
Notoungulata	Toxodontidae	Undescribed Taxon <i>Nesodon imbricatus</i> <i>Adinotherium</i> sp. indet. Toxodontidae ?new taxon [?Palyeidodon (?) sp. of Bond and Garcia, 2002]
	Mesotheriidae	<i>Altitypotherium paucidens</i> <i>Altitypotherium chucalensis</i> <i>Eotypotherium chico</i>
	Hegetotheriidae	<i>Hegetotherium</i> cf. <i>H.</i> <i>mirabile</i>
Litopterna Incertae sedis	Macrauchenidae	<i>Theosodon</i> sp. indet. Tiny Undescribed Taxon 1
Anura		*Undescribed Taxon 1

*Indicates new identifications or occurrences.

available material. If the indeterminate glyptodontid specimen described above does not pertain to *Parapropalaeohoplophorus septentrionalis*, then 19 species of mammals are present. Compared to the last published Chucal faunal list (Croft et al., 2004), this revision adds two new mammal occurrences (*Acarechimys* and a second undescribed chinchillid), possibly a third (if SGO PV 5097 does not pertain to *Parapropalaeohoplophorus septentrionalis*), and clarifies the identities of two others (the caenolestid, ?*Pichipilinae* sp. indet., and the dasypodid, *Stenotatus*). The anuran is the first non-mammalian tetrapod recorded from the Chucal Formation.

The taxonomic composition of the Chucal Fauna is depauperate compared to other Santacrucian faunas, which typically are characterized by high mammal diversity. The upper (*Protyppotherium australe*) and lower (*P. attenuatum*) biozones of the Santa Cruz Formation in Argentina include 36 and 31 mammal species, respectively (Tauber, 1997); 36 species are known from the Pampa Castillo Fauna of southern Chile (Flynn et al., 2002b). No complete faunal list has been published for the Pinturas Formation of Argentina (Kramarz and Bellosi, 2005; Kramarz and Bond, 2005), but the rodents and litopterns of that fauna are vastly more speciose than the corresponding elements of the Chucal Fauna. The Pinturas Formation also includes several species of primates (Fleagle, 1990; Tejedor, 2002). The high diversity of mammals from the Santa Cruz Formation suggests that at least partly forested conditions were present at the time of deposition (Croft, 2001), although the peculiar taxonomic composition of the fauna and other non-analog aspects have hampered comparisons with modern faunas and habitats (Croft and Townsend, 2005).

The low diversity of mammals in the Chucal Fauna probably is due, in part, to sampling (specimens are more abundant at other Santacrucian localities), but also likely reflects habitat differences between Chucal and Patagonian localities. The high proportion of hypsodont ungulates at Chucal suggests a relatively open habitat (e.g., savanna grassland; but see MacFadden, 2005 and Townsend and Croft, 2005, in press, for examples of non-grazing hypsodont notoungulates), an interpretation further supported by the abundance of high-crowned chinchillid rodents and the paucity—both in diversity and abundance—of low-crowned rodents (only octodontoids; Croft et al., 2004). The xenarthrans present also are compatible with the inferred open habitat. The three cingulates described above are all open habitat forms (Fariña and Vizcaíno, 2001; Vizcaíno et al., 2006) whereas sloths, usually more typical of closed habitats, are absent. The green layers of the Chucal Formation Member W3, characterized by abundant chinchillid remains and frogs, suggest the presence of bofedal or vega (low meadow/wetland vegetation) conditions (Charrier et al., 2002, 2005). Leaves and pollen from the Chucal Formation include a mix of taxa typical of the altitudinal transition from forest to steppe conditions (Charrier et al., 1994b). These data do not permit the relative amount of tree cover to be estimated, however. The low diversity of ostracods suggests extreme/seasonal conditions at Chucal, perhaps partly reflecting frequent ashfalls from nearby volcanoes (Charrier et al., 1994b).

The preliminary phylogenetic analysis presented here clearly supports a fairly basal position for *Parapropalaeohoplophorus* within the Glyptodontidae. Among traditionally recognized glyptodontid subfamilies, *Parapropalaeohoplophorus* might be included in the Glyptatelinae based on its morphology, but given the apparently paraphyletic nature of this group and the large amount of missing character data for 'glyptatelines' in general, referral of *Parapropalaeohoplophorus* to the Glyptatelinae is premature. Neither is it appropriate to refer *Parapropalaeohoplophorus* to the Propalaeohoplorinae, however, given that it differs dramatically from, and lacks derived features shared by, *Propalaeohoplophorus* and other closely related species. The unusual

