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Evidence for advanced carnivory in fossil armadillos (Mammalia: Xenarthra: Dasypodidae)

Sergio F. Vizcaíno and Gerardo De Iuliis

Abstract.—The euphractine *Macroeuphractus outesi*, from the late Pliocene Chapadmalalan SALMA of Buenos Aires Province, Argentina, is one of the largest dasypodids known. Its skull preserves features remarkable for an armadillo. Its complete dental arcade and large caniniform teeth have received attention in the literature as indicative of scavenging behavior. This report considers the degree of carnivory within the context of the generally omnivorous feeding behavior of euphractine armadillos through morphological and biomechanical analyses. Morphological analyses reveal that the main differences between *M. outesi* and other euphractines are the enlargement of the cranium, particularly of the temporal fossa; more prominent muscular scars for origin of the temporalis muscle; a more expanded rostrum, particularly in dorsoventral height; a more powerful anterior dentition, especially in the great enlargement and caniniform modification of M2; and a deeper and more robust zygomatic arch. Biomechanical analyses indicate that the moment arm of the temporalis musculature is greater than that recorded for other armadillos. These analyses indicate that the temporalis was probably larger and played a more important role in *Macroeuphractus* than in other euphractines, a pattern that is more usual for carnivorous mammals. Combined with the second upper molariform, which is caniniform, the features suggest that *Macroeuphractus* occupied an extreme position in the carnivorous-omnivorous feeding behavior of euphractines. Its large size indicates that it could have easily preyed on hare-sized vertebrates.

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Introduction

The pig-sized *Macroeuphractus outesi* Ameghino is one of the largest armadillos (Dasypodidae) known. It is known only from the late Pliocene (Chapadmalalan SALMA) of Buenos Aires Province, Argentina. Lydekker's (1894) misinterpretation of its geographic and stratigraphic provenance was corrected by Ameghino (1895; see also Scillato-Yané 1980). Although its remains are scarce, the skull and some postcranial elements preserve several remarkable features. Two other species are known for the genus: *M. retusus*, from the late Miocene–Pliocene (Huayquerian, Montehermosan, and Chapadmalalan SALMAs) includes a mandible; *M. moreni*, from the late Miocene and Pliocene (Huayquerian SALMA in northwest Argentina and probably Montehermosan SALMA in Bolivia [Castellanos 1947, 1958; Mones and Mehl 1990]) includes a skull.

Scillato-Yané (1980) placed *Macroeuphractus*

and 11 other genera in the tribe Euphractini (sensu Simpson 1945), which includes the extant *Euphractus*, *Chaetophractus*, and *Zaedyus*. Engelmann's (1985) phylogenetic analysis of the Xenarthra (Fig. 1A) united the armadillos (except the eutatines and pampatheres) in the Dasypoda on the basis of the presence of simple teeth that are oval in section, and the assumption that lobate dentition is primitive for cingulates. Within the Dasypoda he recognized the Dasypodidae, as modified from Simpson's classification (1945), and the Euphracta as sister taxa. The Euphracta coincides nearly with the Euphractini of Scillato-Yané (1980, 1986) and includes *Macroeuphractus*. Engelmann (1985) noted that this is a fairly uniform morphological group, with most of the similarities being plesiomorphic, although its members share the presence of an ossified bulla with a characteristic configuration.

In a recent analysis based on features of the exoskeleton, Carlini and Scillato-Yané (1996) proposed that, within the euphractines, *Ma-*

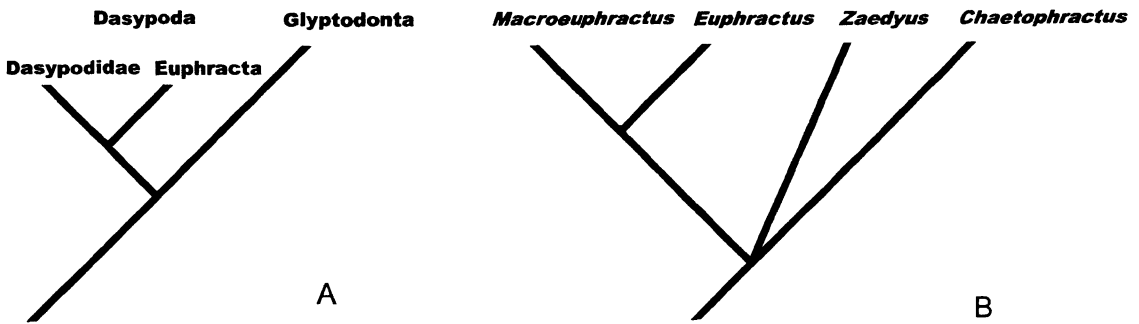


FIGURE 1. Phylogenetic relationships of *Macroeufractus* with other armored xenarthrans. A, Following Engelmann (1985). B, Following Carlini and Scillato-Yané (1996).

croeufractus is related to the *Chorobates*, *Macrochorobates*, and *Proeufractus* clade (Fig. 1B). They also stated that this group represents a radiation independent from that of the living genera and that they lived in temperate to warm environments of central and northern Argentina.

