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Skeletal anatomy and the fossil history of the Vermilingua

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Resumen

La diversidad taxonómica de los osos hormigueros de América del Sur o Vermilingua (Familias Myrmecophagidae y Cyclopedidae) está limitada a solo tres géneros y cuatro especies. El registro certero más temprano de Vermilingua corresponde al Oligoceno tardío-Mioceno temprano, aunque hay algunas propuestas dudosas más antiguas. Los restos son escasos y muchos de los taxones fósiles están basados en huesos aislados. Este registro tan parcial limita la capacidad de entender algunas de las tendencias evolutivas dentro del grupo, como sus especializaciones craneanas para la alimentación basada en insectos coloniales y la transición de hábitos terrestres a arborícolas o viceversa. En esta contribución presentamos una síntesis de las características más salientes del esqueleto de los Vermilingua vivientes y el estado actual del conocimiento de los fósiles, incluyendo una lista sinóptica de los especimenes disponibles en colecciones de museos.

Resumo

A diversidade taxonômica dos tamanduás na América do Sul (Vermilingua: Famílias Myrmecophagidae e Cyclopedidae) está limitada apenas a três gêneros e quatro espécies. O registro confiável mais antigo dos Vermilingua corresponde-se com o Oligoceno superior-Mioceno inferior, embora haja propostas duvidosas anteriores. Os restos achados têm sido escassos, e muitos dos táxons fósseis baseiam-se em ossos isolados. Este registro tão parcial limita a nossa capacidade de entendermos algumas das tendências evolutivas dentro do grupo, como suas especializaões craneanas para a alimentação baseada em insectos coloniais e a transição de hábitos terrestres para arborícolas ou vice-versa. Nesta contribuição apresentamos uma síntese das características mais salientes do esqueleto dos Vermilingua atuais e o estado presente do conhecimento das fósseis, incluindo uma relação sinóptica dos especimes disponíveis em coleções de museus.

Introduction

An insectivorous diet is common in many extant mammals and is implied as the primitive condition in the earliest eutherian mammals, as all proximal outgroups to the Eutheria were apparently insectivorous (Kielan-Jaworowska et al. 2004). However, specialization for feeding on colonial insects such as ants and termites (myrmecophagy) has evolved in only a limited number of mammals, although trace fossils considered to be termite nests are known from the Triassic (Hasiotis and Dubiel 1995) and body fossils of colonial insects are known from the Cretaceous (Grimaldi and Agosti 2000; Krishna and Grimaldi 2003). This dietary specialization is reflected in numerous morphological features, resulting in convergent evolution among a number of unrelated groups. Many of the skeletal characters associated with myrmecophagy first appear in the Jurassic in the enigmatic *Fruitafossor* (Luo and Wible 2005). Modern forms displaying these adaptations (to various degrees) include monotremes (the echidna, Murray 1984), marsupials (the numbat, *Myrmecobius fasciatus*, Reiss 2001), the pholidotes, tubulidentata, xenarthrans, and a carnivore (the aardwolf, *Proteles cristatus*). The greatest number of similar morphological characters is shared by the xenarthran anteaters (Vermilingua) and pangolins (Pholidota) and these similarities have been interpreted as indicative of a close phylogenetic

relationship (Englemann 1985; Reiss 1996; Asher et al. 2003) or that at least the two lineages should be considered sister groups (Novacek and Wyss 1986).

Contrary to these earlier systematic investigations, recent morphological studies of the South American anteaters (Vermilingua) and the Eurasian pangolins (Pholidota) have shown that the two groups are not closely related (Rose and Emry 1993; Gaudin and Wible 1999; Gaudin and McDonald this volume). Instead, the anatomical similarity represents an outstanding example of convergent evolution reflecting common dietary specialization on colonial insects. This more distant relationship between the Vermilingua and Pholidota has been supported by recent molecular studies (Delsuc et al. 2001, 2002, 2003; Springer et al. 2005; Delsuc and Douzery this volume), which place Xenarthra (including the Vermilingua) as one of the four major subdivisions of placental mammals and the Pholidota within the Laurasiatheria. The term anteater in this paper will refer to dietary specialization/habits for feeding on colonial insects such as termites and ants, whereas the term Vermilingua is used taxonomically to refer to the South American xenarthrans with this dietary specialization and includes all members, fossil and living, of the two currently recognized extant families, Myrmecophagidae and Cyclopedidae, and possibly one or two poorly known taxa from the Miocene (Santacrucian). The highly specialized feeding apparatus of the Vermilingua has been studied in detail (Naples 1985, 1999; Reiss 1997) and the reader is referred to these articles for details concerning modifications to the cranium and its musculature.

F. Ameghino (1894) described the family Adiastaltidae to include his genera *Adiastaltus* 1893 and *Plagiocoelus* 1894. Originally Ameghino (1893) considered *Adiastaltus* and *Anathitus* to be closely related to monotremes, with the latter possibly a link between theriodonts and monotremes. In 1894 he included *Adiastaltus* and *Plagiocoelus* (Fam. Adiastaltidae), *Anathitus* (Fam. Anathitidae), *Scotaeops* (Fam. Scotaeopsidae; an armadillo now known as *Stegotherium*) and *Dideilotherium* (Fam. Dideilotheridae) within the Monotremata. An evaluation of the status of these families is being undertaken, but for the purposes of this review, based on the morphology of the distal humerus, we provisionally consider the families Adiastaltidae and Anathitidae as junior synonyms of the Myrmecophagidae and all members to be poorly known Vermilinguans. A complete analysis is not possible at this time given the paucity of material available for these taxa, which limits a comprehensive morphological assessment of their relationships to either the Vermilingua or any other group of South American mammals.

The relationship of *Eurotamandua* from Germany, originally considered a member of the Vermilingua (Storch 1981) has been thoroughly discussed elsewhere (Gaudin and Branham 1998; Szalay and Schrenk 1998; Delsuc et al. 2001; Storch 2003; Rose et al. 2005) and will not be considered here, except to note that we do not consider it a member of the Xenarthra, let alone a Vermilinguan, but merely another outstanding example of the convergent evolution that has occurred in mammals adapted for "anteating."

Morphology of the Vermilingua

Members of the Vermilingua possess numerous distinctive modifications of the skeleton and soft anatomy indicative of their adaptive specializations for feeding on colonial insects. While a comprehensive description is not possible, a brief overview of the major modifications of the skeleton of the living forms is provided to illustrate features useful for classifying fragmentary fossil material.

Cranial morphology

Gaudin and Branham (1998, see also appendix 3.1 of Gaudin and McDonald this volume) list several cranial synapomorphies of Vermilingua, including curvature of the basicranial/basifacial axis, reduced maxillary orbital exposure, and the posteromedial orientation of the eustachian tube. Other specializations in the skull are related to the use of the slender, elongated, sticky tongue, the feature from which the group derives its name (Vermilingua = worm tongue), as the primary means of capturing prey. These include an elongation of the rostrum and the hard palate and a complete loss of dentition (figure 6.1A,B,C). The zygomatic arch is incomplete and the jugal is reduced to a small process attached to the zygomatic process of the maxilla in *Tamandua* and *Myrmecophaga*, while in *Cyclopes* it has been lost. A septomaxilla has been documented in *Tamandua* (Zeller et al. 1993) and *Cyclopes* (Gaudin and Branham 1998). The premaxilla remains small and lengthening of the skull is accomplished primarily through an elongation of the nasal and maxilla.

In *Tamandua* and *Myrmecophaga* the hard palate is elongated as a result of a slight elongation of the palatines and a joining of the pterygoids at the midline, so that the internal nares are shifted posterior to the gle-

noid fossa. The elongated secondary palate allows these genera to accommodate the retracted tongue within the oropharynx without interfering with the ability to breathe (Naples 1999). In this regard these two genera are more derived than *Cyclopes*, where, like the others, the pterygoids and soft palate are elongated posteriorly, but the internal nares remain in the same plane as the orbit (Patterson et al. 1992; Reiss 1997). In all Vermilingua the pterygoids extend posteriorly to form the anterointernal portion of the tympanic cavity, whereas the basioccipital forms its posterointernal wall. The contribution of these two bones to the formation of the tympanic cavity is a distinctive feature of the Vermilingua that distinguishes them from other Xenarthra (Patterson et al. 1992). The anterior edge of the tympanic is well behind the glenoid in *Cyclopes* but in *Tamandua* and *Myrmecophaga* the anterior margin of the tympanic forms its posterior edge. There is no mastoid process. The stapes in *Myrmecophaga* is bicrurate while in *Cyclopes* it is columelliform and lacks a perforation, which presumably has been lost secondarily (Patterson et al. 1992; Gaudin et al. 1996).

Whereas *Cyclopes* retains prominent coronoid and angular processes on the mandible, in the other two extant genera they are reduced. The mandibular symphysis is unfused in all three genera. This permits mandibular rotation during feeding and effectively increases the gap of the mouth opening (Naples 1999).

Postcranial morphology

The primary postcranial modifications of the skeleton are in the forelimbs, which are modified for digging. These modifications cannot be viewed as fossorial in a strict sense because the forelimbs are used only for digging earth in *Myrmecophaga*, whereas in *Cyclopes* and *Tamandua* they are used to remove bark from trees or rip open the hard nests of ants or termites in order to feed. Detailed descriptions of various postcranial features follow in the next sections.

Scapula

The scapula has a coracoid (or scapular) foramen, a character shared with sloths and used to define the Pilosa (Flower 1882), although the coracoid is greatly reduced in *Cyclopes* and the foramen has been secondarily lost. The foramen is formed between the procoracoid (= anterior coracoid), which is a separate center of ossification, and the supraspinous fossa. Characteristic of all Xenarthra is a secondary scapula spine, with the attachment area for the teres major muscle greatly enlarged in *Myrmecophaga* and *Tamandua*, but not as much in *Cyclopes*. The teres major serves to retract the humerus and the enlargement of its origin on the scapula and its more distal insertion on the humerus increases its moment arm, thus increasing the amount of force it contributes during digging (Taylor 1978). The acromion process is well developed in all forms and the metacromion process is present in *Myrmecophaga* and *Tamandua* but absent in *Cyclopes*. The acromion process extends more medially than in other mammals and increases the capability of the acromiodeltoid muscle to protract the humerus because it positions the muscle in front of the shoulder and not to the side. This may aid in climbing or defensive posturing (Taylor 1978).

Humerus

The humerus is robust in the Vermilingua, with well-developed muscle scars and ridges for the origin of muscles that both extend and flex the forearm. The deltoid tubercle is well developed and curves posteriorly in all three extant genera. An entepicondylar foramen is present in all forms. The distal end is greatly expanded, primarily by the enlargement of the supinator crest, which provides the origin of the extensor carpi radialis, extensor carpi ulnaris, and extensor digitorum communis. One head of the supinator, along with the extension of the medial epicondylar process, provides the origin of the pronator teres, flexor carpii radialis, flexor digitorum sublimis, flexor carpi ulnaris, and flexor digitorum profundus muscles on the anterior surface and the epitrochleo-anconeus muscle on the posterior surface (Taylor 1978). In *Tamandua* the medial head of the triceps is fused with the flexor digitorum profundus by a common tendon that passes under the distal border of the medial epicondyle to insert on the third digit. The enlargement of the entepicondylar process and notch can be used to infer this unique muscle arrangement in fossil Vermilingua, but both characters are also present in a variety of other forms (e.g., pangolins and palaeanodonts) that lack this specialized muscle arrangement. The supinator crest may be further extended proximally by a delto-epicondylar ligament that connects the crest with the deltoid tubercle (Taylor 1978).

Ulna

The olecranon process is enlarged compared to non-fossorial mammals, but not to the extent seen in armadillos (Vizcaíno et al. 1999). The index of fossorial ability (IFA), calculated as the length of the olecranon process divided by the difference between ulnar length

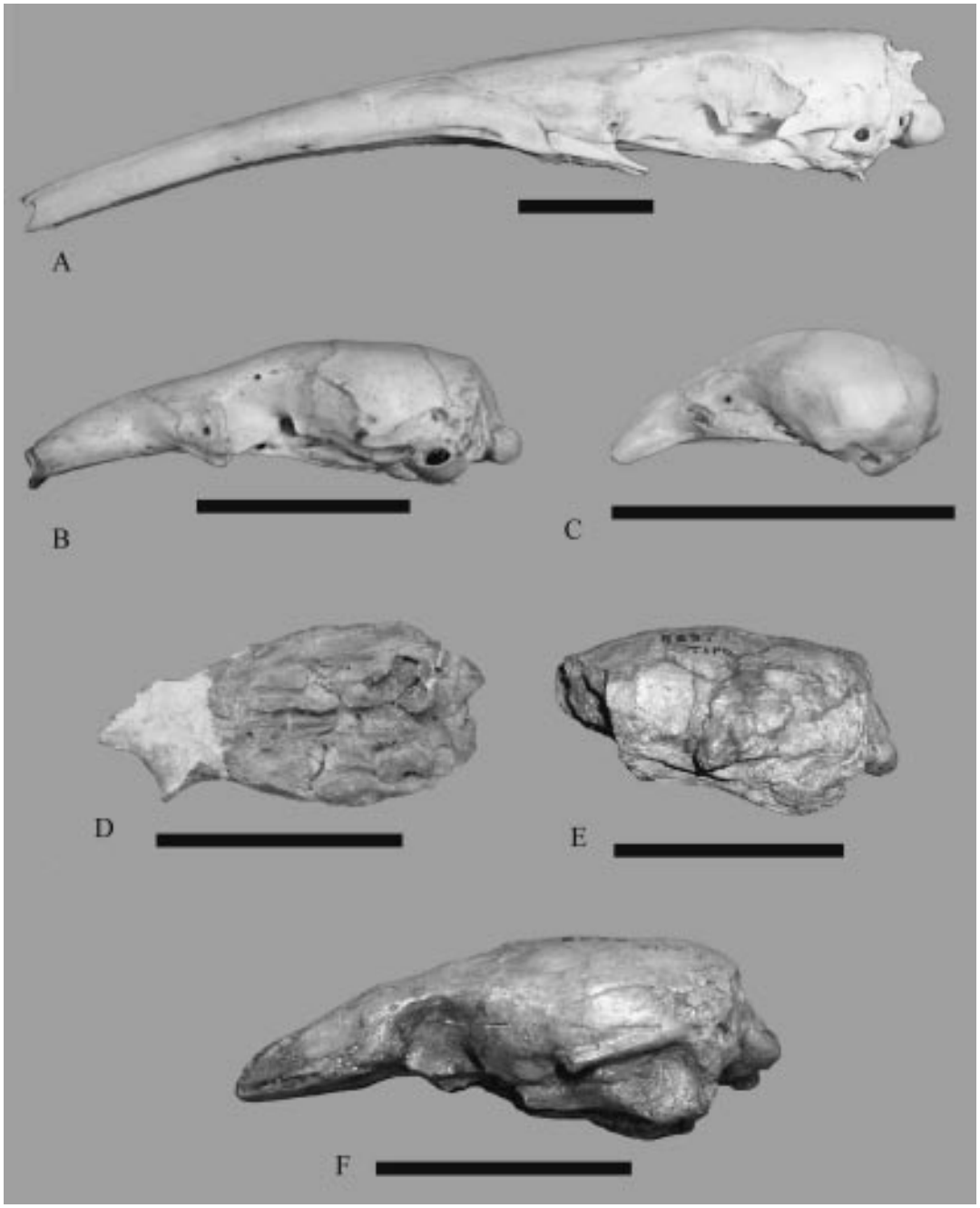

Figure 6.1. Skulls of extant (A–C) and fossil (D–F) Vermilingua. A. *Myrmecophaga trydactyla* (MACN 49.405). B. *Tamandua tetradactyla* (MACN 33.255). C. *Cyclopes didactylus* (no catalog number). D. *Protamandua rothi* (YPM 15267). Note that because this specimen is extremely flattened dorsoventrally, we decided to include a ventral view, which is more informative in terms of showing various vermilinguan features. E. *Neotamandua conspicua* (MACN 8097). F. *Palaeomyrmidon incomptus* (MACN 8098). Scale bar 5 cm. See Appendix 6.1 for full names of museum acronyms.

and olecranon length x 100, is 24.2 in *Myrmecophaga*, *Tamandua*, and *Cyclopes*. This is considerably less than the value of 101.17 ± 34.5 in the most fossorial armadillo, *Priodontes*, and not even half that obtained for the least fossorial and most cursorial armadillo, *Tolypeutes* (58.02 ± 9.16, Vizcaíno and Milne 2002).

White (1993) noted that climbing and digging mammals often have a rather long, proximally extended olecranon, with little dorsal extension and often a slight ventral orientation, whereas in more terrestrial mammals the olecranon tends to project dorsally. She developed an index based on the length and depth of the trochlear notch to clearly distinguish the three extant vermilinguan genera with relation to their locomotor habits. *Cyclopes* had the lowest index (ca. 1.1), *Myrmecophaga* the highest (ca. 1.7), and *Tamandua* was intermediate (ca. 1.4).

In all extant forms, the anconeal process is only moderately developed, permitting a greater extension of the forearm, and there is no coronoid process. Both *Myrmecophaga* and *Tamandua* have a well-developed styloid process that is absent in *Cyclopes*.

Radius

The radius in the Vermilingua has a distinct curvature so that the distal end is offset anteriorly relative to the proximal end, and the distal anterior edge is flared. This increases the moment arm of axial rotation by the pronator teres and hence the force generated, even though the range of pronation and supination is more limited than in other mammals (about 50˚ in *Tamandua* and 40˚ in *Myrmecophaga*, Taylor 1978). This modification is less pronounced in *Cyclopes*. Orr (2005) noted that in *Myrmecophaga* there is a distal projection of the dorsal ridge of the distal end and a deeper concavity of the distal articular surface that limits the range of extension of the antebrachiocarpal joint to 10–15˚, compared to 60˚ in *Tamandua*. This ridge acts as a brace, and Orr considered this to be a hallmark of a locomotor style that involves the manus being held vertical relative to the substrate. The presence or absence of this feature in fossil Vermilingua can be used to infer terrestrial versus arboreal habits in extinct forms.