nature of *Parapropalaeohoplophorus* seems to owe more to its derivation from a poorly sampled biogeographic region of South America (i.e., the low-middle latitudes) than to its slightly greater antiquity (≤ 2 m.y.) compared to glyptodontids from the Santa Cruz Formation of Patagonia. Much older (ca. 10 m.y.) yet more advanced ('propalaeohoplorine') osteoderms are known from southern Argentina (Scillato-Yané, 1977b), apparently indicating the presence of later diverging glyptodontids during this interval, and hence a long ghost lineage for *Parapropalaeohoplophorus*. As one of the earliest-diverging glyptodontids known, as well as the oldest glyptodontid represented by good craniodental, postcranial, and exoskeletal material, this new Miocene species from the Altiplano is important for understanding the early diversification of this clade. Discovery of *Parapropalaeohoplophorus*, like the Chucal Fauna in general, underscores the importance of filling both temporal and spatial gaps in the South American fossil record for clarifying Neotropical mammal evolution.

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APPENDIX 1. Characters and character states used in phylogenetic analysis of glyptodontids. Characters are polarized based on Pamphateriidae as the outgroup.

- (1) Cephalic shield osteoderm sculpture: like that of carapace (0); unlike that of carapace (1).
- (2) Cephalic shield osteoderms: many, small (0); few, large (1).
- (3) Osteoderm sculpturing: shallow/faint (0); deep/pronounced (1).
- (4) Position of principal figure in dorsal osteoderms [ordered]: along posterior edge (0); near posterior edge (1); roughly central (2).
- (5) Dorsal osteoderm medial and lateral peripheral figures [ordered]: absent or scarcely discernable (0); present and easily discernable but small relative to more anterior peripheral figures (1); present, easily discernable, and close in size to anterior peripheral figures (2).
- (6) Dorsal osteoderm piliferous pits: large/prominent (0); small/faint (1).
- (7) Osteoderms of the carapace: unfused (0); fused (1).
- (8) Dorsal osteoderm principal figure: flat or smoothly convex or concave (0); with central elevation or knob (1).
- (9) Dorsal osteoderm principal figure: straight-sided (0); round (1).
- (10) Margins of carapace: smooth (0); serrate (1).
- (11) Moveable bands in anterolateral carapace: present and pronounced (0); absent in adult (1).
- (12) Tail sheath: long and tapering (0); with blunt termination (1).
- (13) Tail sheath: without osteoderm spikes (0); with spikes (1).
- (14) Tail sheath: rings and imbricated osteoderms (0); rings and solid club (1).
- (15) Mandibular symphysis: unfused (0); fused (1).
- (16) Mandibular angle: approximately in line with ascending ramus (0); extended posteriorly (1).
- (17) Coronoid process: vertical (0); angled anteriorly (1).
- (18) Osteodentine figure [ordered]: absent (0); simple, following main axes of tooth (1); complex, with additional branches (2).
- (19) n1-3 [unordered]: subcircular/reniform (0); lobed (1); triangular with distobuccal extension (2).
- (20) n2-3: simpler than n5-8 (0); as complex as n5-8 (1).
- (21) n4: similar in morphology to n2-3 (0); similar in morphology to n5-8 (1).
- (22) Vertical groove on posteroexternal lobe of N6-8: present/distinct (0); absent/faint (1).
- (23) Posterior teeth: asymmetrical (0); roughly symmetrical (1).
- (24) Fused vertebral "dorsal tube": absent (0); present (1).
- (25) Position of third trochanter of femur: near midshaft (0); close to distal end (1).
- (26) Greater trochanter: much higher than femoral head (0); at approximately same level as femoral head (1).

APPENDIX 2. Character-taxon matrix used for phylogenetic analysis of glyptodontids. Missing character states are indicated by a question mark (?). Taxa polymorphic for state 0 and 1 are coded as 'A.'

	00000	00001	11111	11112	22222	2
	12345	67890	12345	67890	12345	6
Pamphateriidae	00000	00000	00000	00A00	A?000	0
<i>Glyptatelus</i>	??011	0001?	?????	?????	?????	?
<i>Neoglyptatelus</i>	??001	00000	??0??	?????	??0??	?
<i>Propalaeohoplophorus</i>	00022	10111	1100A	11110	10010	0
<i>Cochlops</i>	00022	10111	11001	??110	1001?	?
<i>Eucinepeltus</i>	11022	00010	1???0	??100	0101?	?
<i>Asterostemma</i>	??022	10010	?0000	1?120	1A0??	?
<i>Metopotoxus</i>	10022	0001?	?????	??1??	?00??	?
<i>Hoplophorus</i>	00122	00010	21001	11110	1A11?	?
<i>Doedicurus</i>	101??	010?0	21111	11111	11111	1
<i>Glyptodon</i>	10122	01A11	2010A	11211	11111	1
<i>Parapropalaeohoplophorus</i>	??000	10011	1???0	00120	0?0?0	0