Patterson and Pascual (1972: p. 266) stated that *Macroeufractus* "is outstanding, not only for its size but for its closed dentition with incisiform and large caniniform teeth. It may have been primarily a scavenger." This hypothesis is tested here through biomechanical analysis and comparison with living relatives. Analyses were conducted on the composite masticatory apparatus composed of the skull of *M. outesi* and the dentary of *M. retusus* (Figs. 2, 3). The use of a composite is required because neither species is known from both skull and dentary. In addition, possible phylogenetic constraints imposed on the evolution of the masticatory apparatus of *Macroeufractus* are discussed.

Armadillos were common elements of South American Cenozoic faunas and among the successful wave of immigrants into North America during the Great American Biotic Interchange, the intermingling of southern and northern faunas following emergence of the Panamanian Land Bridge about 3 million

years ago. With over 100 species named (Scillato-Yané 1980), the fossil armadillos attained a much greater diversity than the living representatives (about 25 species [Wetzel 1985]). Different authors have proposed that either insectivory (e.g., Patterson and Pascual 1972; Webb 1985) or omnivory (Smith and Redford 1990) was the primitive feeding pattern of armadillos. Several clades, such as the peltephilines, eutatines, and pampatheres, have been recognized as herbivores. *Peltephilus* was traditionally considered a carnivore but was demonstrated to have been herbivorous by Vizcaíno and Fariña (1997). This leaves *Macroeufractus*, one of the largest armadillos recorded except for pampatheres, as the only probable member of the Cingulata (and possibly all armored mammals) specialized for carnivory.

Materials and Methods

Acronyms and Abbreviations (see Appendix for list of specimens studied)

FMNH: Field Museum of Natural History, Chicago, U.S.A.

MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina

MLP (DCPV): Museo de La Plata, Depart-

FIGURE 2. Skull of *Macroeufractus outesi* (MLP 69-IX-9-3) in lateral (A), dorsal (B), and occlusal (C) views (from Lydekker 1894). A larger temporal fossa is due mainly to anterior and posterodorsal expansion of the parietals and posterior expansion of the squamosal, particularly as compared with *Euphractus*. Also, the temporal lines converge much more abruptly than in other cingulates and extend into a stout, rugose, and posteriorly rising sagittal crest, whereas the cranial profile is nearly horizontal in other cingulates. The massive, robust arch is intermediate between those of *Euphractus* and pampatheres.

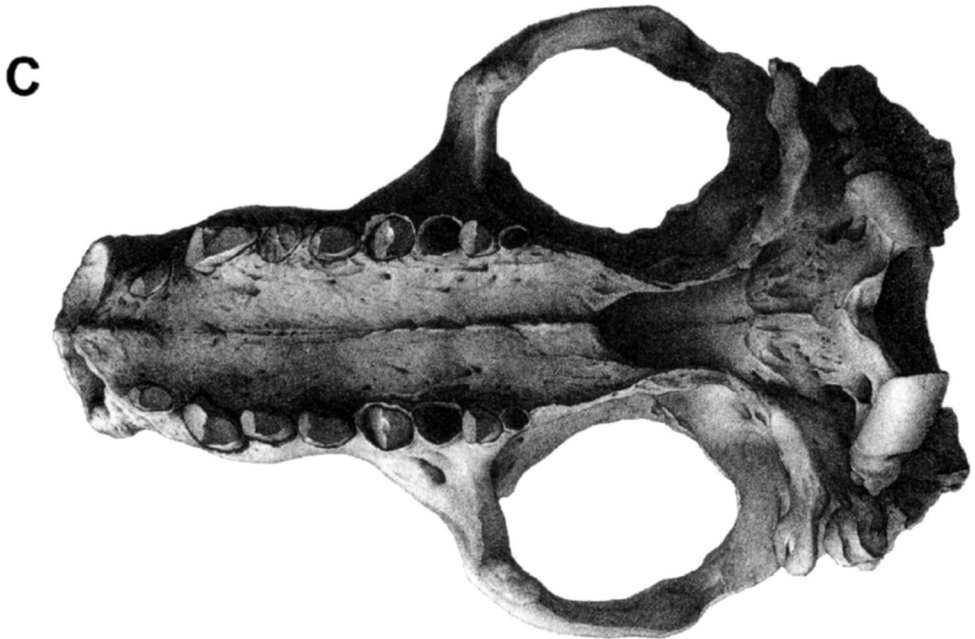




FIGURE 3. Mandible of *Macro euphractus retusus* (MLP 64-VIII-25-1) in lateral (A) and occlusal (B) views (from Lydekker 1894). The more robust dentary has nearly constant width in occlusal view, whereas in *Euphractus* it tapers anteriorly. Note also the medial bulging anteriorly to accommodate the alveolus of the caniniform in *Macro euphractus*.