Manus

While metacarpals two and three are roughly the same length and slightly shorter than metacarpals four and five, the manus is dominated by the third metacarpal, which is roughly rectangular in morphology and more robust than the other metacarpals (Taylor 1978). The distal end is strongly keeled, with the keel angled to the axis of the bone so that it slopes medially. Its distinctive morphology in Vermilinguans has been discussed by Hirschfeld (1976), Shaw and McDonald (1987), and Gaudin and Branham (1998). The fifth metacarpal is reduced, lacks an ungual (present on all other digits), and is bound in a pad of fat and connective tissue with the fourth metacarpal. The proximal phalanx is proximodistally shortened and there is no flexion or extension between it and either the metacarpal or second phalanx. The animal's weight is carried on the back of the unguals, primarily the third (the largest) and fourth, which can be flexed at ninety degrees to the manus in *Myrmecophaga* (Orr 2005). In contrast, *Tamandua* walks on the sides of its hands, supported by the padded fourth and fifth digits.

Femur

The head of the femur in all three extant genera extends above the greater trochanter. The angle at which the head of the femur is oriented relative to the shaft varies, though, with the highly arboreal *Cyclopes* having the smallest angle (extending more proximally); in the fully terrestrial *Myrmecophaga* it extends more medially, and the angle is intermediate in *Tamandua* (White 1993). The lesser trochanter is prominent in all three taxa. There is no distinct third trochanter in *Cyclopes*, but it is represented by a thin lip of bone along the distal half of the lateral edge of the shaft that is continuous with the lateral epicondyle. The third trochanter in *Tamandua* is a slightly raised ridge on the midshaft of the femur. In *Myrmecophaga*, the third trochanter is represented as a thickening of a prominent crest that extends from the greater trochanter to the lateral epicondyle. The distal end of the femur in *Cyclopes* is flattened more than in the other two genera, reflecting the greater flattening of the diaphysis. There is a prominent epicondylar process above the medial condyle in *Tamandua* and *Myrmecophaga* that is absent in *Cyclopes*. The patellar surface is continuous with the articular surfaces of the condyles in all three genera.

Because the shape of the distal femur is highly correlated with the mode of locomotion in many mammals, White (1993) utilized an index of distal femur shape (maximum depth of the distal end divided by its width) that clearly demonstrated differences between the modes of locomotion in the three extant genera. *Cyclopes* had the lowest value (ca. 0.65) and *Myrmecophaga* the highest (ca. 1.05). This index is partially determined by the degree to which the medial side of the patellar

surface is raised relative to the lateral edge. There is no raised edge in *Cyclopes* but there is a prominent one in *Myrmecophaga*. This index, along with the femoral neck angle, can be applied to fossil forms as a means of determining the extent to which they were arboreal or terrestrial.

Tibia

The shaft of the tibia is flattened in *Cyclopes*, and the distal articular surface is also anteroposteriorly flattened. The distal tibial articular surface is shallow and the grooves for the tendons of the tibialis caudalis, flexor digitorum longus, and flexor hallucis longus are greatly reduced in *Cyclopes* but are large and prominent in *Myrmecophaga* and *Tamandua*. In *Tamandua* the diaphysis of the tibia is more oval, but it tends to be more triangular in *Myrmecophaga*. The articular surface for the astragalus is deeper in *Myrmecophaga* than in the other two genera, thus restricting lateral movement.

Pes

The pes is plantigrade in *Myrmecophaga* and *Tamandua* but highly modified for grasping branches in *Cyclopes*, as the derivation of the generic name suggests. All Vermilingua have an astragalus with a concavity on the navicular facet and a navicular possessing a complementary mamillary process. There is a tibial sesamoid next to the entocuneiform.

Vertebral column

In *Myrmecophaga* there are four sacral vertebrae, with the first three articulating with the ilium and the fourth articulating with the ischium, as does the first caudal. In *Tamandua* the number of sacral vertebrae is three, with the first two articulating with the ilium and the third having no contact with the pelvis, while the first caudal articulates with the ischium to form the synsacrum. The number of sacral vertebrae in *Cyclopes* is four, with the first three articulating with the ilium, the fourth having no contact with the pelvis, and the first caudal vertebra articulating with the ischium.

The caudal vertebrae differ between *Myrmecophaga*, *Tamandua*, and *Cyclopes*, reflecting the presence or absence of a prehensile tail. In *Myrmecophaga* the anterior caudal centra are short, robust, and round, with a massive neural arch and neural spine, and the zygapophyses are deep to limit lateral movement. The anterior caudal series in *Tamandua* have centra with flat ends, short neural arches, and zygapophyses that are broad and shallow. *Tamandua* and *Cyclopes* have bifurcate transverse processes on the mid and posterior caudals, indicative of their prehensile tails. The bifurcation of the transverse process is absent in the caudals of *Myrmecophaga*. The transverse processes of the caudals in *Tamandua* are longer anteroposteriorly than in *Myrmecophaga* for attachment of the muscles that flex the tail. The posterior caudal vertebrae in *Tamandua* are phalanxlike, with convex posterior ends that allow for flexibility in the end of the tail (Hirschfeld 1976). Gaudin and Branham (1998) note that bifurcated, elongated transverse processes of the caudal vertebrae are found in *Protamandua* (FMNH 13134), implying that this taxon, like *Cyclopes* and *Tamandua*, had a prehensile tail.

Ribs

All three extant genera of Vermilingua have anteroposteriorly expanded ribs. A similar pattern of rib expansion is present in some genera of armadillos. In *Cyclopes* the expansion of the ribs is more pronounced than in the other two genera so that successive ribs imbricate. The expansion of the ribs may increase the stability of the thorax and vertebral column and can facilitate both arboreal and fossorial habits (Jenkins 1970).

Fossil record of the Vermilingua

Given the relative rarity of fossil Vermilingua, we have provided a synoptic list (appendix 6.1) of all specimens either described in the literature or known to us through our visits to various collections. That it is even possible to provide such a list indicates just how few specimens have been collected.

Except for an enigmatic metacarpal from the early Eocene of Patagonia that shows some similarities with Vermilingua (Carlini et al. 1989), the earliest certain fossil of the group is from the Colhuehuapian (late Oligocene to early Miocene) from the Atlantic coast of Chubut province, Argentina (Carlini et al. 1992). The specimen consists of half a mandible, numerous vertebrae, ribs, scapula, a fragment of the distal humerus, an almost complete manus, both femora, the proximal portion of the tibia, and an almost complete pes. The specimen has not been formerly described but is similar in size to *Tamandua*, although more robust. What makes the discovery of this specimen even more remarkable is that it was recovered from the marine sediments of the Gaiman Formation.

A large number of taxa from the Santacrucian (early-middle Miocene) have been referred to the Ver-

milingua, including *Protamandua rothi*, *Promyrmephagus dolichoarthrus*, *Promyrmephagus euryarthrus*, *Adiastaltus habilis*, *Adiastaltus procerus*, *Plagiocoelus obliquus*, *Anathitus revelator*, *Argyromanis patagonica*, and *Orthoarthrus mixtus*. The large number reflects the generally fragmentary nature of the types, and the fact that each new discovery was described as a new taxon. Because different skeletal elements often were utilized as a type, it has not been possible to make any comparisons between taxa that would permit their synonomy. Some taxa, among them *Adiastaltus habilis*, *Adiastaltus procerus*, *Anathitus revelator*, *Argyromanis patagonica*, and *Orthoarthrus mixtus*, were considered Xenarthra *incertae sedis* by Mones (1986), whereas *Plagiocoelus obliquus* was considered Mammalia *incertae sedis* by the same author, reflecting the need for a critical re-examination of this material. A preliminary step in this direction was undertaken by Hirschfeld (1976), who noted that the type specimen of *Protamandua rothi* (a calcaneum) easily articulated with the type of *Promyrmephagus euryarthrus* (an astragalus), indicating that not only were the taxa the same but the two specimens probably represented the same individual. She proposed that *P. euryarthrus* and *P. dolichoarthrus* be considered junior synonyms of *Protamandua rothi*. Carlini et al. (1993) considered *Promyrmephagus euryarthrus* to be congeneric with *Protamandua* but retained it as a distinct species.

There has been no recent study of the family Adiastaltidae and its genera, *Adiastaltus* and *Plagiocoelus*, or the Anathitidae with *Anathitus*. As indicated earlier, for the practical purposes of this review, we consider them to be synonymous with the Myrmecophagidae, as was preliminarily proposed by Vizcaíno, Bargo, et al. (2004), based on the similarity of the distal humerus to other Vermilingua. However, these genera require re-examination to determine their validity. Likewise, a re-examination of *Argyromanis patagonica* and *Orthoarthrus mixtus* is needed to determine their validity, possible synonomies, and systematic relationships.

Pending further study of the Santacrucian material, only one taxon can be confidently referred to the Vermilingua, *Protamandua rothi* (figure 6.1D). This is a small animal, intermediate in size between *Tamandua* and *Cyclopes*. The morphology of the manus and pes are similar to those of *Tamandua* and *Myrmecophaga*, but lack any of the specializations in the limbs for either arboreal or terrestrial locomotion seen in these genera. The only specialization seen in *Protamandua* is modification of the caudals, indicating that it had a prehensile tail (Hirschfeld 1976; Gaudin and Branham 1998).

Neotamandua? *australis* was described by Scillato-Yané and Carlini (1998) from the Colloncuran (their Friasian, Collón Curá Formation) of Río Negro province, Argentina. The type specimen is a complete right humerus. A distal left humerus was also found. Assignment of the new species to *Neotamandua* was tentative given the limited amount of material. The humerus is similar in size to *Tamandua* but about 50% wider for its length. Scillato-Yané and Carlini (1998) considered its overall structural appearance to be most similar to *Tamandua* and *N. conspicua*. They considered *Neotamandua* to be ancestral to *Tamandua* and *Myrmecophaga* and postulated without discussion that the two forms evolved allopatrically, with *Myrmecophaga* evolving in the northern part of South America and *Tamandua* in the south.

In the late Miocene (Laventan), *Neotamandua* is represented by *N. borealis*, based on a partial skeleton from La Venta, Colombia. This taxon is intermediate in size between *Tamandua* and *Myrmecophaga* and is also intermediate in most characters of the manus and pes (Hirschfeld 1976). Preserved caudal vertebrae indicate that the tail was not prehensile as in extant *Tamandua*. Hirschfeld (1976) considered *N. borealis* a possible common ancestor to *Tamandua* and *Myrmecophaga*. Both Engelmann (1985) and Gaudin and Branham (1998) considered *Neotamandua* to be the sister taxon to *Myrmecophaga*, that is, to be more closely related to *Myrmecophaga* than to *Tamandua*, rather than the ancestor to both modern genera. Patterson et al. (1992) suggested that *Neotamandua* (*N. conspicua*, FMNH P14419) was congeneric with *Myrmecophaga*, although Gaudin and Branham (1998) treated it as a separate taxon and recognized at least one autapomorphy not shared with the modern genus. This taxon occurs during the interval identified by Delsuc et al. (2001) as the time of divergence of *Tamandua* from *Myrmecophaga*.

Neotamandua conspicua was described by Rovereto (1914) based on a posterior part of a skull from the Huayquerian (late Miocene) of Catamarca province, Argentina (figure 6.1E). Based on some skull measurements, this species is slightly larger than *Tamandua*.

The type specimen of *Neotamandua greslebini* from the Huayquerian (late Miocene) of Tíopunco in Tucuman province, Argentina, consists of a partial skeleton that includes the proximal third of both femora, the distal end of the left femur, the body of the

right astragalus, the left calcaneum, distal left humerus, proximal right ulna, and distal right radius (Kraglievich 1940b). Unfortunately, the specimen cannot be located at the moment (but see notes in synoptic list of specimens).

Also present in the Huayquerian is one of the better-known fossil Vermilingua, *Palaeomyrmidon incomptus* (figure 6.1F), represented by a nearly complete skull (without a mandible), and a few postcranial fragments that are tentatively assigned to the genus. This small taxon is generally considered closely related to the extant *Cyclopes* by most workers (Hirschfeld 1976; Gaudin and Branham 1998). Delsuc et al. (2001) calculated that the pygmy anteater diverged from other anteaters 35–45 MYA; Barros et al. (2003) place the divergence at 32 MYA. Either way, these results indicate a long hiatus in the fossil record between the proposed origin of the lineage and the first appearance of a member in the fossil record between 7 and 9 MYA. This may not be surprising given the high degree of arboreality in *Cyclopes*, which would not lend itself to being readily preserved, particularly if this adaptation became established early in the group's history.

Patterson and Pascual (1968, 1972) cite a cranium with a partial rostrum they referred to *Myrmecophaga* from the Montehermosan (early Pliocene) of Catamarca province, Argentina. Hirschfeld (1976) noted that this specimen is larger than the living form. However, there is no formal description and no photos or illustrations have been published. The specimen, MLP 31-XI-12-15, is currently cataloged as *Neotamandua*. The skull is from a juvenile individual; the frontals and parietals have separated along their common suture and other sutures are visible. A detailed examination of the specimen indicates that the suture patterns and shape of the cranial bones do not match any known Vermilinguan, and the dorsal profile of the skull is not compatible with its interpretation as a member of this group. We do not consider this specimen to be a Vermilinguan.

Nunezia caroloameghinoi was also described from the Montehermosan (Kraglievich 1934). *Nunezia* comes from the type locality for this age and was recovered from lithostratigraphic unit 1, which Tonni et al. (1992) consider the type for the Montehermosan. This taxon is currently considered a synonym of *Myrmecophaga* (McKenna and Bell 1997). By extrapolation, C. Ameghino's (1919) *Neotamandua magna* should also be considered *Myrmecophaga* because Kraglievich (1934) transferred this taxon to *Nunezia*. If these synonomies are correct, then the earliest record of *Myrmecophaga* is in the Huayquerian. The next record of *Myrmecophaga* is from the early Irvingtonian (roughly equivalent to the Uquian) locality of El Golfo in Mexico (Shaw and McDonald 1987). The El Golfo specimen is a third metacarpal that permits direct comparison with the type of *Nunezia caroloameghinoi*, also a third metacarpal, but not with *Neotamandua magna*, which is known only from a pelvis.

In the Lujanian (late Pleistocene/early Holocene), we have good records of both *Tamandua tetradactyla* and *Myrmecophaga tridactyla*, based primarily on specimens recovered from the caves of Minas Gerais, Brazil, by P. W. Lund (Winge 1915), with additional records of *Myrmecophaga* from Bahia, Brazil (Cartelle and Leite 1989), and Uruguay (Mones and Ximenez 1980). *Tamandua tetradactyla* is known from three other localities (all caves) in Bahia, Brazil (Cartelle and Leite 1989). There are no fossil records of either *T. mexicana* or *Cyclopes didactyla*.

Phylogeny of the Vermilingua

The most recent phylogeny of the Vermilingua is the cladistic study by Gaudin and Branham (1998) utilizing 107 osteological characters of the skull and skeleton (figure 6.2). Along with the three extant genera, they were able to include only three extinct genera in their analysis (*Palaeomyrmidon*, *Protamandua*, and *Neotamandua*) because most of the other putative vermilinguan taxa consist of single bones. Their analysis essentially confirms the conclusions of previous workers such as Hirschfeld (1976) and Engelmann (1985), in which *Palaeomyrmidon* is the sister group of *Cyclopes*, *Protamandua* is the sister group to the other Vermilingua taxa, and *Neotamandua* is the sister group to *Myrmecophaga*. It is unfortunate that more fossil taxa were not included in the analysis. As already mentioned, this was due partly to the general paucity of fossil Vermilingua, but inclusion was further hampered by lack of any recent detailed studies of existing material or re-evaluations of alpha-level taxonomy.

Using a molecular clock, Delsuc et al. (2001) calculated divergence times for various stages in the evolution of the Xenarthra, including events within Vermilingua (table 6.1). While it may never be possible to obtain DNA from the older Vermilingua taxa in order to refine this phylogeny using molecular data, their work does provide a hypothesis that can be tested by the fos-

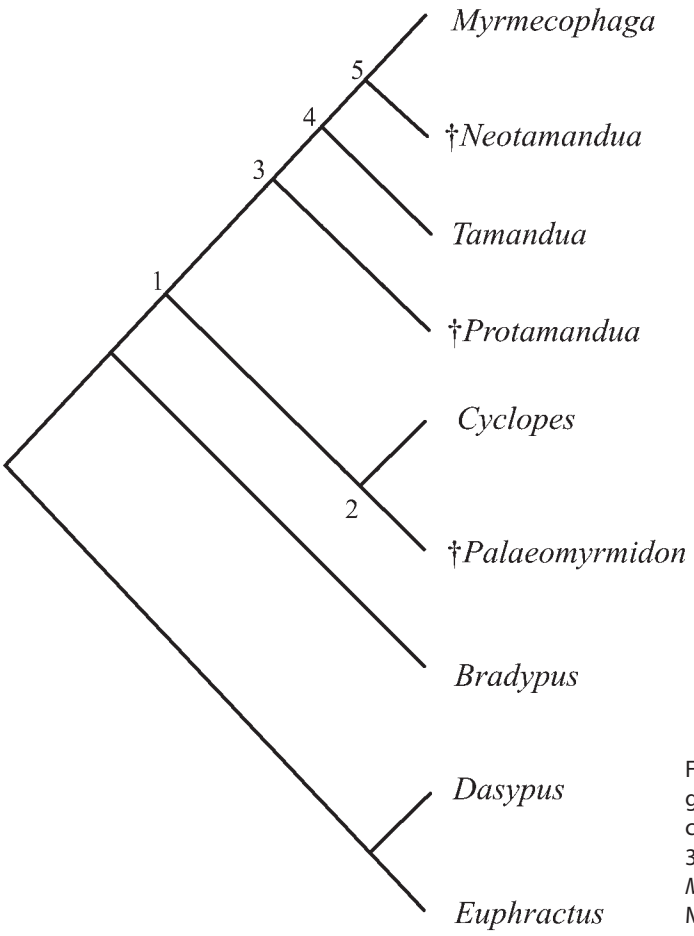

Figure 6.2. Hypothesized phylogeny of the Vermilingua based on PAUP analysis utilizing 107 osteological characters. Nodes are: 1-Vermilingua, 2-Cyclopedidae, 3-Myrmecophagidae, 4-*Tamandua*, *Neotamandua*, and *Myrmecophaga*, 5-*Myrmecophaga* and *Neotamandua*. Modified from Gaudin and Branham (1998).

sil record. However, this is difficult at present because, as can be seen in table 6.1, there are significant gaps in the vermilinguan fossil record. Thus, at this time, fossil data are insufficient to answer some very critical questions about vermilinguan evolutionary history. For example, we cannot say at what stage the Vermilingua lost their dentition and the pattern (if any) of tooth reduction. Regarding *Tamandua*, an unresolved question is whether its semiarboreal habits represent a primitive retained condition or were derived from a terrestrial ancestor. Neither is it known whether the terrestrial habits of *Myrmecophaga* represent a derived condition from a semiarboreal ancestor. Continued field work and detailed description and analysis of new finds will be necessary in order to utilize the fossil record to understand the evolutionary history and phylogenetic relationships of these taxa, including the timing of major divergences and the acquisition of major adaptations.