mento Científico Paleontología Vertebrados, La Plata, Argentina

MLP (DCZV): Museo de La Plata, Departamento Científico Zoología Vertebrados, La Plata, Argentina

ROM: Royal Ontario Museum, Department of Palaeobiology, Toronto, Canada

D: RFTRA distance

Mm: moment arm of the masseter

Mt: moment arm of the temporalis

Mb: moment arm at the bite point

RFTRA: Resistant Fit Theta-Rho Analysis

SALMA: South American Land Mammal Age

Methods

Shape Analysis.—The skull shape of *M. outesi* is compared with that of the living euphrac-

tine *Euphractus sexcinctus* and the pampatheres *Vassallia maxima*, *Pampatherium*, and *Holmesina occidentalis* through the superposition of one form onto another using the position of landmark points. For each pair of RFTRA comparisons, *V. maxima*, *P. typum*, and *H. occidentalis* were used as base specimens. Shape was analyzed through RFTRA, which was developed to identify and measure homologous regions of change in shape by establishing congruence among those that have not changed (Benson et al. 1982; for detailed information see Chapman 1990a,b, and references therein). The software for performing RFTRA analyses was developed by Chapman in 1989. The landmarks (homologous and geometric points) used in analyses are presented in Figure 4.

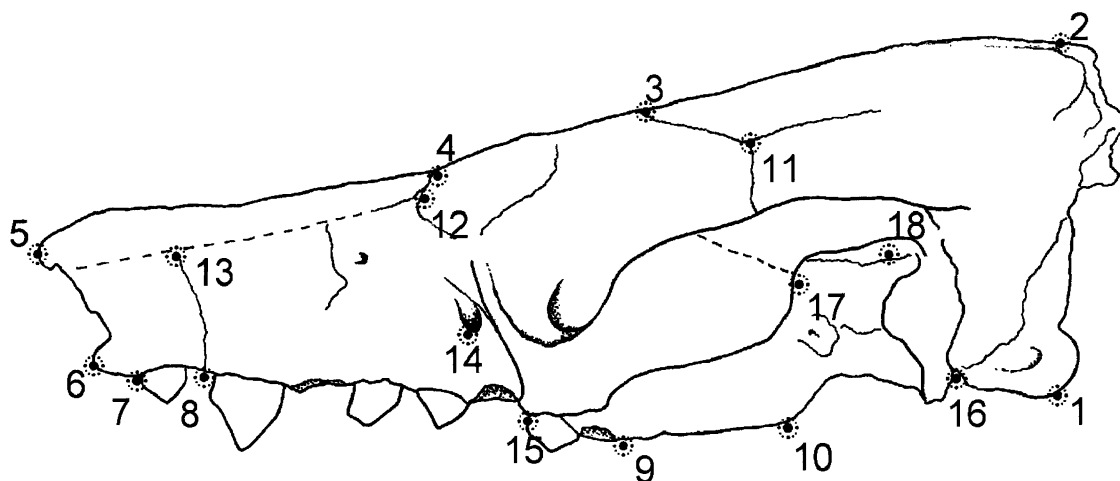


FIGURE 4. Skull of *Macroeufractus outesi* showing the landmarks used for RFTRA. 1 = ventral margin of occipital condyle; 2 = dorsal margin of sagittal crest; 3 = parietofrontal suture on the sagittal plane; 4 = nasofrontal suture on the sagittal plane; 5 = anterior end of nasal; 6 = anterior end of premaxilla; 7 = mesial margin of first molariform; 8 = premaxillomaxillary suture on the ventral margin; 9 = distal margin of last molariform; 10 = posterior end of pterygoid; 11 = squamoso = parieto-frontal suture; 12 = lacrimo-maxillo-frontal suture; 13 = naso-maxillo-premaxillary suture; 14 = infraorbital foramen; 15 = ventral-most level of zygomatic arch; 16 = ventral end of mastoid process; 17 = zygomaticosquamosal suture on the ventral margin of the arch; 18 = mandibular fossa.

Masticatory Musculature.—The areas of origin and insertion of the masticatory musculature of *M. outesi* (skull) and *M. retusus* (dentary) were reconstructed from features of the skeletal elements, following the methods of Turnbull (1976), Finch (1982), Vizcaíno et al. (1998), and De Iuliis et al. (2000), and from the patterns of musculature in modern mammals (Maynard Smith and Savage 1959; Turnbull 1970), particularly those in armadillos (Mcalister 1869; Smith and Redford 1990). The musculature reconstructed and used for analyses includes the temporalis and masseter (see Vizcaíno et al. 1998).