Despite these problems, the historical record does suggest certain plausible evolutionary scenarios. Although there is considerable variation in size and locomotor habits (terrestrial to fully arboreal), all extant forms possess a generally uniform morphology, suggesting a strong phylogenetic constraint on the group's musculoskeletal anatomy (Taylor 1985). The presence of a prehensile tail like that of *Cyclopes* and *Tamandua* in the Santacrucian *Protamandua*, the oldest well-known described anteater, plus the fact that two of the three modern genera have arboreal adaptations, led Gaudin and Branham (1998) to infer that arboreality is likely the primitive condition for Vermilinguans. If the ancestral form was semiarboreal, like extant *Tamandua*, then its distribution was probably restricted to closed canopy forests. Therefore, the evolutionary appearance of *Myrmecophaga* may be closely tied to the development of savanna and open-country habitats in South America, and with the appearance of ground-dwelling termites and other colonial insects in these same areas. Woodland savanna was present in South America from the late Paleocene to early Miocene, but by the Eocene open savanna woodlands with abundant grasses and shrubby elements had differentiated from tropical

Table 6.1. Chronologic Distribution of Fossil Vermilingua

South American Land Mammal Age (SALMA)	Duration (MYA)	Taxa present	Time since divergence
Present		*Myrmecophaga tridactyla* *Tamandua tetradactyla* *Tamandua mexicana* *Cyclopes didactylus*	
Lujanian	0.5–0.01	*Myrmecophaga tridactyla* *Tamandua tetradactyla*	
Ensenadan	1–0.5		
	GAP		
Irvingtonian (Uquian)	3.8–1.5	*Myrmecophaga tridactyla*	
	GAP		
Chapadmalalan	4–3.8		
Montehermosan	7–4	*Myrmecophaga* (= *Nunezia*) *caroloameghinoi*	
Huayquerian	9–7	*Palaeomyrmidon incomptus* *Neotamandua greslebini* *Neotamandua conspicua*	
Chasicoan	10–9		
Mayoan	12–10		
Laventan	14.2–12	*Neotamandua borealis*	Giant anteater from collared anteater 13 (15–12) MYA
	GAP		
Colloncuran	15.5–14	*Neotamandua*? *australis*	
Friasian	16.5–15.5		
Santacrucian	17.5–16.5	*Protamandua rothi*	
	GAP		
Colhuehuapian	21–19	Undescribed taxon	
	GAP		
Deseadan	29–25		
	GAP		
Tinguiririan	36–31.5		
	GAP		Pygmy anteater from other anteaters 38 (45–35) MYA
Divisaderan	42–40		
	GAP		
Mustersan	48–45		
	GAP		
Casamayoran	54–51		Vermilingua from sloths 54 (65–51) MYA
	GAP		
Riochican	54.8–55.5		
	GAP		
Itaboraian	59–57.5		
	GAP		
Peligran	62.5–61		Cingulata and Pilosa diverge 63 (76–59) MYA
	GAP		
Tiupampan	64.5–63		

Sources: Time of divergence of major taxa based on the molecular data of Delsuc et al. (2001) and Barros et al. 2003. South American Land Mammal Age chronology based on Flynn and Swisher (1995).

rainforest (Webb 1978). Some open park savanna was present by the early–middle Miocene (Santacrucian ca. 17.5–16.5 MYA), and Webb (1978) noted that at this time anteaters (Vermilingua) were abundant, along with the myrmecophagus armadillo, *Stegotherium*, thus suggesting abundant termitaria. This slightly precedes the estimate of Delsuc et al. (2001) for the divergence of the *Tamandua* and *Myrmecophaga* lineages (table 6.1), but is suggestive that expansion of South American savanna habitat played an important role in the evolution of *Myrmecophaga*. Given the importance of colonial insects living in open savanna habitat in the diet of extant *Myrmecophaga* (Rodrigues et al. this volume), it is safe to assume its evolutionary history is closely tied to the evolution of this ecosystem in South America.

The fossil record provides little help in understanding other aspects of the evolution of *Myrmecophaga*. For example, the earliest preserved cranial material of the giant anteater already resembles the modern form, so provides no insight into how the extreme modification of the skull was achieved or how rapidly it occurred. Likewise, except for the late occurrence of *Palaeomyrmidon* in the Huayquerian, very little is known about the ancestry of *Cyclopes* and when it became an obligate arboreal form. Given the high degree of specialization in the living form, its evolution must be closely tied to the history of the Neotropical rain forest. Both *Cyclopes* and *Tamandua* have evolved prehensile tails as part of their adaptation to an arboreal habitat. This may be a primitive feature retained by these two taxa from *Protamandua* but secondarily lost in the terrestrial *Myrmecophaga*, or, given their early divergence, it is possible this feature was independently acquired in each lineage.

An equally fruitful area of potential research is to thoroughly review the numerous Santacrucian taxa currently placed in the families Adiastaltidae and Anathitidae or as Xenarthra *incertae sedis*, although this will definitely require the discovery of additional material. In the past these taxa have been variously referred to Pholidota and Monotremata, as well as to Vermilingua. Although the sample is limited, the robustness of the preserved humeri suggest there may have existed in the Santacrucian a branch within Vermilingua that was more fossorially adapted than any other members of the group (Vizcaíno, Bargo, and Kay 2004). A better understanding of the range of morphological adaptations within Vermilingua and their evolutionary history, particularly as related to the utilization of colonial insects, can certainly enhance our ability to compare them with myrmecophagous mammals from other parts of the world, and consequently provide more insight into this fascinating example of convergent evolution.

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Appendix 6.1. Synoptic list of fossil Vermilingua

An extinct taxon is indicated by †. Institutional Abbreviations: FMNH = Field Museum of Natural History, Chicago; MACN = Museo Argentino de Ciencias Naturales, Buenos Aires; MCL = Museu de Ciências Naturais, Belo Horizonte; MLP = Museo de La Plata, La Plata; MNHN = Museo Nacional de Historia Natural, Montevideo; SDMNH = San Diego Museum of Natural History, San Diego; MPT = Museo Provincial de Tucumán, San Miguel de Tucumán; UCMP = University of California Museum of Paleontology, Berkeley; YPM = Yale Peabody Museum, New Haven; ZMUC = Zoological Museum of the University of Copenhagen, Copenhagen.

FAMILY CYCLOPEDIDAE

Cyclopes Gray 1821

Species: *Cyclopes didactyla*
No fossil record

FAMILY MYRMECOPHAGIDAE

Myrmecophaga Linneaus 1758

Species: *Myrmecophaga tridactyla* Linneaus 1758
Locality: Lapa da Escrivania #1, Lagoa Santa, Minas Gerais, Brazil
Material: ZMUC 3407 posterior part of skull, 3742 right astragalus, 3743 second phalanx digit III manus, 4681 proximal caudal, 4677 patella
Age: Pleistocene
Reference: Winge 1915

Locality: Lapa da Cerca Grande 2, Minas Gerais, Brazil
Material: ZMUC 11007 distal epiphysis left tibia, 11041 neural arch of thoracic, 11043 distal end metapodial, 3572 second phalanx digit III manus, 11042 left scaphoid
Age: Pleistocene
Reference: Winge 1915

Locality: Lapa da Escrivanía No. 5, Lagoa Santa, Minas Gerais, Brazil.
Material: Probably a single individual represented by ZMUC 5243 left femur, 5622 right third metacarpal, 5247 left second metatarsal, 5672 left tibia, 5689 proximal left humerus, 5362 distal right radius, 4245 distal right fibula, 5244 distal half left tibia, 8885/7234 left acetabulum, 12382 right ulnar, 5245 left third metacarpal, 11890 right third metatarsal, 5673 thoracic, 5361, 11889 lumbar, 5625 caudal, No # proximal right femur, 8652 diaphysis, 5246 left fourth metatarsal, 11888 head femur, 5623 second phalanx, 9743 distal end right second metacarpal, 5624 ungual; 10761 posterior skull of juvenile, 9733 left astragalus juvenile, 8858 left calcaneum, -12 distal epiphysis left humerus
Age: Pleistocene
Reference: Winge 1915

Locality: Lapa da Escrivanía No. 11, Lagoa Santa, Minas Gerais, Brazil
Material: ZMUC 7354 distal left humerus, No # proximal left ulna, 10759 midshaft right ulna, No # ungual digit III manus, 11891 proximal phalanx digit III manus, 6711 second phalanx digit III manus, 6580 distal epiphysis third metacarpal, 10762 neural arch of thoracic, 10760 proximal epiphysis radius, 12552 right third metatarsal, 12549 right fourth metatarsal, 12481 left fourth metatarsal, 12548 right fourth metacarpal, 12551 left second metacarpal, 12553 right second metacarpal
Age: Pleistocene
Reference: Winge 1915

Locality: Lapa dos Tatus, Lagoa Santa, Minas Gerais, Brazil
Material: ZMUC 9410 partial right pelvis, 9385, 9386, 9387, thoracic, 9330 caudal, 11913 thoracic neural arch, 11892 patella, 9422 right calcaneum, 2071 partial sacrum
Age: Pleistocene
Reference: Winge 1915

Locality: Lapa Vermelha No.1, Lagoa Santa, Minas Gerais, Brazil
Material: ZMUC 930 left second metacarpal, 931 second phalanx, 1916 left astragalus
Age: Pleistocene
Reference: Winge 1915

Locality: Gruta dos Brejões, Município de Morro do Chapéu, Bahia, Brazil
Material: MCL 1603 partial skeleton
Age: late Pleistocene, Lujanian
Reference: Cartelle and Leite 1989

Locality: El Golfo, Sonora, Mexico
Material: SDMNH 20323 right third metacarpal
Age: Pleistocene, Irvingtonian
Reference: Shaw and McDonald 1987

Locality: Departamento de Rocha, Costa del Río Cebollatí (Arrocera de Saglia), Uruguay
Material: MNHN-M 2573 posterior half of skull
Age: Pleistocene
Reference: Mones and Ximenez 1980

† *Neotamandua* Rovereto 1914

Species: *Neotamandua*? *australis* Scillato-Yané and Carlini 1998
Locality: Commallo, Rio Negro Province, Argentina
Material: Type = MLP 91-IX-6-5 complete right humerus, and MLP 91-IX-4-23 distal third of left humerus
Age: middle Miocene, Collocuran (originally Friasian), Collón Curá Formation
Reference: Scillato-Yané and Carlini 1998
Species: *Neotamandua conspicua* Rovereto 1914
Locality: Andalhuala, valley of Santa Maria, Catamarca Province, Argentina
Material: Type = MACN 8097 posterior part of cranium
Age: late Miocene, Huayquerian (= "Araucanense")
Reference: Rovereto 1914
Species: *Neotamandua conspicua* Rovereto 1914

Locality: Corral Quemado, Department of Belen, Catamarca Province, Argentina
Material: FMNH P14419 skull, jaws, ulna
Age: late Miocene-Pliocene, Corral Quemado Formation
Reference: Gaudin and Branham 1998, Patterson et al. 1992
Comment: Patterson et al. (1992) suggest this material is congeneric with *Myrmecophaga*, but Gaudin and Branham (1998) provisionally accept it as a separate genus.
Species: *Neotamandua greslebini* Kraglievich 1940b
Locality: Tíopunco, Tucuman Province, Argentina
Material: MACN no holotype designated and the material cannot currently be found in the collections; referred specimens proximal third of both femora, distal end left femur, body of right astragalus, left calcaneum, distal fragment (condyle and epicondyle) left humerus, proximal right ulna, distal right radius
Age: late Miocene, Huayquerian (= "Araucanense")
Reference: Kraglievich 1940b
Comment: No catalog number was given at the time the species was described and no mention of this species is available in the museum catalog; it is possible that the material listed above is the same as *Neotamandua?* MACN 2403, 2405, 2406, 2407, 2408, and *Paleomyrmidon?* MACN 2934 listed below, but it is not currently possible to confirm this.
Species: *Neotamandua borealis* Hirschfeld 1976
Locality: San Nicholas locality, Department of Huila, La Venta, Colombia
Material: Type = UCMP 39847 incomplete manus, pes, and fragmentary postcranial elements of a mature individual
Age: middle Miocene, Laventan, Honda Formation
Reference: Hirschfeld 1976
Species: *Neotamandua magna* C. Ameghino 1919
Locality: Tíopunco, Tucuman Province, Argentina
Material: Type = MPT 58 pelvis
Age: late Miocene, Huayquerian (= "Araucanense")
Reference: C. Ameghino 1919, p. 152, lam. VI
Comment: Kraglievich (1934) transferred this to his genus *Nunezia*
Species: *Neotamandua*?
Locality: Andalhuala, Catamarca Province, Argentina
Material: MACN 2403 7 fragments of bone (includes fragments of diaphysis and fragment of the olecranonean apophysis, which is left; Kraglievich indicated it as right).
Age: late Miocene, Huayquerian (= "Araucanense")
Reference: unpublished
Comment: collected by Col. J. Méndez, 1911
Species: *Neotamandua*?
Locality: Andalhuala, Catamarca Province, Argentina
Material: MACN 2405 left caput humeralis
Age: late Miocene, Huayquerian (= "Araucanense")
Reference: unpublished
Comment: collected by Col. J. Méndez, 1911
Species: *Neotamandua*?
Locality: Andalhuala, Catamarca Province, Argentina
Material: MACN 2407 left proximal femur.
Age: late Miocene, Huayquerian (= "Araucanense")
Reference: unpublished
Comment: collected by Col. J. Méndez, 1911
Species: *Neotamandua*?
Locality: Andalhuala, Catamarca Province, Argentina
Material: MACN 2408 right distal radius
Age: late Miocene, Huayquerian (= "Araucanense")
Reference: unpublished
Comment: collected by Col. J. Méndez, 1911
Species: *Neotamandua*?
Locality: Andalhuala, Catamarca Province, Argentina
Material: MACN 2406 right astragalus, incomplete
Age: late Miocene, Huayquerian (= "Araucanense")
Reference: unpublished
Comment: collected by Col. J. Méndez, 1911
Species: *Neotamandua*?
Locality: Andalhuala, Catamarca Province, Argentina
Material: MACN 2411 left calcaneum, incomplete
Age: late Miocene, Huayquerian (= "Araucanense")
Reference: unpublished
Comment: collected by Col. J. Méndez, 1911

† *Nunezia* Kraglievich 1934

Species: *Nunezia caroloameghinoi* Kraglievich 1934
Locality: Monte Hermoso, Buenos Aires Province, Argentina
Material: Type = MACN 6215 left third metacarpal
Age: late Miocene/early Pliocene, Montehermosan
Reference: Kraglievich 1934, Tonni 1974
Comment: McKenna and Bell (1997) include *Nunezia* as a junior synonym of *Myrmecophaga*

† *Palaeomyrmidon* Rovereto 1914

Species: *Palaeomyrmidon incomptus* Rovereto 1914
Locality: Andalhuala, Catamarca Province, Argentina
Material: Type = MACN 8098 nearly complete skull
Age: late Miocene, Huayquerian, "Araucano" Formation
Reference: Rovereto 1914
Species: *Palaeomyrmidon*?
Locality: Valley of Santa María, Catamarca Province, Argentina
Material: MACN 2934 left proximal tibia, and both distal portions; right proximal femur and left distal femur.
Age: late Miocene, Huayquerian (= "Araucanense")
Reference: unpublished
Comment: collected by J. Méndez, 1908.

†*Promyrmephagus* Ameghino 1904

Species: *Promyrmephagus dolichoarthrus* Ameghino 1904
Locality: Santa Cruz, Argentina
Material: Type = MLP ? right astragalus (specimen lost). Cast of the type in MACN A-4621b.
Age: early/middle Miocene, Santacrucian
Reference: Ameghino 1904, Hirschfeld 1976
Species: *Promyrmephagus euryarthrus* Ameghino 1904
Locality: Santa Cruz, Argentina
Material: Type = MACN A-11530 right astragalus
Age: early/middle Miocene, Santacrucian
Reference: Ameghino 1904, Hirschfeld 1976

† *Protamandua* Ameghino 1904

Species: *Protamandua rothi* Ameghino 1904
Locality: Santa Cruz, Argentina
Material: Type = right calcaneum (specimen lost). Cast of the type in MACN A-10901b.
Age: early/middle Miocene, Santacrucian, Santa Cruz Formation
Reference: Ameghino 1904
Comment: Hirschfeld (1976) noted that the type of *P. rothi* articulates with the type of *Promyrmephagus euryarthrus* and is not only the same taxon but probably also the same individual.
Species: *Protamandua rothi*
Locality: La Costa farm, 8 miles south of Coyle, Santa Cruz Province, Argentina
Material: FMNH P13134 partial skull with postcranial elements including calcaneum and astragalus (material currently missing)
Age: early/middle Miocene, Santacrucian, Santa Cruz Formation
Reference: Patterson et al. 1992, Gaudin and Branham 1998
Comment: collected by G. F. Sternberg, 1923
Species: *Protamandua rothi*
Locality: Güer Aike Department, 10 miles south of Coy Inlet, Santa Cruz Province, Argentina
Material: YPM-PU 15267 partial skull
Age: early/middle Miocene, Santacrucian, Santa Cruz Formation
Reference: Patterson et al. 1992, Gaudin and Branham 1998
Comment: collected by O. A. Petersen

Tamandua Gray 1825

Species: *Tamandua tetradactyla* Linneaus 1758
Locality: Toca dos Ossas, Município de Jacobina, Bahia, Brazil
Material: MCL 1604 skull, 30 vertebrae, 23 rib fragments, partial scapula, right radius, both ulnae, partial pelvis, left femur, both tibiae, ungual from digit 3 pes
Age: Pleistocene, Lujanian/Holocene
Reference: Cartelle and Leite 1989

Locality: Gruta dos Brejões, Município de Morro do Chapéu, Bahia, Brazil
Material: MCL 1602 partial skeleton
Age: Pleistocene
Reference: Cartelle and Leite 1989

Locality: Gruta do Impossível, Município de Palmeiras, Bahia, Brazil
Material: MCL 7190 partial skeleton
Age: Pleistocene
Reference: Cartelle and Leite 1989

Locality: Lapa do Bahu No. 1, Lagoa Santa, Minas Gerais, Brazil
Material: ZMUC 780 left fourth metatarsal
Age: Pleistocene
Reference: Winge 1915
Species: *Tamandua mexicana* Saussure 1860
No fossil record

Myrmecophagidae indeterminate

Locality: Santa Cruz Province, Argentina
Material: MLP 69-IX-8-8a left humerus lacking the proximal epiphysis.
Age: early/middle Miocene, Santacrucian, Santa Cruz Formation.
Reference: Vizcaíno, Bargo, et al. 2004
Comment: Lydekker (1894) attributed this specimen to the armadillo *Peltephilus* (Peltephilidae). Recently it was referred to Myrmecophagidae by Vizcaíno, Bargo, et al. 2004.

FAMILY ADIASTALTIDAE

† *Adiastaltus* Ameghino 1893

Species: *Adiastaltus habilis* Ameghino 1893
Locality: Corriguen Aike, Santa Cruz Province, Argentina
Material: Type = MACN A-7772 almost complete left humerus with the deltoid tuberosity broken, and A-7773 left ulna.
Age: early/middle Miocene, Santacrucian, Santa Cruz Formation
Reference: Ameghino 1893, 1894
Comment: collected by C. Ameghino, 1891–1892. The size and morphology of this specimen fits with the description of the type of *Adiastaltus habilis*, Ameghino 1893.

Locality: Killik Aike, Rio Gallegos, Santa Cruz Province, Argentina

Material: MACN A-5801 distal humerus
Age: early/middle Miocene, Santacrucian
Reference: Ameghino 1894, Hoffstetter 1958
Comment: collected by C. Ameghino, 1891. This specimen was mislabeled as the type of *Adiastaltus habilis*.
Species: *Adiastaltus procerus* Ameghino 1894
Locality: Monte Observación, Santa Cruz Province, Argentina
Material: Type = MACN A-7779, distal humerus
Age: early/middle Miocene, Santacrucian
Reference: Ameghino 1894
Comment: collected by C. Ameghino, 1890–1891

† *Plagiocoelus* Ameghino 1894

Species: *Plagiocoelus obliquus* Ameghino 1894
Locality: Monte Observación, Santa Cruz Province, Argentina
Material: Type = MACN A-7780, distal humerus
Age: early/middle Miocene, Santacrucian, Santa Cruz Formation
Reference: Ameghino 1894
Comment: collected by C. Ameghino, 1890–1891
Species: *Plagiocoelus*? *latus*
Locality: Monte Observación, Santa Cruz Province, Argentina
Material: MACN A-7781, distal humerus
Age: early/middle Miocene, Santacrucian, Santa Cruz Formation
Comment: collected by C. Ameghino, 1890–1891. It appears that this species was never formally described. The specimen cannot be assigned to *Plagiocoelus* and is probably not a vermilinguan.

FAMILY ANATHITIDAE

† *Anathitus* Ameghino 1894

Species: *Anathitus revelator* Ameghino 1894
Locality: Monte Observación, Santa Cruz Province, Argentina
Material: Type = MACN A-7782 distal right humerus (pathological), A-7783 lumbar (missing)
Age: early/middle Miocene, Santacrucian
Reference: Ameghino 1893, 1894
Comment: collected by C. Ameghino, 1892–1893

FAMILY MANIDAE AMEGHINO 1904, MAMMALIA *INCERTAE SEDIS* MONES 1986

† *Argyromanis*

Species: *Argyromanis patagonica* Ameghino 1904
Locality: Santa Cruz, argentina
Material: Type = MACN A-11687 left astragalus
Age: early/middle Miocene, Santacrucian
Reference: Ameghino 1904

† *Orthoarthrus* Ameghino 1904

Species: *Orthoarthrus mixtus* Ameghino 1904
Locality: Argentina
Material: Type = MLP 69-IX-5-16 left astragalus
Age: early/middle Miocene, Santacrucian
Reference: Ameghino 1904
Comment: originally described as a pangolin.

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The evolution of armored xenarthrans and a phylogeny of the glyptodonts

JUAN CARLOS FERNICOLA, SERGIO F. VIZCAÍNO, AND RICHARD A. FARIÑA

Resumen

Los xenartros con coraza (Cingulata) son uno de los grupos más característicos de los mamíferos fósiles sudamericanos desde el principio del Terciario y también son conocidos en América Central y del Norte. Considerados un grupo natural, han sido tradicionalmente divididos en armadillos (incluyendo a los extintos pampaterios) y los completamente extinguidos gliptodontes. El primer análisis cladístico reconoció una dicotomía basal, con los pampaterios, armadillos eutatinos y gliptodontes como el grupo hermano del resto de los armadillos. Un análisis más reciente, basado en caracteres craniodentales, no sustenta esta dicotomía ni la monofilia de los diferentes agrupamientos clásicos. Además, la clasificación y la filogenia tradicionales de los gliptodontes estaban basadas en el estudio de la superficie exterior de las placas óseas y del tubo caudal, al contrario que en el enfoque común para los mamíferos, en el cual los caracteres craniodentales son fuente privilegiada de información. Un reciente análisis cladístico de este destacablemente uniforme grupo monofilético, basado en 84 caracteres craniodentales, desafió la división tradicional en hasta cinco grupos a los niveles de familia o subfamilia: Propalaehoplophoridae/nae, Glyptatelinae, Hoplophoridae/nae (= Sclerocalyptidae/nae), Glyptodontidae/nae y Doedicuridae/nae. En este enfoque, se encontró una dicotomía basal de los gliptodontes, basada en cinco sinapomorfías inequívocas, con la subfamilia Propalaehoplophorinae, tradicionalmente considerada parafilética, como el grupo hermano del resto. Más aun, la monofilia de la subfamilia Sclerocalyptinae y de sus tribus no fue sustentada. Los géneros *Neosclerocalyptus*, *Plohophorus*, *Doedicurus*, *Glyptodon*, *Panochthus* y *Urotherium* conforman un grupo monofilético, con la inesperada estrecha relación de *Neosclerocalyptus* y *Panochthus* por un lado y de *Doedicurus* y *Glyptodon*, por el otro. Futuros análisis filogenéticos deberían incluir ambos tipos de información, es decir caracteres craneanos y poscraneanos. Sin embargo, la fuerte sustentación de algunos clados (como *Panochthus* + *Neosclerocalyptus*) permite sugerir que las propuestas tradicionales deben ser modificadas.

Resumo

Os xenarthros com carapaça (Cingulata) são um dos grupos mais característicos dos fósseis de mamíferos sul-americanos desde o início do Terciário e também são conhecidos na América Central e do Norte. Considerados um grupo natural, têm sido tradicionalmente divididos em tatus (incluindo os extintos pampatérios) e os completamente extintos gliptodontes. A primeira análise cladística reconheceu uma dicotomia basal, com os pampatérios, tatus eutatinos e gliptodontes como o grupo irmão do resto dos tatus. Uma análise mais recente, baseada em caracteres crânio-dentais não sustenta esta dicotomia nem a monofilia dos diferentes agrupamentos clássicos. Também, a classificação e a filogenia tradicionais dos gliptodontes estavam baseadas no estudo da superfície exterior das placas ósseas e do estojo caudal, ao contrário que no enfoque comum para os mamíferos, segundo o qual os caracteres craniodentais são fonte privilegiada de informação. Uma recente análise cladística deste muito uniforme grupo monofilético, baseada em 84 caracteres crânio-dentais, desafiou a divisão tradicional em até cinco grupos nos níveis de família ou subfamília: Propalaehoplophoridae/nae, Glyptatelinae, Hoplophoridae/nae (= Sclerocalyptidae/nae), Glyptodontidae/nae e Doedicuridae/

nae. Nesta aproximação, encontrou-se uma dicotomia basal dos gliptodontes, baseada em cinco sinapomorfias inequívocas, com a subfamília Propalaehoplophorinae, tradicionalmente considerada parafilética, como o grupo irmão do resto. Ainda mais, a monofilia da subfamília Sclerocalyptinae e de suas tribos não foi sustentada. Os gêneros *Neosclerocalyptus*, *Plohophorus*, *Doedicurus*, *Glyptodon*, *Panochthus* e *Urotherium* conformam um grupo monofilético, com a inesperada estreita relação de *Neosclerocalyptus* e *Panochthus*, por uma parte, e de *Doedicurus* e *Glyptodon*, pela outra. Futuras análises filogenéticas deveriam incluir ambos os tipos de informação, isto é, caracteres cranianos e pós-cranianos. Porém, a forte sustentação de alguns clados (como *Panochthus* + *Neosclerocalyptus*) permite sugerir que as propostas tradicionais devem ser modificadas.

Introduction

Armored xenarthrans (Cingulata) constitute one of the most characteristic groups of fossil mammals in South America, although they are also found in Central and North America. Traditionally they have been divided into two groups, informally known as armadillos and glyptodonts. The former include living and many fossil forms classified as dasypodids and pampatheres. In contrast to the modest current representation of the cingulates (8 or possibly 9 genera; Wetzel 1985; Vizcaíno 1995; Gardner 2005), the fossil record is very rich. Indeed, more than 100 genera have been described, 65 corresponding to glyptodonts (McKenna and Bell 1997). The oldest glyptodont remains, assigned to the genus *Glyptatelus*, include isolated scutes from the middle Eocene of Patagonia, Argentina (Pascual et al. 1996), while *Riostegotherium yanei*, from the middle Paleocene of São José de Itaboraí, Brazil, is not only the oldest armadillo, but also the oldest xenarthran known (Bergqvist et al. 2004).

No doubt, glyptodonts represent one of the most bizarre groups of mammals ever to have evolved. During the terminal Pleistocene, these herbivorous animals reached gigantic sizes, with forms that varied between one and two tons of body mass, yet they were still able to adopt bipedal postures to perform strenuous activities such as intraspecific fights (Fariña 1995; Fariña et al. 1998; Alexander et al. 1999). Their most remarkable anatomical features are the presence of an essentially immobile dorsal carapace, different numbers of trilobate teeth, elephantine hind-limbs, and a masticatory apparatus telescoped well below the cranium (Hoffstetter 1958; Fariña and Vizcaíno 2001).

Historical background

The first mention of a South American armored xenarthran goes back to the mid-eighteenth century. It was Thomas Falkner (1774), an English Jesuit missionary, who reported discovering a great carapace at least three meters long made up of hexagonal scutes and comparable to that of armadillos, in clear reference to what we today know as a glyptodont.

Albeit indirectly, Dámaso Antonio Larrañaga provided the first scientific description of a great armored extinct animal. This fossil material, composed of a femur, carapace fragments and a caudal tube was assigned to "*Dasypus* (*Megatherium* Cuv.)" by Larrañaga, and as such included by Cuvier (1823) in his second edition of *Recherches sur les ossements fossiles*. This subgeneric assignment was advocated because the original material of *Megatherium americanum* (a giant fossil sloth, see McDonald and De Iuliis this volume) was collected jointly with armor fragments (see Méndez Alzola 1950, and references therein). Beyond the reasons that induced Larrañaga to recognize the existence of armored megatheriids, the fact that his opinion was published in Cuvier's work (1823) led to the similar categorization of several incomplete fossils described later (e.g., Weiss 1830; Clift 1835).

In 1838, Richard Owen named the genus *Glyptodon* from material collected in Buenos Aires and shipped to London by the English Secretary Woodbine Paris. One year later, Owen revised all the references to armored megatheres and established that the big armored animals were glyptodonts, related to the armadillos, and that megatheres did not possess a carapace (Owen 1839). Also during this time, knowledge and collection of large armored mammals were increasing in the Río de la Plata region. The pioneering descriptions and functional studies by Teodoro Vilardebó and Bernardo Berro in Uruguay and Francisco P. Muñiz in Argentina, although not very well known, are of particular interest. They collected many fossil mammals, including glyptodonts (Ameghino 1889; Méndez Alzola 1950), which were sent to France during the first half of the nineteenth century. These fossils, along with material from other sources, ultimately became known to science through the extensive and definitive monograph published by Nodot (1857), who described glyptodonts

in great detail. Some years later, Burmeister (1870–1874) wrote a detailed monograph on the comparative anatomy of glyptodonts, taking a complete specimen of *Panochthus* as the main reference.

In regard to armadillos, the first record corresponds to a giant armadillo, *Chlamydotherium* (= *Pampatherium*), discovered and named by Lund (1839) in Brazil. During most of the nineteenth century, the scarce information about fossil armadillos strongly contrasts with the detailed anatomical and morphological knowledge available on glyptodonts. It is possible that this disparity was due to the greater interest in large specimens during those times. In any case, it was Florentino Ameghino (1889, 1891) who increased our knowledge of fossil armadillos considerably. Prior to Ameghino, several authors (Darwin 1839; Pictet 1853; Flower 1882; Schmidt 1887) recognized glyptodonts as ancestors of recent armadillos. This relationship was rejected by Ameghino (1884, 1889), who maintained the opposite, based on a set of morphological and evolutionary inferences. In short, arguing that the fusion of bony elements should be considered a derived characteristic, Ameghino (1889) postulated that the rigid carapace of the glyptodonts should have derived from the flexible armor of the dasypodids, and hence the inverse evolutionary relationship was proposed. At the same time, but using different characters of the dermal carapace, Ameghino (1889) presented the first phylogeny of the glyptodonts, including almost all known taxa. Despite some later anatomical descriptions (e.g., Scott 1903, 1904), this seminal work shifted the study of cingulates to phylogeny and notably influenced all genealogic and classificatory proposals during the twentieth century (Castellanos 1932; Simpson 1945; Hoffstetter 1958; Paula Couto 1979; McKenna and Bell 1997).

Cingulate lineages

Because of the unique postcranial morphology of Cingulata, these peculiar mammals were initially considered a "natural" group (Ameghino 1889; Hoffstetter 1958; Engelmann 1978, 1985). Many of these characteristics (e.g., dermal armor) were discussed recently by McDonald (2003b). In addition, Gaudin (1995, 2004a) and Gaudin and Wible (2006) have described a group of derived cranial features that identify the Cingulata. All these data, plus recent molecular studies (see Delsuc et al. 2003 and references therein) unambiguously support the monophyletic origin of Cingulata.

Traditionally, cingulates have been split into two taxonomic groups: the dasypodids, including armadillos and pampatheres, and glyptodontids (Ameghino 1889; Simpson 1945; Hoffstetter 1958; Paula Couto 1979; Scillato-Yané 1980; see figure 7.1). Engelmann (1978, 1985) was the first author to employ cladistic methodology to work out cingulate phylogeny. He examined a wide range of dasypodids, among them pampatheres, and glyptodonts, with the latter treated as a terminal taxon. Engelmann (1978, 1985) recognized a basal dichotomy of Cingulata but with a different taxonomic composition. He included pampatheres in his Glyptodonta group as the sister group to Glyptodontoidea, formed by eutatine armadillos and glyptodonts, although he recognized that the hypothesis that joins pampatheres and glyptodonts was also possible. The remaining living and extinct armadillos were included in the group Dasypoda. Recently, Gaudin and Wible (2006) reanalyzed the genealogical relationships between extant and extinct armadillos, pampatheres, and glyptodonts, with the latter represented by just the basal, Miocene genus *Propalaehoplophorus*. This cladistic analysis was based on a morphological analysis of 163 craniodental characters. Their proposed phylogenetic scheme did not support any basal dichotomy nor the monophyly of different classic clusters (e.g., eutatine and euphractine armadillos) recognized by earlier authors (Simpson 1945; Hoffstetter 1958; Paula Couto 1979; Scillato-Yané 1980; Engelmann 1978, 1985; Carlini and Scillato-Yané 1996; McKenna and Bell 1997). On the other hand, the alliance of *Dasypus* and *Stegotherium* was clearly supported, a relationship proposed by Engelmann (1978, 1985) and Patterson et al. (1989).

With respect to the sister group of glyptodonts, Gaudin and Wible (2006) found strong support for a clade formed by pampatheres and glyptodonts. This hypothesis, discarded by Engelmann (1978, 1985) and Hoffstetter (1958), had been previously outlined by Ameghino (1889), Castellanos (1937), Patterson and Pascual (1968, 1972), and Patterson et al. (1989).