Jaw Mechanics.—The mandible may be considered as a lever, with a fulcrum at the temporomandibular joint. The input force is generated by the masticatory musculature and the output force is exerted by the teeth on food. The moment arms of the lines of action of the temporalis and masseter muscles are estimated so that the effective strength of each muscle and the relative bite forces may be described and compared with those of dasypodids. We followed the geometric model proposed and described by Vizcaíno et al. (1998). In this model, skull size of the different species is standardized to mandible length, following the methodology of Smith and Redford

(1990). For the masseter, the lines of action are estimated from the most anterior and posterior positions of the origin and insertion. For the temporalis they are estimated from the most anterior, middle, and most posterior origins on the skull, and from a single insertion on the coronoid process. Then, the means of the moment arms are calculated.

Once the moment arms for the temporalis and masseter have been calculated, comparisons among *Macroeufractus* and other dasypodids may proceed according Smith and Redford (1990). Interpretations of the relationships between bite force and velocity may be conducted by comparing the proportions of the combined moment arms of the masseter and temporalis to those based on different tooth positions (i.e., the central point of the anteriormost, middle, and posteriormost teeth). Mandibular movements and occlusal patterns are determined through study of the temporomandibular joint and the form and arrangement of the dentition, including occlusal wear patterns.

Results

Shape Analysis of Skull Morphology

General descriptions of the skull of *M. outesi* and the dentary of *M. retusus* have been given

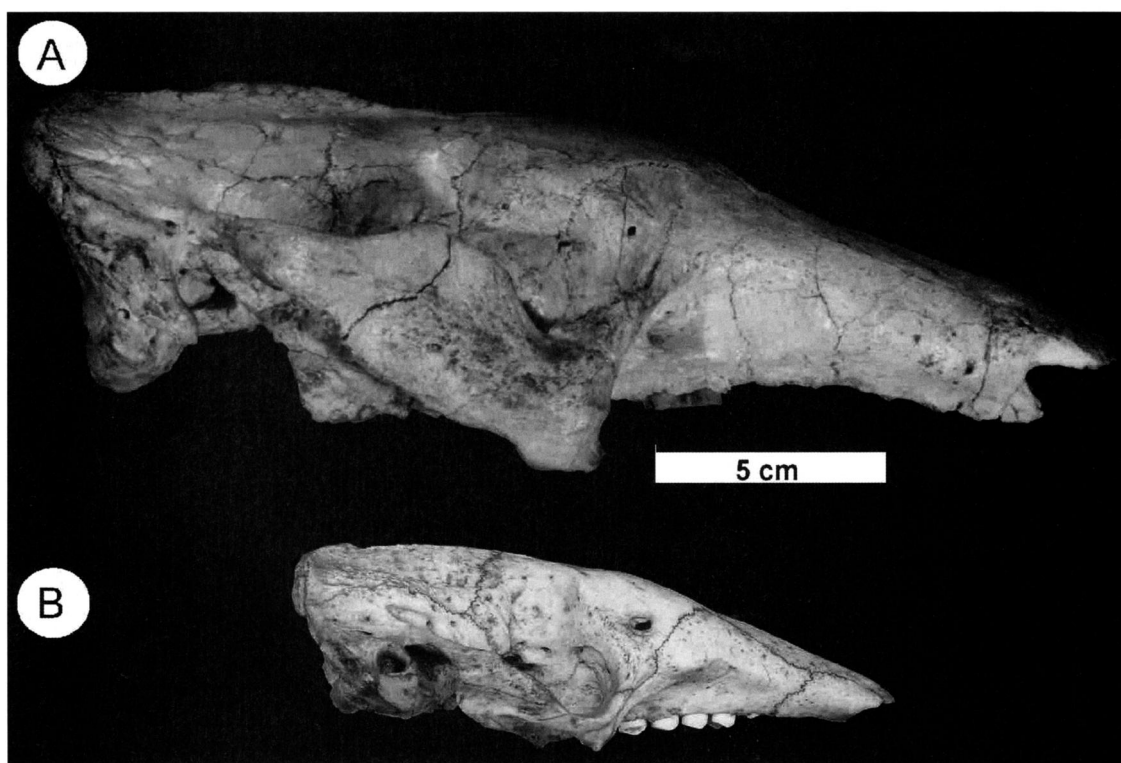


FIGURE 5. Skulls of *Vassallia maxima* (A) and *Euphractus sexcinctus* (B) in lateral view.