The genus *Palaeopeltis* has been controversial. It is the only representative of the family Palaeopeltidae, and was considered closely related to glyptodonts by Ameghino (1895), based on scutes. Later, Kraglievich and Rivas (1951) described parts of a skull and scutes from the head shield and carapace. These authors believed that the teeth of *Palaeopeltis* agreed with the holotype of *Orophodon*, previously described as a sloth by Ameghino (1895). Thus, they relegated *Palaeopeltis* to

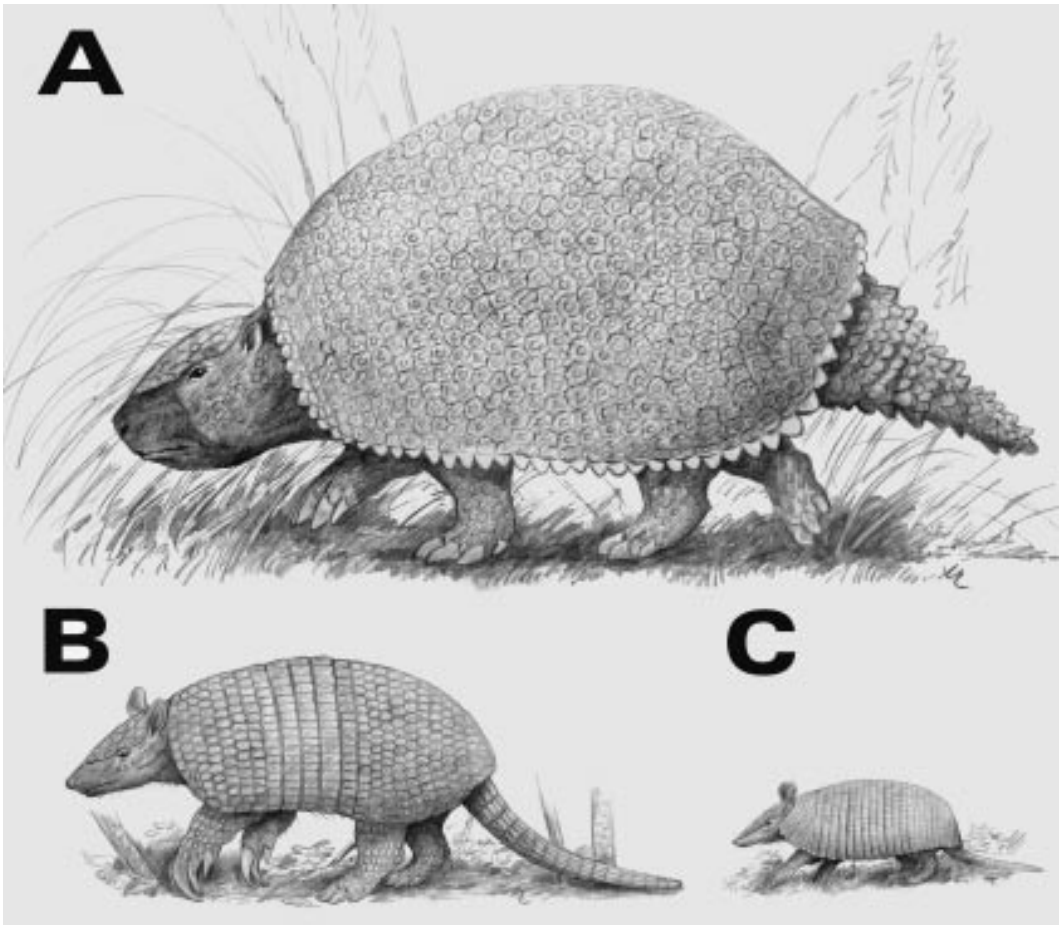

Figure 7.1. Drawing of cingulates. A. *Glyptodon*. B. Giant armadillo *Pampatherium*. C. Armadillo *Eutatus*.

synonymy and founded the superfamily Orophodontoidea, placing it in an intermediate position between dasypodids and glyptodonts within Cingulata. Later, Hoffstetter (1954, 1956) showed that *Orophodon* was a ground sloth and assigned the original scutes of *Palaeopeltis* to two ground sloths: *Orophodon* and *Octodontotherium*. He created a new genus, *Pseudorophodon*, for the specimen described by Kraglievich and Rivas (1951). Hoffstetter (1958) recognized *Pseudorophodon* as a terminal branch to the "horned" peltephiline armadillos. Patterson and Pascual (1968, 1972) discussed the problematic Palaeopeltidae and proposed that the original scutes and the specimen described by Kraglievich and Rivas (1951) corresponded to the genus *Palaeopeltis*, and that *Pseudorophodon* was its synonym. Patterson and Pascual (1968, 1972) did not support the relationship proposed by Hoffstetter (1958), and placed this group as a basal component to their pampatheres-glyptodonts dichotomy.

The Palaeopeltidae have a very poor fossil record. Until now, this group has not been considered in any cladistic analysis. However, the presence of a continuous dental series, similar to that of the "horned" armadillo *Peltephilus*, supports the opinion of Hoffstetter (1958). If this is corroborated in the future, then the relationship between Palaeopeltidae and glyptodonts should be discarded, following Gaudin and Wible's (2006) view, who placed *Peltephilus* as the sister taxon to all remaining cingulates.

Phylogeny of glyptodonts

Traditionally, the classification and phylogeny of the glyptodonts were based on study of the external surface of bony scutes and the morphology of the caudal tube. This contrasts with other mammals, where skull features have played a central role. This oversight was addressed by Fernicola (2005), who studied the craniodental morphology (n = 84 characters) of 12 genera in order to describe glyptodont phylogeny using cladistic methodology. The analyses included representatives of the following taxa: Propalaehoplophorinae (*Propalaehoplophorus* and *Eucinepeltus*), Doedicurinae (*Doedicurus*), Glyptodontinae (*Glyptodon*), and Sclero-

calyptinae with the following tribes: Sclerocalytini (*Neosclerocalyptus*, *Eosclerocalyptus*, and *Hoplophractus*), Plohophorini (*Plohophorus*, *Stromaphorus*, and *Pseudoplohophorus*), Panochthini (*Panochthus*), and Lomaphorini (*Urotherium*). In accord with Engelmann (1978, 1985) and Gaudin and Wible (2006), the genera *Pampatherium*, *Eutatus*, *Euphractus*, and *Dasypus* were included as outgroups.

Historically, glyptodonts have been considered a natural group characterized by a remarkable morphological uniformity (Engelmann 1978, 1985). This author recognized as unique characters of the group the absence of mobile transverse bands in the dorsal carapace, strongly trilobated last cheek teeth, presence of a bony groove defining the course of the optic nerve, and a very short face. These last three characteristics, together with 12 others, were identified by Fernicola (2005) as unambiguous synapomorphies that partially support the monophyly of glyptodonts. Support was only partial because Fernicola (2005) did not include representatives from all taxa of rank higher than genus in his analyses.

In the past, glyptodonts were split into at least four groups at the familial (Ameghino 1895; Castellanos 1932, 1940) or subfamilial level (Simpson 1945; Hoffstetter 1958; Paula Couto 1979; McKenna and Bell 1997): Propalaehoplophoridae/nae, Hoplophoridae/nae (= Sclerocalyptidae/nae), Glyptodontidae/nae, and Doedicuridae/nae. However, a fifth subfamily, Glyptatelinae, erected by Castellanos (1932, 1940), was also recognized by Hoffstetter (1958), Scillato-Yané (1977), Carlini et al. (1997), and McKenna and Bell (1997), while Simpson (1945) and Paula Couto (1979) included the corresponding genera in the Propalaehoplophorinae.

The taxonomy of the oldest glyptodont group, the glyptatelines, was discussed recently by Vizcaíno et al. (2003). These authors included in the glyptatelines the genera *Clypeotherium*, *Glyptatelus*, *Neoglyptatelus*, and, tentatively, *Pachyarmatherium*, a taxon previously described by Downing and White (1995) as a dasypodid. With regard to the last three taxa, some cranial elements have been described, although of doubtful taxonomic assignment. Among the elements confidently assigned to these taxa, scutes revealed a carapace without mobile bands (Vizcaíno et al. 2003). Although not always set in a phylogenetic context, this character has been considered diagnostic of glyptodonts by several authors (e.g., Burmeister 1870–1874, Flower 1882, Ameghino 1889, Hoffstetter 1958, Engelmann 1978, 1985, Vizcaíno et al. 2003). The presence in *Pachyarmatherium* and *Neoglyptatelus* of free, dasypodid-like dorsal vertebrae (Carlini et al. 1997; Vizcaíno et al. 2003) contrasts with the different fusion grades observed in the vertebral column in the remaining glyptodonts (Hoffstetter 1958; Gillette and Ray 1981). This mixture of glyptodont-like and dasypodid-like characters suggests placement of the Glyptatelinae in its own taxonomic rank and a possible basal position within the glyptodonts. This hypothesis needs to be further assessed in future phylogenetic studies.

Phylogenetic relationships among the remaining glyptodont groups, as proposed by Ameghino (1889), Castellanos (1931, 1932), and Hoffstetter (1958), were tested by Fernicola (2005) and the results do not support the monophyly of the classic groups. Fernicola's (2005) study yielded three hypotheses of maximum parsimony. This was attributed to the fluctuating position of the genus *Urotherium* in the derived portion of the tree (figure 7.2). The exclusion of this taxon yielded only one hypothesis of phylogenetic relationships, which will be the basis of the following discussion. It is not the aim of this chapter to provide a comprehensive analysis, as in Fernicola (2005). Instead, the approach will involve examination of the most strongly supported groups. However, it is worth mentioning that trees consistent with the classifications of Castellanos (1932), Simpson (1945), Hoffstetter (1958), and Paula Couto (1979) were as much as 23 to 25 steps longer than the most parsimonious tree of Fernicola (2005).

Within the glyptodonts, Fernicola (2005) proposed, for the first time, the existence of a basal dichotomy, with the subfamily Propalaehoplophorinae positioned as the sister group of the remaining glyptodonts (figure 7.2). This contradicts the traditional paraphyly of the group proposed by, among others, Ameghino (1889), Castellanos (1931, 1932), and Hoffstetter (1958). These authors concurred, although with slight differences, in deriving the different groups of glyptodonts from different genera of Propalaehoplophorinae. In Fernicola's analysis, five unequivocal synapomorphies support Clade A (figure 7.2). Within this, four genera, included by Hoffstetter (1958) in the tribes Sclerocalyptini and Plohophorini, were positioned basally. The successive arrangements that define the positions of these genera (*Stromaphorus*, *Hoplophractus*, *Eosclerocalyptus*, and *Pseudoplohophorus*) were weakly supported. However, the monophyly of the two tribes, as well as that of the subfamily Sclerocalyptinae, was contradicted by the allocation of the genera, as was the derived position of the Sclerocalyptini *Neosclerocalyptus* and Plohophorini

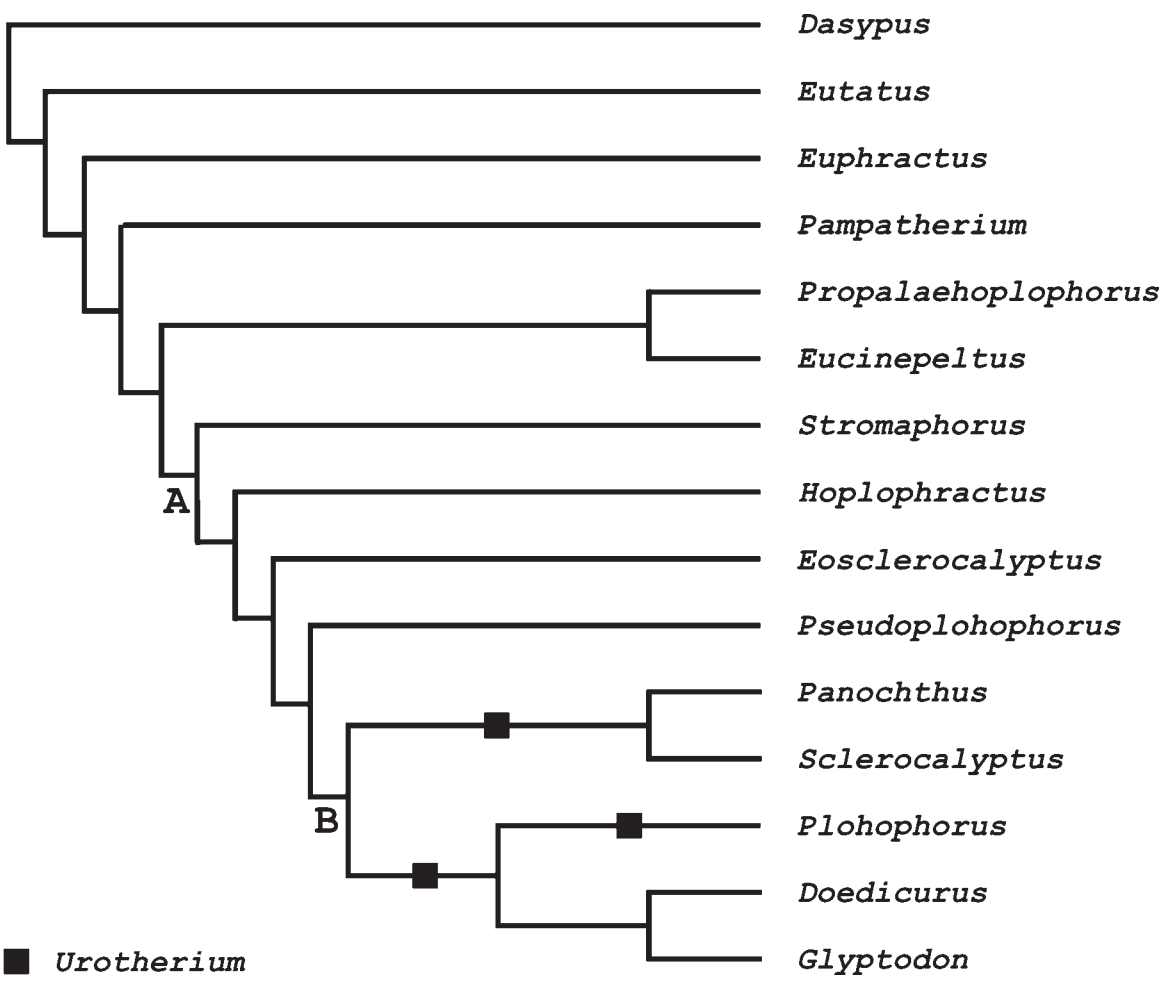

Figure 7.2. Phylogenetic relationships of glyptodonts (modified from Fernicola 2005). Possible allocations of the genus *Urotherium* in solid squares.

Plohophorus. These last two genera, together with *Doedicurus*, *Glyptodon*, *Panochthus* and *Urotherium*, formed a monophyletic group. Within this nameless group (Clade B), none of the recovered groupings had been proposed previously. In particular, the close relationship between *Panochthus* and *Neosclerocalyptus* was quite unexpected. Clade B had the strongest support in the analysis, with 6 unequivocal synapomorphies.

Ameghino (1889) viewed panochthines and doedicurines as independently derived groups of plohophorines. Castellanos (1931, 1932, 1940) and Simpson (1945) partially supported this hypothesis, putting doedicurines and panochthines in the family/subfamily Doedicuridae/nae, while the plohophorines were positioned in the family/subfamily Hoplophoridae/nae. Hoffstetter (1958) and Paula Couto (1979) included panochthines in Hoplophoridae/nae, relating them to the plohophorines, while putting doedicurines in a separate subfamily.

The relationship between plohophorines and doedicurines as originally proposed by Ameghino (1889) was partially recovered in Fernicola (2005) in that the genus *Plohophorus* was identified as the sister taxon of the clade formed by *Glyptodon* and *Doedicurus*. However, a clade of *Glyptodon* and *Doedicurus* had not been proposed previously because the Glyptodontinae/dae was always interpreted as a group with several primitive characters (e.g., absence of a caudal tube) and as such derived directly from the Propalaehoplophoridae/nae.

Discussion and conclusions

For many years after the remarkable phylogenetic synthesis of Hoffstetter (1958), the study of glyptodonts

did not include cladistic methodology. This could be explained by the fact that the taxonomy of these mammals was historically dominated by the external morphology of carapace scutes and the caudal tube. In this respect, it is interesting to carefully recall the opinion of Hoffstetter (1958: 572): "Le sectionnement en sous-familles et en tribus est plus délicat. Beaucoup de formes sont très imparfaitement connues, certaines par une seule plaque. Dans ces conditions, il est illusoire d'essayer d'établir des relations phylétiques et des divisions naturelles . . ."

The first phylogenetic study using a cladistic methodology, and carried out at the generic level, was that of Fernicola (2005). This author questioned virtually all the previously proposed clusters. As described above, he found monophyletic groups previously considered paraphyletic (e.g., Propalaehoplophorinae), while others, formerly considered monophyletic, were solved otherwise (e.g., Sclerocalyptini, Plohophorini). Recent studies (Gaudin and Wible 2006) have reinforced the monophyly of the clade pampatheres + glyptodonts, a hypothesis clearly influenced by Ameghino's ideas. Fernicola's study showed partial, but strong, support for the monophyly of glyptodonts.

The scarce and dubious cranial record of the Glyptatelinae prevented them from being phylogenetically assessed by Fernicola (2005). In this chapter, we consider them as glyptodonts because of their immobile armor, but the presence of free dorsal vertebrae, as in dasypodids, may indicate a basal position within glyptodonts. However, at present it is not possible to rule out a closer relationship with the dasypodids.

It is worth pointing out that, just as demonstrated by Fernicola (2005) for the glyptodonts, the results obtained by Gaudin and Wible (2006) for the dasypodids show a marked discrepancy between postcranial and cranial data. Because of this, future phylogenetic analyses should include both sources of characters. Even so, the data presented in this chapter, and in particular the strong support for some clades (e.g., *Panochthus* + *Neosclerocalyptus*), suggests that traditional phylogenies should be reconsidered (Fernicola 2005).

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Form, function, and paleobiology in xenarthrans

SERGIO F. VIZCAÍNO, M. SUSANA BARGO, AND RICHARD A. FARIÑA

Resumen

La historia de los estudios de la biología de los xenartros fósiles es muy rica y se inicia con la descripción del perezoso terrestre gigante *Megatherium americanum* realizada por Cuvier en 1796. Los xenartros fueron ejemplos destacados de las colecciones realizadas por Darwin y de los estudios de Owen. El grupo ya se registra en América del Sur en los comienzos del Terciario, en sedimentos del Paleoceno, es decir, alrededor de 55 millones de años antes del presente, convirtiéndose luego en uno de los elementos más abundantes y característicos de las faunas fósiles de ese continente y llegando a América Central y del Norte a partir del Pleistoceno y hasta la actualidad. El registro fósil muestra una gran diversidad morfológica, mucho más acusada que en la actualidad, que incluye mamíferos de tamaño corporal gigantesco y con rasgos muy peculiares, especialmente los de la megafauna del Pleistoceno de América del Sur. Debido a su morfología tan peculiar y a la falta de análogos modernos, los xenartros fósiles han incentivado una serie de estudios paleobiológicos y propuestas novedosas. En este capítulo se resume cómo se ha estimado el tamaño corporal en xenartros fósiles, mediante el uso de modelos a escala y geométricos generados por computadora, así como a través de ecuaciones alométricas. Algunos estudios biomecánicos contribuyeron a la interpretación de la capacidad de soportar flexiones de los huesos de los miembros de los gliptodontes, la velocidad de extensión del antebrazo en *Megatherium*, el bipedalismo o las habilidades cavadoras de otros perezosos terrestres. El aparato bucal ha sido estudiado en una amplia variedad de xenartros y ha permitido comprender diversas posibilidades adaptativas en cingulados y tardígrados (incluyendo carnivoría, mirmecofagia, necrofagia, alimentación selectiva o al bulto en herbívoros y omnivoría). Las investigaciones sobre la relación entre el área de la superficie oclusal dentaria (OSA) y el tamaño corporal ha proporcionado interesantes resultados sobre la dieta y metabolismo; los perezosos milodóntidos tienen OSAs mucho menores que las esperadas para animales de su tamaño, lo que indica bajos metabolismos, mientras que *Megatherium* tiene una OSA aún mayor que la predecible indicando mayor capacidad de procesamiento del alimento en la cavidad oral, baja capacidad de fermentación intestinal y/o mayores requerimientos metabólico. Con respecto a las interpretaciones paleoecológicas de las faunas de América del Sur, han sido abordadas desde varios aspectos, incluyendo los hábitos alimenticios, locomotores y relaciones tróficas. Este último estudio propuso la novedosa hipótesis de que algunos xenartros, previamente considerados herbívoros estrictos, podrían haber tenido una dieta más amplia, lo que despertó un interés renovado hacia otros aspectos ecológicos, como la partición de nichos durante el Pleistoceno, reinterpretaciones de la sistemática de algunos Carnivora sudamericanos y otras más.