by Lydekker (1894). The present descriptions note only differences related to the masticatory system as compared with *Euphractus sexcinctus*, *Vassallia maxima*, *Pampatherium typum*, and *Holmesina occidentalis*. In general skull morphology, *M. outesi* strongly resembles euphractine armadillos and pampatheres (Fig. 5). RFTRA indicates approximately equal shape distances between *M. outesi* and *E. sexcinctus* and between *M. outesi* and the pampatheres (see Fig. 6). *M. outesi* is slightly larger than *V. maxima* (nuchonasal lengths = 26.4 and 25.7 cm, respectively; condylobasal lengths = 25.2 and 23.4 cm, respectively). Several morphological differences are demonstrated by the size and direction of the vectors that indicate the position of the landmarks of the target specimen in relation to the base specimen.

Macroeuphractus is more similar to the pampatheres in the wider and less narrowly tapered rostrum, but to *Euphractus* in the outline of the cranium, so that the temporal fenestrae are wide and rounded. This is due to the more

anterior position of the postorbital constriction in *Euphractus* and *Macroeuphractus*. The temporal fossa is larger in *Macroeuphractus* than in the other cingulates (Figs. 2, 5, 6). A measure of the relative space available for musculature passing through the temporal fenestrae is given by the following ratio: (Maximum Zygomatic Width – Interorbital Width)/Condylobasal Length. This ratio is 0.44 in *Macroeuphractus*, compared with only 0.36 in *Euphractus*.

Macroeuphractus and *Euphractus* differ most markedly in the degree of enlargement of the cranium, particularly in the region dorsal to the zygomatic arch. Comparison with pampatheres (e.g., *Vassallia*, Fig. 6) reveals considerable increase in size of the temporal region as well. The rostrum, particularly in the prefrontal region, is shorter in *Macroeuphractus* than in *Euphractus* (the premaxillae do not extend as far anteriorly), but the snout is clearly larger, especially in dorsoventral height (Fig. 6). The premaxilla is only slightly shorter than in pampatheres and the snout nearly as high

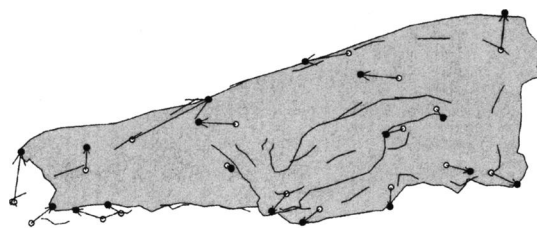
and elevated. The maxillae bulge laterally in *Macroeuphractus* compared with the other cingulates to accommodate the enlarged canini-forms (see below).

The elongated temporal fossa is more rugose and bears more prominent muscular attachment scars than in the other cingulates. Anteroventrally its margin is marked by a laterally projecting ledge that gradually expands laterally into the posterior zygomatic buttress. The ventral surface of the ledge is concave and its lateral edge is thicker and more rugose than in other cingulates. The dorsal surface of the buttress is scarred, probably for the origin of the pars zygomatica of the temporalis. In the other cingulates these structures are low, smooth, and much less prominent.

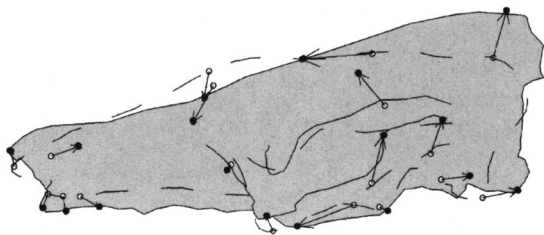
The zygomatic arches are prominently bowed and project farther laterally than in the other cingulates, resulting in wider temporal fenestrae (see Fig. 2B). The zygomatic arch is deeper and its descending process projects further ventrally in *Macroeuphractus* than that of *Euphractus*. The anteroventral protuberance is well developed, as it generally is in euphractines and pampatheres, but is not as prominent, robust, or rugose as in the latter. The wide and slightly transversely convex glenoid fossa of *Macroeuphractus* and *Euphractus* differs from that of pampatheres mainly in being more constricted by the auditory region, which slopes markedly anteroventrally to form a prominent postglenoid process.

Mandible

RFTRA was not performed on the dentary because the positions of many of the landmarks, as established for example by Vizcafno et al. (1998), De Iuliis et al. (2000), and Bargo (2001), are uncertain as the element is incomplete. The partial dentary of *M. retusus* nevertheless permits a wide range of comparisons. The anterior edge of the coronoid is similar, but wider than in *Euphractus*, and the deep, well-defined masseteric fossa is in marked contrast to the nearly flat ascending ramus of *Euphractus*. The preserved portion of the dentary is relatively less elongated compared with that of *Euphractus*, suggesting that the complete element was shorter. A hypothesized shorter dentary is supported by the



Euphractus-Macroeuphractus



Vassallia-Macroeuphractus

FIGURE 6. Results of RFTRA of the skulls. The figures show landmarks and vectors, with polygonal diagrams superimposed. Discontinuous line = base specimen; continuous line = target specimen. RFTRA indicates approximately equal shape distances between *Macroeuphractus* and *Euphractus* ($D = 0.23$) and *Macroeuphractus* and the pampatheres (D to *Vassallia maxima* = 0.24, to *Pampatherium typum* = 0.24, and to *Holmesina occidentalis* = 0.23).

presence of fewer teeth and abbreviated premaxillae in *Macroeuphractus*. Moreover, the premaxilla extends anteriorly much farther beyond the first tooth in *Euphractus*.

Dentition

The teeth in *Macroeuphractus* (8/8) and *Euphractus* (9/10) are elliptical, with their major axes oriented mesiodistally (but see below), in both. The mesial and distal surfaces are worn to produce a beveled pattern, which contrasts sharply with the flattened and generally bilobed dentition of pampatheres. The dentitions of *Macroeuphractus* and *Euphractus* differ most conspicuously in that the second upper tooth in *Macroeuphractus* is enlarged into a powerful canini-form that extends notably beyond the occlusal plane of the other teeth (Fig. 2A). In *Euphractus* the dentition is essentially functionally homogenous (Fig. 5B), with a tendency toward enlargement of the teeth in the central part of the tooth row. In *Macroeuphrac-*

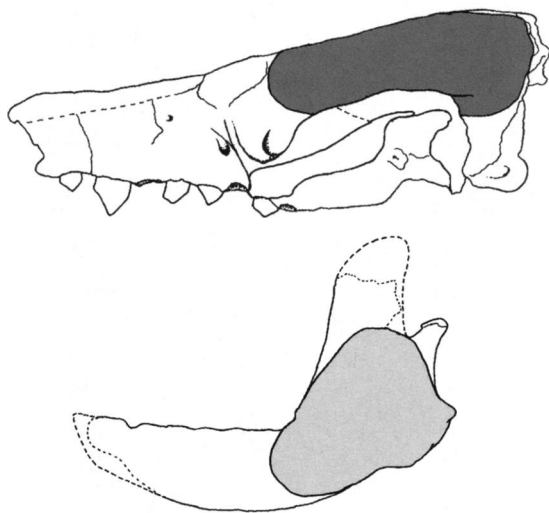


FIGURE 7. Reconstruction of areas of origin and insertion of the main masticatory muscles. Dark gray area = temporalis; light gray area = masseter.

tus the small first molariform is separated from the second by a diastema, which received the lower caniniform. The teeth distal to the caniniform (except the final two) are equally large and stout, and relatively less elongated mesiodistally. The last two teeth are markedly smaller than the preceding teeth than is the case in *Euphractus*. The wear facets are flat and the crest formed between mesial and distal facets is sharp and prominent. In *Euphractus* each facet is concave, and the crest is a much less conspicuous element, as it assumes the concave contours of the facets.

The most mesial preserved alveolus of the dentary of *M. retusus* carried the enlarged caniniform. The teeth in the central part of the tooth row were stout, apparently more so than those of the maxilla relative to *Euphractus*, in which the lower teeth are particularly elongated and delicate. The final tooth is relatively smaller than in *Euphractus*. Further, the main axes of the alveoli following that for the caniniform are obliquely oriented.

Masticatory Musculature

A reconstruction of the masticatory musculature of *Macroeuphractus* is provided in Figure 7. Comparisons of the origin and insertion sites indicates that the masticatory musculature was relatively larger in *Macroeuphractus* than in *Euphractus*. This is particularly evident

for the temporalis, which has a considerably larger origin area. Also, the relative width of the temporal fenestrae, and hence the space available for musculature, is nearly 25% greater in *Macroeuphractus* (see ratio of (Maximum Zygomatic Width – Interorbital Width)/Condylonasal Length, above). The increased prominence and strength of the temporalis in *Macroeuphractus* is supported by the presence of numerous, prominent attachment scars on the temporal fossa that suggest internal subdivision of the temporalis into at least superficial and deep layers. Such evidence is lacking for other cingulates (see Vizcaíno et al. 1998; De Iuliis et al. 2000). The origin and insertion areas suggest that the masseteric musculature was only marginally larger in *Macroeuphractus*, a condition that is also reflected by the slightly higher and more robust zygomatic arch.

Differences between *Macroeuphractus* and pampatheres are more marked. The temporalis was relatively greatly enlarged in the former, but the masseter was slightly reduced as is particularly evident from the insertion area and the less well developed and less robust zygomatic arch.