Resumo

A biologia dos xenartros fósseis mostra uma rica história, começando pela descrição da preguiça gigante *Megatherium americanum* por Cuvier, em 1796. Os xenartros foram exemplos proeminentes nas coleções de Darwin e nos estudos de Owen. Os xenartros aparecem na América do Sul no começo do Terciário, em sedimentos do Paleoceno, isto é, cerca de 55 milhões de anos antes do presente e se tornaram membros muito abun-

dantes e característicos das faunas de mamíferos neste continente, com mais de 150 gêneros, e alcançaram as Américas Central e do Norte desde o Pleistoceno e até o presente. Seu registro fóssil mostra uma maior diversidade morfológica da observada no presente incluindo mamíferos de grande tamanho corporal e características muito peculiares, especialmente na megafauna pleistocênica da América do Sul. Sendo tão peculiares e faltando os análogos modernos, os xenartros fósseis têm estimulado os enfoques paleobiológicos criativos. Neste capítulo, exploramos como o tamanho corporal tem sido estimado nos xenartros fósseis, incluindo o uso de modelos de escala e geométricos gerados por computador, e também equações alométricas. Ainda mais, os estudos biomecânicos realizados em grandes gliptodontes e preguiças terrícolas permitiram compreender a capacidade dos ossos longos das extremidades em gliptodontes de resistir forças de flexão, extensão do antebraço e velocidade em *Megatherium* e bipedalismo ou capacidade de excavar em outras preguiças terrícolas. O aparato mastigador também tem sido estimado em diversos xenartros, o que levou a entender as variadas possibilidades adaptativas nos cingulados e tardigrados (incluindo mirmecofagia, necrofagia, carnivoria, herbivoria seletiva e não-seletiva e omnivoria). Entre outros enfoques, a relação entre a área oclusal (OSA) e a dieta tem sido pesquisada com resultados interessantes sobre dieta e metabolismo; a maioria das preguiças têm OSAs menores do que o esperado, o que sugere um metabolismo baixo, ao passo que *M. americanum* tem a OSA esperada para um mamífero do seu tamanho, ou ainda maior, o que indica um maior processamento oral do alimento, menor capacidade de fermentação e/ou um maior metabolismo. Quanto às interpretações paleoecológicas, houve enfoques diferentes no estudo das faunas do Cenozóico sul-americano, incluindo hábitos alimentares, locomoção e relações tróficas. Este último tipo de estudos levou à idéia contra-intuitiva de que alguns dos xenartros que tinham sido considerados herbívoros estritos possam ter tido uma dieta mais ampla, e isto, pela sua vez, aumentou o interesse em outros tópicos ecológicos, como partição de nichos no Pleistoceno, reinterpretação da sistemática de alguns Carnivora da América do Sul e outros.

Some history

The biology of fossil xenarthrans has deservedly received the attention of many scientists since the description of the giant sloth *Megatherium americanum* by Cuvier in 1796. This species has played a significant role in the history and development of vertebrate paleontology and evolutionary science (De Iuliis et al. 2005). The first specimen was a nearly complete individual that, as usual for the period, was packaged and shipped to a European center of study. The remains, considered marvelous and aberrant, made a great impression on the scientific community. Its gigantic size and strange anatomical features defied explanation in the hands of the specialists. These extraordinary remains arrived at the Real Gabinete de Historia Natural de Madrid, where they were mounted and illustrated in a lifelike position, the first fossil skeleton to be so mounted, and illustrated by Juan Bautista Bru de Ramón (figure 8.1). His illustrations reached Cuvier, at the Muséum National d'Histoire Naturelle in Paris, who described and named the remains. Cuvier considered the giant sloth important for several reasons. One of these dealt with the idea of extinction. Using the powerful new methods of comparative anatomy, Cuvier clarified phylogenetic relationships of *Megatherium*, for it was he who realized that *M. americanum*, aberrant as it must have seemed, was a giant ground sloth and thus its closest living relatives were tree sloths. But Cuvier went further, for he was able to reconcile the odd anatomy of the gigantic beast, demonstrating that its parts contributed to a harmonious whole, in contrast to the opinions of other naturalists who viewed the anatomy of *M. americanum* as proof that it was ill adapted for life and therefore led a miserable existence. Several interesting exchanges followed and led ultimately in 1831 to a famous Academy dispute between Cuvier and Étienne Geoffroy Saint-Hilaire, primarily about their particular interpretations of animal form and the effects of function on structure (Ramírez Rozzi and Podgorny 2001).

Additional large extinct mammals from South America, including *M. americanum* and other xenarthrans, were first found by Darwin or made better known through his efforts while collecting in South America between 1832 and 1833. As usual, the specimens were sent back to England. Darwin sent them for study primarily to Richard Owen, who made magnificent descriptions and illustrations of *M. americanum* (Owen 1842, 1851, 1856) that became a model for the presentation of information on fossils. More than 150 years later, this is still the standard text on the anatomy of the giant sloth. Owen considered giant sloths terrestrial forms, barely able to climb, with their weight resting on the outer margins of the manus and pes. They were able to raise themselves on their hind limbs, using

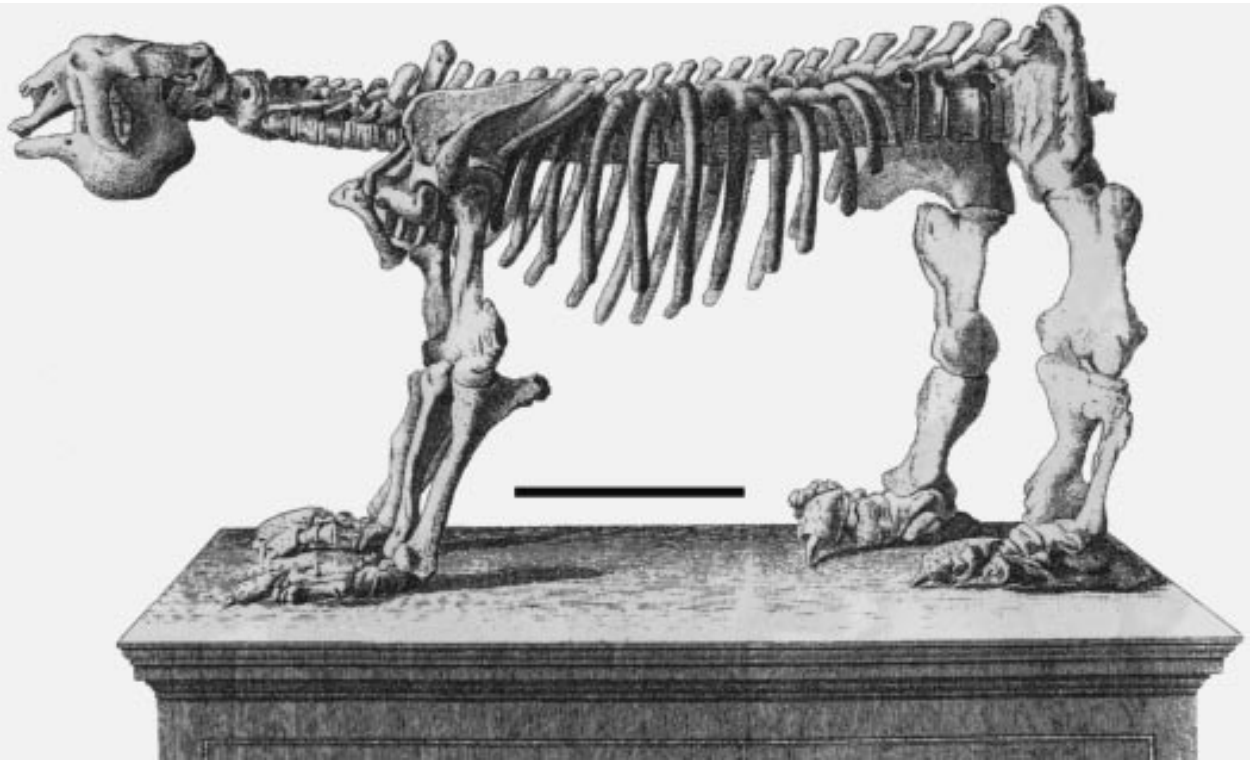

Figure 8.1. Early drawing of *Megatherium americanum* by Juan Bautista Bru de Ramón in 1793, first published by Cuvier in 1796. Modified from López Piñero and Glick 1993. Scale bar: 10 cm.

the tail as a support, so that the forelimbs were freed for other activities such as feeding on the foliage of trees. Such an image has had a profound influence on the way the habits of this species have been, and are, conceived. Indeed, the dominant reconstruction shows the great beast as an indolent herbivore that needed to bear its weight on the branch of a tree whose leaves were torn off with a long tongue. As we will see below, new studies based on functional morphology and biomechanics, joined with evidence coming from other sources, are providing us with a very different view.

Diversity of fossil xenarthrans

Xenarthra represents one of the four major clades of placental mammals (see Delsuc and Douzery this volume). The other three, Afrotheria, Euarchontoglires, and Laurasitheria, were previously believed to be a single clade, Epitheria (McKenna 1975).

As described by Vizcaíno and Loughry (this volume) xenarthrans have a long history in South America, beginning about 55 MYA during the Paleocene and becoming one of the most prominent and abundant fossils of South America. During the latest Tertiary and the Pleistocene, xenarthrans also became abundant in Central and North America. Today, there are 31 species of living xenarthrans, a diversity that cannot be regarded as very numerous. They include armadillos (Cingulata), digging mammals with a complete, flexible armor and diets ranging from omnivory to myrmecophagy (McDonough and Loughry this volume), the strictly myrmecophagous anteaters (Vermilingua), which range from fully terrestrial to fully arboreal in habits (Rodrigues et al. this volume), and the almost completely arboreal, largely folivorous tree sloths (Tardigrada, also known as Phyllophaga or Folivora; see the preface for a discussion of this nomenclatural issue; see Chiarello this volume for more discussion of sloth behavior).

On the other hand, the fossil record of the group shows a striking morphological diversity. It includes mammals of very peculiar features and great body size, particularly in the Pleistocene megafauna. Among them are large cingulates, including armadillos (Dasypodidae), pampatheres (Pampatheriidae) and glyptodonts (Glyptodontidae), and tardigrades, with four families (Mylodontidae, Megalonychidae, Nothrotheriidae, and Megatheriidae), some of them with body masses greater than a ton (see below).

Reconstructing paleobiology: form and function in xenarthrans

Paleobiologists are interested in reconstructing the external form of fossils as living animals and describing their habitat, ecological role, behavior, and basic biology. As direct observation of behavior or the measurement of physiological variables is impossible in extinct species, a different way of inferring habits must be devised. One important tool is the principle of actualism, according to which past events are surmised by analogy with currently observable processes. Mammals are very diverse in present times and most of them have fossil forms. Reciprocally, most fossil mammals can be assigned to extant orders. Perhaps this is the reason paleomammalogists have applied actualism with a more restrictive criterion than other vertebrate paleontologists, by assuming that fossil species had similar habits to their current relatives.

However, this methodology is of little use when phylogenetic affinity is not very close or fossil lineages possess morphologies not represented in extant species (Vizcaíno, Fariña et al. 2004a). Organisms reflect a duality between adaptation to environmental requirements and an inherited tendency to remain constant, that is, the historical contingency of evolutionary constraint. Therefore, if a lineage develops a phenotype that is adapted to a certain environmental condition, its species will not necessarily be identical to the current models. This circumstance is particularly applicable to those mammalian faunas that evolved in isolation in South America during a good part of the Tertiary. For instance, xenarthrans show important dental, skeletal, and muscular peculiarities that make them differ greatly from other mammals (Vizcaíno and De Iuliis 2003, and references therein).

In vertebrate paleontology, the main sources of information are fossilized bones and teeth. Therefore, even though indirect evidence can be used (ichnites or fossil tracks, taphonomic data, etc.), the majority of the paleobiological information comes from these data. Thus, the "form-function correlation approach" (Radinsky 1987) applies. According to this principle, function can be inferred from form. If appropriate homologies are lacking, biological analogues must be used; if biological ones are not available, then mechanical analogs can be helpful.

Although various features of skeletal anatomy, some of them very peculiar, characterize xenarthrans (McDonald 2003b) and make them ideal for studies relating form and function, some authors (Hirschfeld 1976; Webb 1985a; Mendoza et al. 2002; Vizcaíno and De Iuliis 2003) have recognized that xenarthrans have not only historical, but also functional and biomechanical constraints. For instance, the dentition (teeth are hypselodont and lack enamel, but are composed of osteodentine, a biomaterial with different structural properties) probably imposed a severe functional and biomechanical constraint in subsequent adaptations to different diets among the various clades.

Several methods can be applied to interpret form-function relationships: functional morphology, biomechanics, and ecomorphology. Functional morphology analyzes how form causes, allows, or restricts the functions an organism can perform; biomechanics studies the relationships between form and function using the principles of physics and engineering; finally, ecomorphology investigates form and function in regard to environment (Plotnick and Baumiller 2000). All of these can be complemented by other techniques, such as morphogeometrical analyses. This particular approach was developed in the early 1980s (Benson et al. 1982) and is especially useful for comparing morphologies in the context of evolutionary transformations (Chapman 1990) and has proved applicable in morphofunctional interpretations of xenarthrans (Vizcaíno and Bargo 1998; Vizcaíno et al. 1998; De Iuliis et al. 2000; Bargo 2001a,b; Vizcaíno and De Iuliis 2003).

A basic protocol in paleobiological studies implies the definition of three biological attributes that are essential for each taxon: size, diet, and usage of substratum or type of locomotion. Morphological study of the masticatory and locomotor apparatuses should permit predictions about the movements they were designed for performing. In addition, analyses of mastication are useful for formulating hypotheses about the diet of the organism, while analyses of the locomotor apparatus allow inferences about the type of locomotion or preferences in the use of substratum: runner, hopper, digger, burrower, etc. Obviously, these two aspects, added to body size, yield much relevant data for the interpretation of an organism in a paleobiological context.

Although actualism is problematic in studies of some lineages of fossil xenarthrans (e.g., ground sloths and glyptodonts, figures 8.2 and 8.3), relationships between form and function in living species are still needed. It was not until the second part of the 1990s that some authors began to apply biomechanical, morphogeometrical, and ecomorphological methods to the study of morphology in living xenarthrans as part of

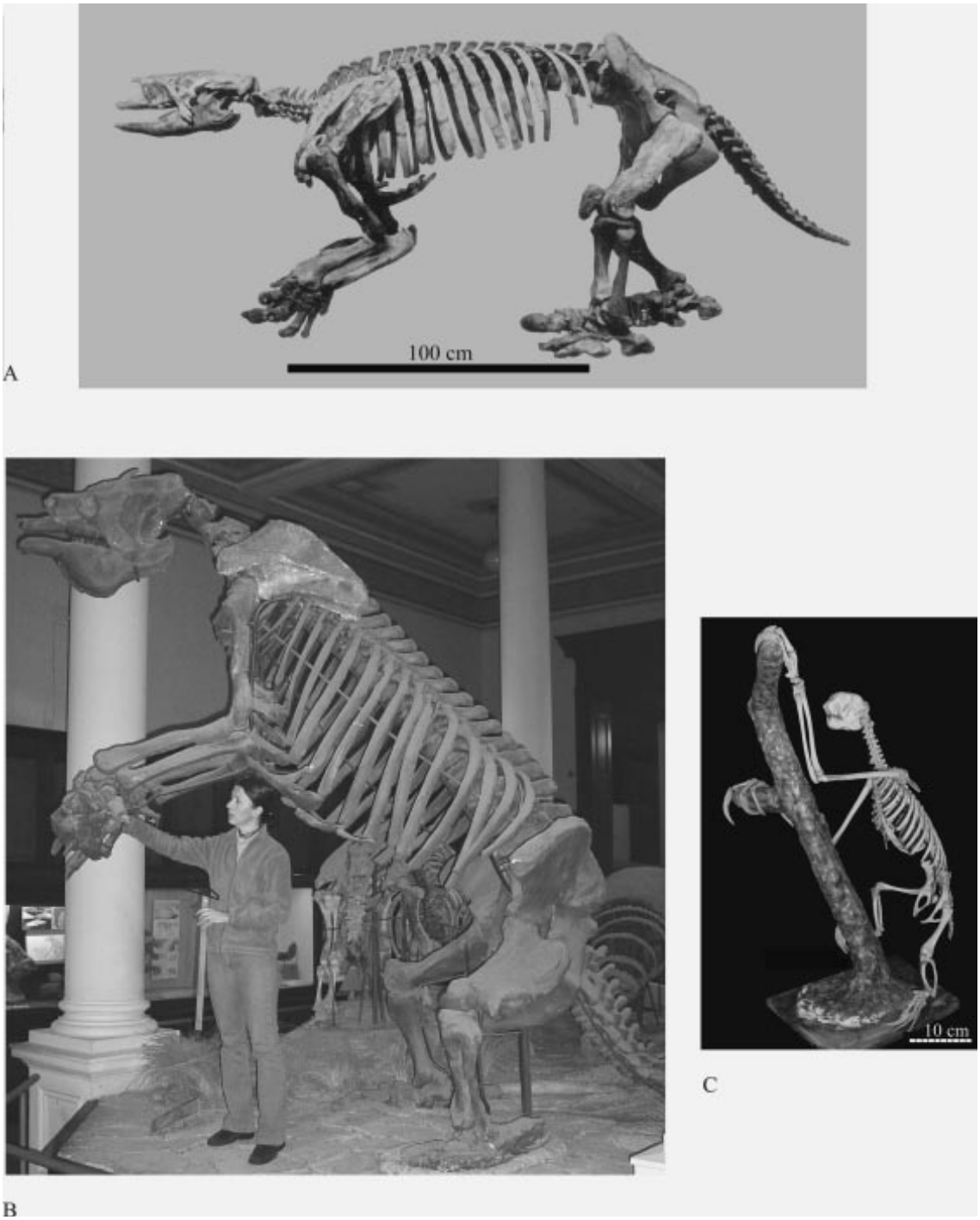

Figure 8.2. Skeletons of fossil and extant tardigrades. A. *Scelidotherium leptocephalum* (MLP 3-401) from Lydekker 1894, Pl. LVI. B. *Megatherium americanum* (MLP 27-VII-1-1) on display at the exhibition hall of Museo de La Plata. By permission of Museo de La Plata, La Plata, Argentina. C. *Bradypus tridactylus* (MACN 4412).