Jaw Mechanics

Moment Arms.—Before presenting results, we note several methodological assumptions. Estimation of masticatory muscle moment arms has proved to be a useful adjunct in biomechanical interpretations of the masticatory apparatus of fossil edentates (see Vizcaíno and Fariña 1997; Vizcaíno et al. 1998; De Iuliis et al. 2000; Bargo 2001). This method requires the reconstruction of the origins and insertions of the masticatory musculature. Unfortunately, the skull and mandible are not known for any one species of *Macroeuphractus*. The only dentary recovered, that of *M. retusus*, is too large for the skull of *M. moreni*, but only slightly smaller (by approximately 10%) than required to fit the skull of *M. outesi*. Thus, the current analyses were performed on a geometrically scaled and graphically reconstructed model of this dentary. Reconstruction of the coronoid process and anterior part of the horizontal ramus was based on the morphology of other fossil (*Chorobates* and *Macrocho-*

robates) and living (*Euphractus*, *Chaetophractus*, and *Zaedyus*) euphractines. The dentary was scaled so that the condyle articulated with the glenoid fossa and the lower caniniform occluded with the diastema between the upper first tooth and caniniform. The latter position was chosen because there is no space between the upper caniniform and the tooth distal to it to accommodate the lower caniniform. Because the analyses were conducted on a composite individual, we have made every attempt to explain the results obtained as conservatively as possible.

Results of the analyses of moment arms (Fig. 8) are summarized and compared in Table 1 with those of *Euphractus sexcinctus*, *Dasypus novemcinctus*, and the pampatheres. The value of M_t for *Macroeuphractus* is higher than those for *Euphractus* and the pampatheres, and much higher than that for *Dasypus*. The value of M_m is higher than that for *Euphractus*, much higher than for *Dasypus*, similar to those for *Holmesina* and *Pampatherium*, and smaller than for *Vassallia*. The ratios of the muscle moments to bite moments at the different tooth positions are the same as in *Euphractus*. They are almost twice those of *Dasypus* at the last tooth, but nearly the same at the first tooth. Compared with the pampatheres values are virtually identical for the middle and mesial-most tooth, but lower at the last tooth.

Discussion

Macroeuphractus outesi is undoubtedly the largest euphractine dasypodid and one of the largest armadillos that has ever existed. Its body mass was estimated at nearly 100 kg from both allometric equations for limb bones (Fariña and Vizcaíno 1997) and geometric