Table 8.1. Estimations of Body Mass (Kg) of Some Fossil Xenarthrans

Species	Estimation Technique (reference)		
	Allometric equation	Geometric model	Scale model
Glyptodon clavipes			2,000 (1)
Glyptodon reticulatus	862 (3)		
Panochthus tuberculatus	1,061 (3)		1,100 (1)
Doedicurus clavicaudatus	1,468 (3)		1,400 (1)
Sclerocalyptus ornatus			280 (1)
Glossotherium robustum	1,713 (3)	1,200 (4)	1,500 (4)
	1,376[a,b] (6)	750[b] (6)	
Lestodon armatus	3,397 (3)	3,750 (4)	4,100 (4)
Mylodon darwini	1,650[c] (6)		
Scelidotherium leptocephalum	1,057 (3)	830 (4)	850 (4)
Megatherium americanum	6,073 (3)	3,950 (5)	3,800 (2)

Sources: (1) Fariña 1995, (2) Casinos 1996, (3) Fariña et al. 1998, (4) Bargo et al. 2000, (5) Blanco and Czerwonogora 2003, (6) Christiansen and Fariña 2003.

a. Mean value of craniodental and limb measurements.

b. Values for the gracile morph of *G. robustum*, proposed to have been the female (Christiansen and Fariña 2003).

c. As mentioned in the text, craniodental measurements yield underestimates of body mass in ground sloths. This value was corrected from appropriate factors (see Christiansen and Fariña 2003 for further discussion).

a major project aimed at understanding the great paleobiological diversity of the South American extinct forms (but see Naples 1987, 1989). These results allow the development of novel interpretations of xenarthran modes of life that, coupled with paleoenvironmental data (geology, paleoclimatology, and reconstruction of paleovegetation), provide insightful information on the paleoecological context in which these animals existed. Recently Bargo (2003) provided a review of paleobiologic studies in xenarthrans. The following sections of this chapter constitute an updated summary of our knowledge, primarily on sloths and cingulates because the fossil material of vermilinguas is too limited (see McDonald et al. this volume).

Body size in fossil xenarthrans

Body size has a remarkable influence on an animal's life because it can be correlated, among other features, with metabolism, limb bone dimensions and biomechanics of locomotion, or particular solutions for food intake. Body size in living xenarthrans ranges from 100 g in the fairy armadillo (*Chlamyphorus truncatus* Harlan) to 50 or 60 kg in the giant armadillo (*Priodontes maximus* Kerr) and giant anteater (*Myrmecophaga tridactyla* Linné). Fossil forms range from about 1 kg to almost 6 tons in *M. americanum*. The oldest xenarthrans recorded during the Paleocene were relatively small armadillos similar in size to the living Patagonian pichi, *Zaedyus pichyi* (Desmarest). Like other mammalian lineages (Bargo 2004), there was a tendency to increase body size all through the Cenozoic, particularly since the late Miocene and Pliocene. Within the Pleistocene fauna, the abundance and diversity of large-sized forms (armadillos, pampatheres, glyptodonts, and ground sloths) represent a fertile soil for biomechanical studies.

This section is a brief overview of the approaches used in estimating body size in xenarthrans. The results obtained are then related to the remarkable adaptations of the locomotor and masticatory apparatuses, as well as to the paleoecology of xenarthrans. These issues will be explored in the following sections, where a complex, interrelated landscape of conclusions will be drawn.

Three different methods have been used to estimate body mass in fossil xenarthrans: scale and computer-generated (geometric) models, and allometric equations (table 8.1). Scale models were applied by Fariña (1995) in some large Pleistocene species of Glyptodontidae and, coupled with computer-generated models, by Bargo et al. (2000) in Pleistocene mylodontid ground sloths. The same geometric model was used by Blanco and Czerwonogora (2003) for assessing body mass in the Pleistocene megatheriid *M. americanum*. Casinos (1996) estimated the body mass of *M. americanum* by means of a scale model and allometric equations. Fariña et al. (1998) estimated the body masses of 7 species of xenarthrans (3 glyptodonts and 4 ground sloths) and 7 other large placental species, using a set of allometric equations previously developed from craniodental (Damuth 1990; Janis 1990) and limb bone dimensions

(Scott 1990) in modern mammals. Christiansen and Fariña (2003) also calculated body masses of three specimens of mylodontid ground sloths using a geometric model and allometric equations.

However, estimation itself is not without difficulties. For example, Fariña et al. (1998) demonstrated that dental measurements are not appropriate for xenarthrans because homologies within the group are unclear, and many xenarthrans have significantly reduced and/or homodont dentitions, producing clear underestimates of body size. Some postcranial measurements, such as femoral transverse diameter in ground sloths, had to be discarded too because they produced ridiculous overestimates of one order of magnitude. As arithmetic means yielded larger estimates, Fariña et al. (1998) suggested that this statistic should be used to estimate body size only in studies in which larger size is the conservative hypothesis.

Limbs and function

In the last decade limb proportions have been used to interpret adaptation in fossil xenarthrans. Biomechanical studies performed on large glyptodonts and ground sloths provided insight into the capacity of the limb bones to withstand bending forces, forearm extension and velocity, and bipedalism or digging abilities.

Within cingulates, Fariña (1995) analyzed limb bone strength and locomotor habits in some glyptodonts, using a strength indicator developed by Alexander (1983, 1985). The strength of a bone is obtained from its cross-sectional area and is inversely related to the bone's length and to the fraction of the weight of the animal that is supported by the corresponding pair of limbs. Hence, as a first step, Fariña estimated body masses and centers of mass, and then calculated the distribution of weight between the anterior and posterior limb pairs. The femur strength indicators of large Pleistocene glyptodonts were equivalent to those of large living mammals capable of galloping (i.e., buffalos and rhinos), but values of the humerus were similar to those of elephants, which cannot gallop. Although the anatomy of their long bones is not consistent with such activity (see figure 8.3A), the muscular insertions suggest that glyptodonts were able to adopt bipedal postures to perform strenuous activities, such as the intraspecific fights proposed by Fariña (1995). Consistent with this hypothesis, Alexander et al. (1999) estimated the energy that the tail muscles could have supplied for a blow and the energy required to fracture the carapace in a large glyptodont. They interpreted observed damage in carapaces as resulting from fights.

Studies of living armadillos provide the larger sample sizes necessary for statistical and comparative studies on the correlations between limb proportions, body size, and behavior. Fariña and Vizcaíno (1997) found that armadillos scale their humeri, ulna, and, partially, tibia like other digging mammals and their femora as generalized mammals. Efforts to identify limb variables that correlate with fossorial ability demonstrated that forelimb indices correlate well with digging habits (particularly the development of the olecranon, see figure 8.3B, Vizcaíno et al. 1999). Hindlimb indices do not, but seem more related to weight bearing (Vizcaíno and Milne 2002). These results have been applied to the study of different extinct armadillos. For example, Vizcaíno and Fariña (1997) used olecranon length as indicative of fossorial ability for the previously proposed cursorial Miocene armadillo *Peltephilus* Ameghino. All limb indices were applied to the Pleistocene form *Eutatus seguini* Gervais, which led to the conclusion that its fossorial ability was comparable to that of living euphractines (Vizcaíno et al. 2003).

White (1997) investigated the influence of a large set of morphological characters on locomotor behavior of early sloths. She found that most of the Santacrucian (early/middle Miocene) sloths were semiarboreal; the smaller forms must have been mostly climbers, while the largest were more terrestrial. This study provides useful evidence for the interpretation of adaptations in the larger Pleistocene ground sloths.

The pes of tardigrades, and particularly of Megatheriinae, is very different morphofunctionally from that of other mammals and merits distinctive terminology, including: "rotated," "pedolateral" (McDonald 1977, Webb 1989), and "traviportal" (both quadrupedal and bipedal stance with obligate slow moving habits, Toledo 1996) postures. Less attention has been paid to the manus, despite the presence of equally anomalous morphofunctional features (Tito and De Iuliis 2003). For the ground sloths, different specializations may have derived from a primitive quadruped way of locomotion in both main lineages of Pleistocene forms, megatheriids and mylodontids. The giant sloth *M. americanum* has been formally proposed as bipedal based on ichnologic and biomechanic evidence (Aramayo and Manera de Bianco 1996; Casinos 1996; Blanco and Czerwonogora 2003; see figure 8.2B). The latter includes analyses of body size, speed, Froude number, indicator

Figure 8.3. Skeletons of fossil and extant cingulates. A. *Glyptodon clavipes* (MLP 16-40) from Lydekker 1894, Pl. V; by permission of the Museo de La Plata, La Plata, Argentina. B. *Tolypeutes matacus* (MLP 1217).

of athletic ability, and bending and resistance moments of the vertebral column, as well as a complete geometric and biomechanical analysis of the footprints assigned to this species found in Pehuén-Có, Buenos Aires Province, Argentina. Bipedalism also implies that the forelimb could have been free to perform activities other than locomotion. Fariña and Blanco (1996) tested the possibility that the forearms of *M. americanum* were designed for optimizing speed rather than strength of extension, and concluded that such a trait must have been associated with a potentially aggressive use of the animal's large claws.

Tito and De Iuliis (2003) provided an analysis of the manus of the tropical ground sloth *Eremotherium laurillardi* (Lund) that lends support to the traditional view that it was normally inverted during locomotion, with weight borne mainly on the lateral margin of digit V. The manus of *E. laurillardi* was unsuited for digging for reasons intrinsic to the manus itself, as well as those associated with the structure of the forelimb,

which is different from the forelimbs of other typical digging animals. In general, the manus was a fairly rigid structure. Movement among its elements, except for the ungual phalanges, was severely restricted. Its structure and form seem ill-suited for use during locomotion, except perhaps for occasional use in uneven terrain; otherwise, we would expect only slow and awkward movement. Similarly, the forelimb was probably not used for manipulating objects, even though it is marked by adaptations allowing a high degree of pronation and supination. More likely, the forearm, capable of striking severe blows, was effective in defense. In addition to being able to resist stresses along the mediolateral plane, the form of the forelimb seems suited to securing overhead branches with the palms facing medially.

Most of the approaches mentioned above were also applied to mylodontid ground sloths. Bargo et al. (2000) analyzed limb proportions and resistance to bending forces in *Scelidotherium leptocephalum* Owen, *Glossotherium robustum* Owen and *Lestodon armatus* Gervais to infer their locomotor adaptations. Allometric equations were calculated from the long bones and used to predict linear dimensions from body mass; the strength indicator was estimated for humeri and femora. This analysis, coupled with the anatomical evidence, indicated that *S. leptocephalum* and *G. robustum* were well adapted for strenuous activities in which force was enhanced over velocity, such as digging (figure 8.2A). Based on this work, Vizcaíno et al. (2001) considered these taxa as possible builders of large Pleistocene burrows present in the Pampean region of Argentina. These tunnels, discovered over the past several decades, were interpreted as paleoburrows built by fossil mammals (Zárate et al. 1998). The diameters of the burrows (ranging from 80 to 180 cm) are consistent with the diameters of the sloths, and the tracks found on the roof and walls of the tunnels coincide with the form of the hand skeleton. Although limb proportions of *L. armatus* are comparable to those of the others, its low strength indicator suggests that its limbs were not well designed to perform such demanding activity.

Semi-aquatic habits have been proposed for some nothrotheriid ground sloths (*Thalassocnus*) from late Miocene/late Pliocene marine deposits of Peru (McDonald and Muizon 1995; Muizon and McDonald 1995). *Thalassocnus* probably entered the near shore waters (as suggested by the morphology of the femur and patella), swam by paddling of the hind limbs (according to the morphology of the femur head and tibia length), and moved the tail dorsoventrally (as inferred from the morphology of the caudal vertebrae) to help maintain a head-down feeding position.

The feeding apparatus

As mentioned above, functional morphology and biomechanics were applied to the study of feeding in a wide range of xenarthrans. Although Smith and Redford (1990) did not continue their investigations on the mechanics of the masticatory apparatus in living armadillos, several studies of fossil armadillos and ground sloths were conducted by others using modifications of their method, which involved calculating the moment arms of the masticatory musculature to infer relative bite forces and velocity (Vizcaíno and Bargo 1998; Vizcaíno et al. 1998; De Iuliis et al. 2000; Bargo 2001a,b; Vizcaíno and De Iuliis 2003).

Within cingulates, the great diversity of forms suggests a number of adaptive possibilities, ranging from specialized myrmecophagous species to carrion eaters or predators among the animal eaters; selective browsers to bulk grazers among herbivores; and some omnivores as well (Vizcaíno, Fariña et al. 2004a). Whereas armadillos developed varied habits (mostly animalivorous but also including omnivores and herbivores), pampatheres and glyptodonts were herbivores (figure 8.4). Morphofunctional and biomechanical studies permitted a reevaluation of previous hypotheses based solely on comparative morphology. As a consequence, specialized carnivory in peltephiline armadillos was refuted (Vizcaíno and Fariña 1997), but corroborated in armadillos of the genus *Macroeuphractus* Ameghino (Vizcaíno and De Iuliis 2003). Plant-eating was confirmed in eutatines (Vizcaíno and Bargo 1998), pampatheres (Vizcaíno et al. 1998; De Iuliis et al. 2000) and glyptodonts (Fariña and Vizcaíno 2001), although different kinds of herbivory may have occurred in each group (Vizcaíno and Bargo 1998; Vizcaíno et al. 1998; De Iuliis et al. 2000). Vizcaíno, Fariña et al. (2004a) proposed that such morphological and adaptive diversity suggests a more extensive cladogenesis than that reflected by current systematic schemes. These analyses also revealed that some cingulates evolved mechanical solutions that are not shared by closely related taxa, and do not have current analogues that can be used as models to investigate and interpret adaptations of lineages without living representatives. For instance, the masticatory apparatus in glyptodonts underwent a telescoping process that placed it well below the cranium (Fariña 1985, 1988), creating problems in the way that stresses produced by mastication were absorbed by the

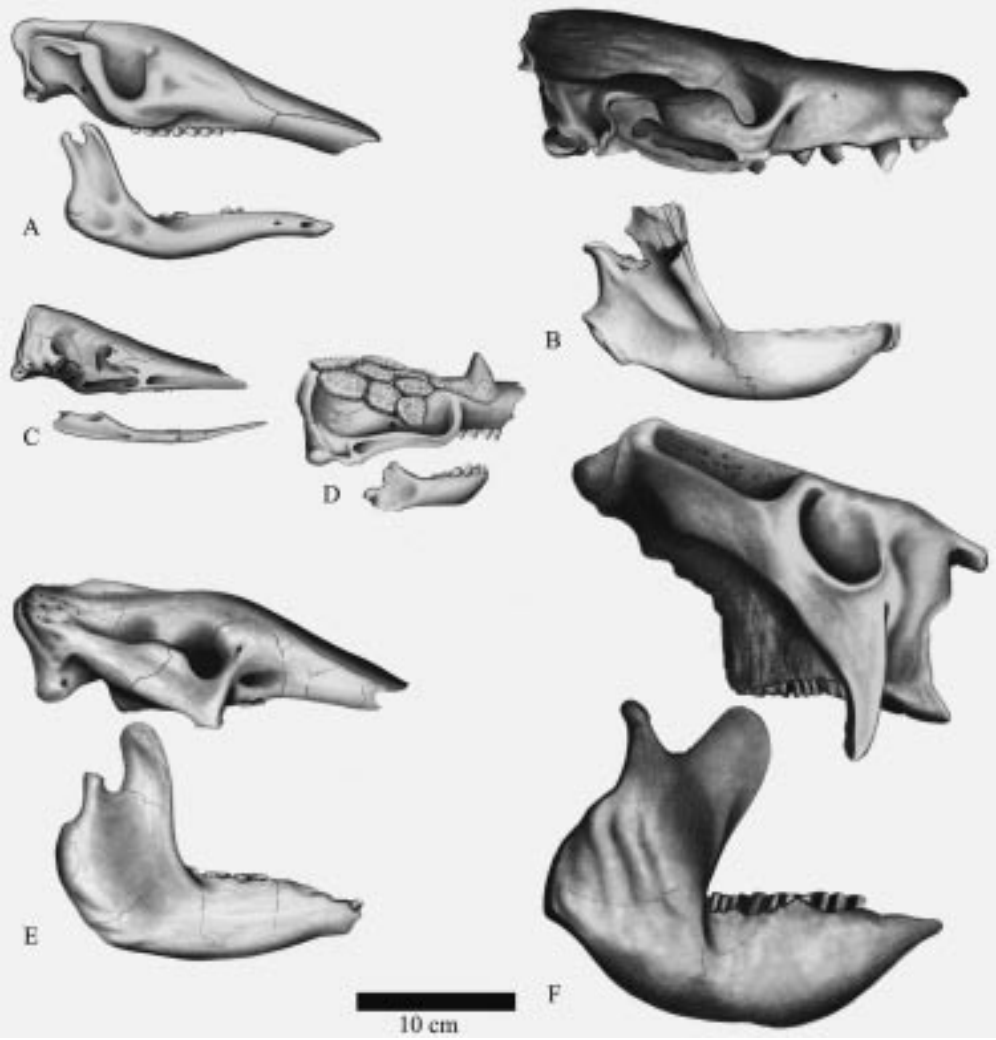

Figure 8.4. Skulls and mandibles of various cingulates. A. *Eutatus seguini* (MLP 69-VIII-1-5). B. *Macroeuphractus outesi* (MLP 69-IX-9-3). C. *Stegotherium tessellatum* (YUPM 15565). D. *Peltephilus pumilus* (MACN 7784). E. *Vassallia maxima* (FMNH P14424). F. *Doedicurus clavicaudatus* (MLP 16-24). By permission of Asociación Paleontológica Argentina, Buenos Aires. Scale bar: 10 cm.

mandible and implying unusual jaw mechanics (Fariña and Vizcaíno 2001).

Using information obtained from living sloths, Naples (1987, 1989) analyzed in detail the morphology and function of the feeding apparatus of two fossil North American ground sloths, proposing generalized anteromedially directed masticatory movements for both. Bargo (2001a,b) studied the masticatory apparatus of the large South American Pleistocene ground sloths (*G. robustum*, *L. armatus*, *Mylodon darwini* Owen, *S. leptocephalum*, and *M. americanum*) with extensive morphological, biomechanical, morphogeometrical, and ecomorphological methods (figure 8.5). Jaw mechanics, morphogeometric analyses, and the correlation between craniodental variables (hypsodonty, dental occlusal surface area, and relative width of the muzzle) and diet all suggested probable niche differentiation among ground sloths based on dietary categories. While the masticatory pattern of mylodontids is rather generalized with a clear anteromedial powerstroke, as previously proposed by Naples (1987, 1989), *M. americanum* was well adapted for strong, mainly vertical biting. This information, in addition to tooth shape, suggests that teeth were used mainly for cutting, rather than grinding, and that fibrous food was not the main dietary component.

Muizon et al. (2004b) analyzed the masticatory apparatus of the five species of aquatic sloths, *Thalassocnus*, from Peru. They showed different feeding adaptations: the three oldest species were probably partial grazers, feeding on stranded seaweeds or sea grasses or in very shallow waters, while the younger were more

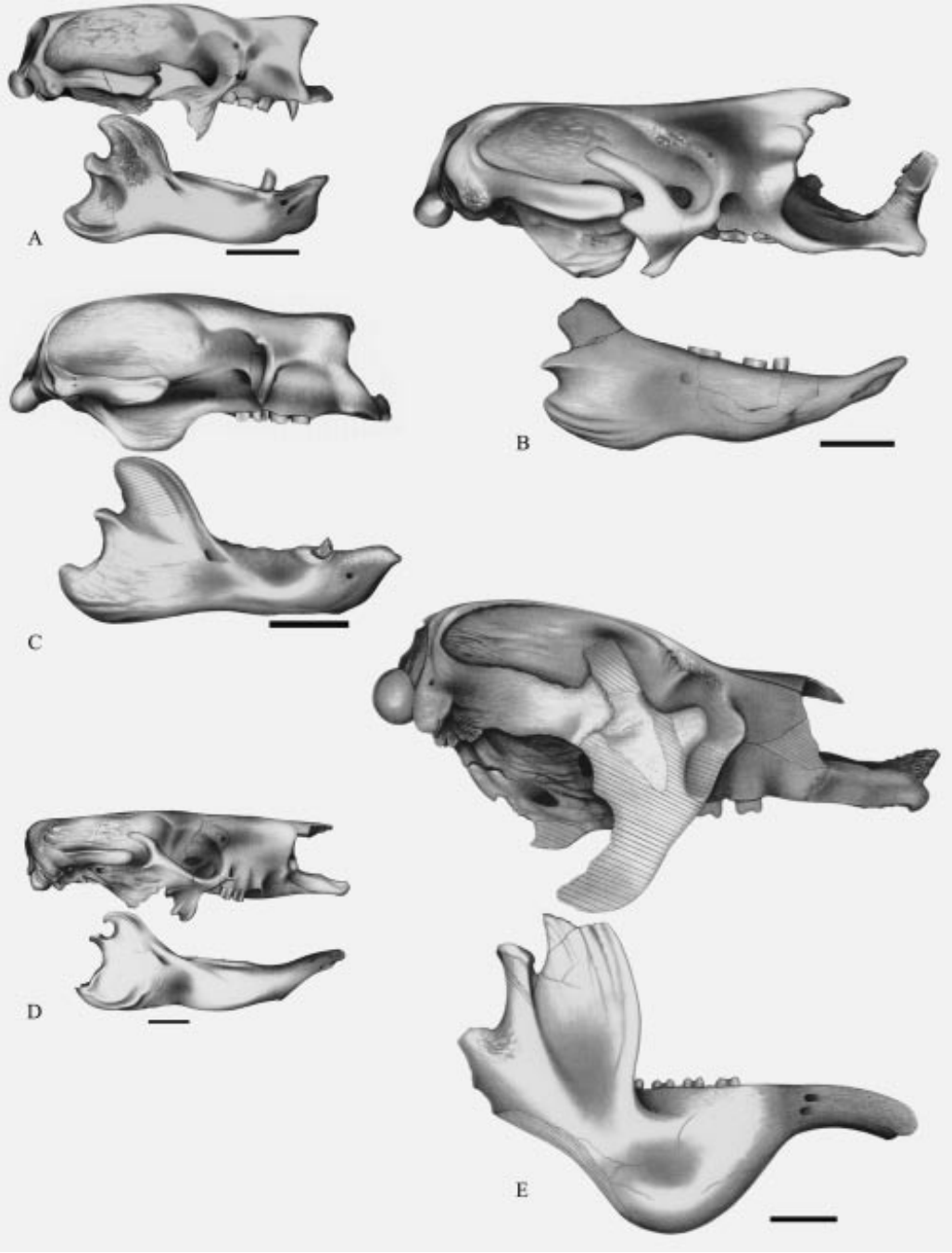

Figure 8.5. Skulls and mandibles of various tardigrades. A. *Glossotherium robustum* (MLP 3-137). B. *Mylodon darwini* (skull MLP 3-764; mandible MACN 991). C. *Lestodon armatus* (MLP 3-29). D. *Scelidotherium leptocephalum* (MMP 458-S). E. *Megatherium americanum* (MLP 2-64). Scale bar: 10 cm.

specialized grazers and probably fed exclusively in the water and at greater depth.

Some other specific traits of the feeding apparatus are also being considered. One of them is hypsodonty, the relative increase in crown height of a tooth, which has been traditionally viewed as a response to dietary shifts toward abrasive vegetation. But recent work indicates that evolution of hypsodonty is also due to the higher prevalence of grit and dust in more open environments (Janis 1988, 1995; Janis and Fortelius 1988). The teeth of sloths are both high crowned and open rooted, that is, hypselodont. A comparative analysis performed in eleven species of Pleistocene sloths by Bargo, De Iuliis, and Vizcaíno (2006) suggests that differences in hypsodonty may be explained by diet, habitat, and behavior. Among mylodontids, morphologic and biomechanical analyses indicate that hypsodonty was unlikely to be due solely to dietary preferences such as grazing. As mentioned above, some mylodontids (e.g., *S. leptocephalum*, *L. armatus*, *G. robustum*, *M. darwini*) were capable diggers that likely dug for food, and ingestion of abrasive soil particles probably played a considerable role in shaping their dental characteristics. Increased hypsodonty over time in *Paramylodon harlani* Owen in North America, however, is apparently due to a change in habitat from closed to more open environments (McDonald 1995). Geographical distributions of the megatheriids *Eremotherium* Spillmann and *Megatherium* indicate differing habitats as possible factors in hypsodonty differences. In summary, although Tardigrada hypsodonty is apparently affected by diet, habitat and behavior, as well as the absence of enamel (which must be responsible for much of the hypsodonty observed in xenarthrans), it is difficult to identify the contribution of each factor.

Fossil xenarthrans are also interesting for the different degrees of lobation in their cheek teeth. Vizcaíno et al. (2006) investigated the relationship between dental occlusal surface area (OSA) and diet, and other physiological factors in fossil xenarthrans. For most fossil xenarthrans OSA is smaller than expected compared to extant herbivorous mammals of equivalent body size. Within xenarthrans, cingulates show the highest OSA values, suggesting more extensive oral food processing than in tardigrades. Among ground sloths, mylodontids have extremely low OSA values, suggesting low efficiency in oral food processing that was probably compensated for by high fermentation in the digestive tract, and/or lower metabolic requirements. On the other hand, *M. americanum* has an OSA expected for, or even higher than, a mammal of its size, which indicates higher oral food processing, lower fermentation capacity, and/or higher metabolic requirements.

Other features besides teeth are important in reconstructing feeding preferences and behaviors. For instance, muzzle shape and facial musculature are important features to consider in relation to food intake, a problem that seems to be emphasized in sloths (Bargo, Toledo, and Vizcaíno 2006) because of the edentulous nature of the muzzle and its varied morphology. The relationship between dietary habits and shape and width of the muzzle is well documented in living herbivores, particularly in ungulates (see Janis and Ehrhardt 1988 and references therein), and has been considered an important feature for the inference of alimentary styles in fossils (Solounias et al. 1988; Solounias and Moelleken 1993a,b; Janis 1995). Bargo (2001a,b) and Bargo, Toledo, and Vizcaíno (2006) used this interesting methodological tool to develop models of food intake in five species of South American Pleistocene giant ground sloths by reconstructing the appearance and shape of the muzzle. Using features of the skull such as the areas of origin and insertion of the musculature, and the patterns of musculature in modern tree sloths and some living ungulates, they reconstructed the nasal cartilages and facial muscles involved in food intake. The preservation of the nasal septum in some fossils, and the scars for muscular attachment in the rostral part of the skulls, permit a conservative reconstruction of muzzle anatomy in fossil sloths. Ground sloths with wide muzzles (*G. robustum* and *L. armatus*; figure 8.5A,C) had a square, nonprehensile upper lip and were mostly bulk-feeders. The lips, coupled with the tongue, were used to pull out grass and herbaceous plants. Sloths with narrow muzzles (*M. darwini*, *S. leptocephalum*, and *M. americanum*; figure 8.5B,D,E) had a cone-shaped and prehensile lip and were mixed or selective feeders. The prehensile lip was used to select particular plants or plant parts.

Characteristics of the tongue may also be important for food intake and intraoral processing, a feature underlined in the aforementioned reconstructions of *Megatherium* tearing off leaves with its purported long tongue. Recently, Tito and De Iuliis (2003) proposed that *E. laurillardi* used its hands to bring overhead branches toward a powerful prehensile tongue that could strip the leaves from the branch. They also stated that it is not unreasonable to presume similar feeding

as well as locomotory habits for *Megatherium*, given the strong similarities in skeletal structures between the hands of these closely related genera.

Of course, these interpretations are based on limited samples because preservation of tongue muscle is extremely rare. However, it is possible to recover information from the hyoid complex, its bony attachment. Recently, functional studies on the hyoid apparatus have been performed in both living and fossil species of xenarthrans (Naples 1986, 1999; Pérez et al. 2000; Pérez 2001). Although fossil preservation of the hyoid complex is itself unusual, studies in progress describe some fine specimens of *Paramylodon*, *Scelidotherium*, *Glossotherium*, *Megatherium*, and *Glyptodon*.

The hyoid apparatus of *Glyptodon* shows a marked fusion of the stylo-, epi-, and ceratohyoid bones of each side into a vertical rod, which is notable also for its general robustness and large areas for muscular insertion. This modification apparently occurred in response to the migration of the masticatory apparatus below the neurocranium that occurred in the evolution of glyptodonts, as described by Fariña (1985, 1988). While other muscles are reduced, the geniohyoideus and ceratohyoideus acted antagonistically, producing powerful movements of protraction and retraction of the tongue, respectively. However, as the geni process is quite far back, the tongue would not have protruded a long distance. Hence, it would have been more important in the reworking of food in the oral cavity than in food intake.

Within Tardigrada, *Glossotherium* has mobile joints. The relationship of the hyoid bones to the skull suggests that these animals were able to make agile movements with their tongues. *Scelidotherium* is somewhat different in that the protrusion capability of the tongue is interpreted as unimportant. In *Megatherium*, the parts of the hyoid show limited ability of movement among themselves or for the positioning and stretching adopted as a whole, following modification in the height of the skull. These features indicate that the classical, pervasive image of the animal tearing off leaves and branches and driving them into its mouth with a long prehensile tongue should be reconsidered. As a matter of fact, current morphofunctional analyses contradict the notion that *Megatherium* was even capable of sticking out its tongue.

Paleoecological interpretation

As described in a recent review (Bargo 2003), studies on body size and locomotor and feeding apparatuses are among the most relevant data for the interpretation of the main aspects of the biology of a fossil mammal (paleoautoecology) and its classification in a paleoecological framework (paleosinecology).

There have been several paleoecological approaches to the study of Cenozoic South American faunas, including xenarthrans (Fariña 1996; Kay and Madden 1997; Tauber 1997; Croft 2001, Vizcaíno, Fariña et al. 2004b). Most examined body mass and feeding habits; locomotion was usually considered only qualitatively or ignored. Fariña (1996) analyzed the trophic relationships between the South American Lujanian and North American Rancholabrean (both ages being late Pleistocene/early Holocene) megamammals from the point of view of body mass, and the ecological implications of these body sizes. According to the author, the fauna contained significant diversity of large herbivores, but did not contain a proportionally diverse suite of large carnivores. In addition, he suggested that the coexistence of so many large herbivores in a poor environment led to strong competition for resources. He concluded that some of the mammals previously considered strict herbivores might have been carnivores to some degree, and proposed that ground sloths were opportunistic carrion eaters.

This challenging view promoted new lines of research. For instance, Vizcaíno (2000) briefly analyzed plant resource exploitation among sympatric Lujanian herbivorous armored xenarthrans (Cingulates). The morphofunctional and biomechanical studies discussed above revealed that the main dietary difference among these cingulates was the coarseness of the vegetation they were capable of processing. On that basis, Vizcaíno (2000) concluded that the coexistence of many herbivorous cingulates could have been sustained through differential exploitation of resources: eutatine armadillos were mainly browsers, and the larger pampatheres and glyptodonts represented increasing degrees of grazing habits. Vizcaíno (2000) has suggested that similar niche differentiation may apply to other herbivores as well. Bargo (2001a) and Bargo, Toledo, and Vizcaíno (2006) proposed a niche differentiation among Lujanian ground sloths. *G. robustum* and *L. armatus* were bulk feeders, whereas *M. darwini* was a mixed feeder. *S. leptocephalum* was a selective feeder that dug using muzzle and claws to search for food (roots and tubers)

or browsed on shrubs and grasses at ground level. *M. americanum* was probably a generalized selective feeder; that is, it fed on a mixture of leaves, shrubs, and fruits, although it may have been more selective, and capable of consuming flesh as an alternative energy source (see above). In all these analyses, in addition to diet, the use of substrate should be considered in order to provide a more complete paleoecological interpretation.

The notion that the review of hypotheses in the light of new evidence is a healthy practice in science applies to these lines of study. For instance, a recent revision of the ursids from South America proposed that during the late Pleistocene there were three species of bears (Soibelzon 2004), instead of one as proposed by Fariña (1996). These species may have acted as large scavengers, which was probably true for other carnivores such as felids and canids as well. If true, this forces reexamination of Fariña's estimates of trophic diversity, at least to a certain extent. In fact, a recent analysis of the paleoecology of the large carnivore guild from the late Pleistocene of Argentina suggests that if high herbivore biomass occurred during the Lujanian, it could have supported a higher density of carnivores (Prevosti and Vizcaíno 2006). As another example, the identification of sexual dimorphism (see Christiansen and Fariña 2003), might diminish the number of herbivore species. Finally, the proposed very low metabolism of the mylodontids (Vizcaíno et al. 2006) suggests that they were probably not as abundant nor required as much food as originally calculated.

Final remarks

Paleobiology reaches its highest degree of interest when it deals with the challenging tasks of interpreting fossil forms having unusual and bizarre morphologies (Hickman 1988), especially those that lack modern analogs. As presented in this chapter, the use of different methodological tools (biomechanics, morphogeometry, ecomorphology) allows a better understanding of the biology of the fossil xenarthrans. Indeed, through the past two centuries, fossil xenarthrans have intrigued many scientists who applied the modern points of view of the day to understand their peculiar morphology.

In recent years, xenarthran paleoecology has been based on the estimation of body size, which was rather impressive in many cases, as in the giant, elephant-sized ground sloths and in many glyptodonts whose body masses exceeded one ton. Such results have allowed the interpretation of autecological, synecological, and morphofunctional aspects of the life history of many members of the group.

Further, limb dimensions have been used to assess locomotor habits, and other biomechanical models yielded results important for inferring mastication and hence diet and metabolism. Other biological traits remain to be addressed. For instance, based on energetic considerations, Fariña (2002) concluded for *M. americanum* that the hide of this giant sloth, like that of modern mammals of similar size, must have been hairless, which represents a significant change in the appearance of the most frequent reconstructions.

These studies demonstrate that extinct xenarthrans were peculiar mammals, not only in their anatomy, but also in their diverse alimentary habits and, in some cases, even in the arrangement of their jaws and in the possible usage of the hands for food processing.

Science is, however, an endless game, and paleontology is no exception. Other kinds of evidence will appear, such as biochemical, palynological, and sedimentological. They will augment our current reconstructions and eventually modify our points of view about the behavior of this striking fossil fauna.

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Note

Abbreviations used in figures: FMNH = Field Museum of Natural History, Chicago, U.S.A., MACN = Museo Argentino de Ciencias Naturales "Bernandino Rivadavia," Buenos Aires, Argentina, MLP = Museo de La Plata, Argentina, MMP = Museo Municipal de Ciencias Naturales de Mar del Plata, Argentina, YUPM = Yale Peabody Museum, New Haven, U.S.A.