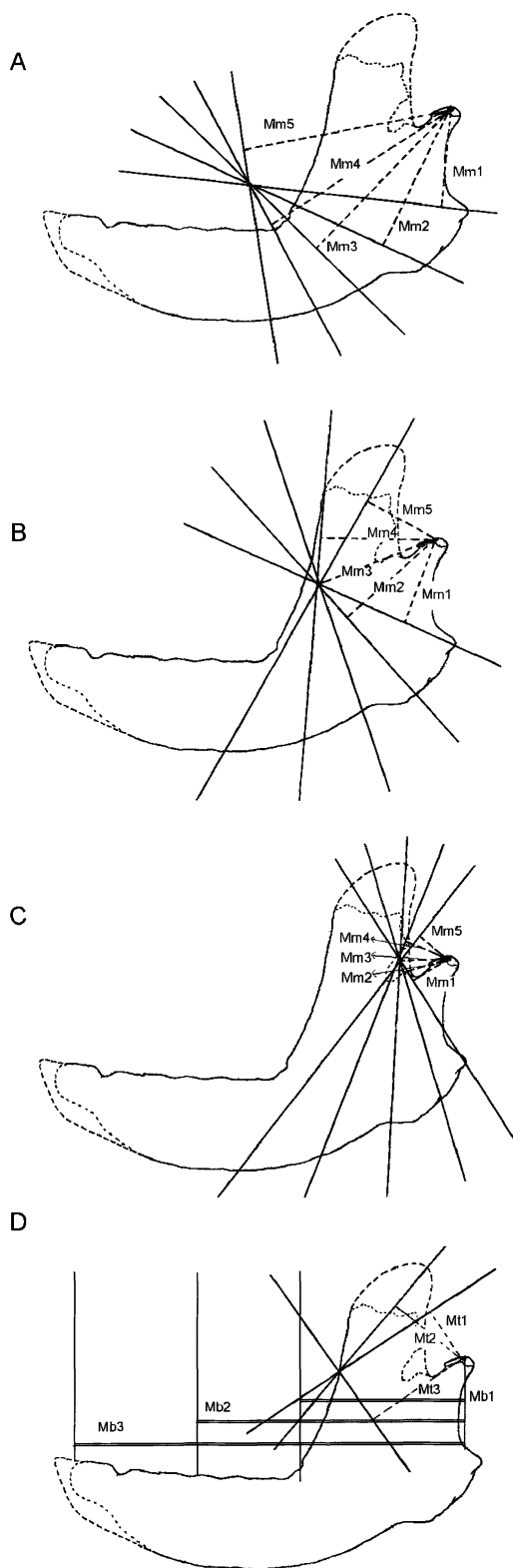


FIGURE 8. Moment arms as calculated in *Macroeuphractus*. A, From the most anterior position of the masseters origin. B, From the middle position of the masseters origin. C, From the posterior position of the masseters origin. D, Moment arms of the temporalis and the bite points. Mm_1 – Mm_5 : moment arms of the masseter; Mt_1 – Mt_3 : moment arms of the temporalis; Mb_1 – Mb_3 : moment arms of the bite points at the distal, middle, and mesial teeth respectively. Thin solid line = lines of action of the muscles; dashed line = moment arms of the masseter and temporalis; heavy solid line = moment arms of the bite point.

TABLE 1. Comparison of the moment arms of the jaw muscles and bite points in *Macroeuphractus*, living armadillos and pampatheres. Mt, moment arm of temporalis. Mm, moment arm of masseter. Mb₁, Mb₂, and Mb₃, moment arms of the bite points at the distal, middle, and mesial teeth respectively. Ratio: ratio of muscle/bite, that is, the combined moment arm of the muscles (Mm + Mt) divided by Mb₁, Mb₂, and Mb₃. P = posterior. M = middle. A = anterior. \bar{x} = mean.

	<i>Macroeuphractus</i>				<i>Euphractus</i>				<i>Vassallia</i>			
	P	M	A	\bar{x}	P	M	A	\bar{x}	P	M	A	\bar{x}
Mt	18.2	20.2	27.8	22.1	10	27	28	21.6	11	28	20	19.6
Mm	13.4	27.3	43.4	28	5.8	27	37.6	23.5	23.2	30.6	44.6	32.9
Mb ₁		38.4				35				25		
Ratio	0.8	1.8	1.9	1.3	0.4	1.5	1.9	1.3	1.4	2.3	2.5	2.1
Mb ₂		68.2				66				61		
Ratio	0.5	0.7	1	0.7	0.2	0.8	1	0.7	0.5	0.9	1	0.8
Mb ₃		97.9				96				91		
Ratio	0.3	0.5	0.7	0.5	0.2	0.6	0.5	0.5	0.3	0.6	0.7	0.5

scaling of skull measurements from living armadillos. Other very large armadillos are known within the peltephilines, eutatines, pampatheres, and dasypodines. The first two have been interpreted as being specialized herbivores (Vizcaíno and Fariña 1997; Vizcaíno and Bargo 1998). Vizcaíno et al. (1998) and De Iuliis et al. (2000) proposed that pampatheres were grazers.

Dasypodines and euphractines are well represented in modern faunas. The Dasypodini are insectivorous to omnivorous. *D. novemcinctus*, the most common living armadillo, is recognized as a generalist insectivore that also includes vertebrates and plants in its diet (Redford 1985). Wetzel (1982: p. 359) noted that "euphractines are generalists with a broad diet that includes small vertebrates, arthropods, carrion, tubers, fruit and seeds." Euphractines constitute Redford's (1985) carnivore-omnivore group, which is characterized by a diet that includes a variety of animal matter, ranging from ants and carrion to birds and mice, in combination with many types of plant material, such as roots and tubers to nuts of a low palm. Nearly 30% of the summer diet of *Chaetophractus vellerosus* consists of vertebrates (Redford 1985).

Smith and Redford (1990) stated that *Euphractus* possesses many features that reflect increased size of the masseter and pterygoid muscles and the moment arm of the masseter, adaptations that reflect greater bite forces and enhanced efficiency of transverse mandibular movements. These authors related the form of the masticatory apparatus of *Euphractus* to its

omnivorous diet (see above). Consideration of the differences between *Euphractus* and *Macroeuphractus* leads to a better understanding of the peculiarities of masticatory mechanics and diet of the latter.

Macroeuphractus is usually regarded as a euphractine, but its skull and jaws bear several distinctive features. Indeed, RFTRA analysis indicates nearly equal distances between *Macroeuphractus* and *Euphractus* and between *Macroeuphractus* and the pampatheres; and it probably reflects adaptations, albeit in different directions, for a more powerful masticatory apparatus. However, the mechanical design, including the dentition, of *Macroeuphractus* is clearly more similar to that of other euphractines (see "Results").

The main skeletal differences of *Macroeuphractus* are that the temporal fossa is enlarged, the rostrum is considerably more robust and dorsoventrally higher, and, perhaps most conspicuously, the teeth are very robust and the second teeth are enlarged into strikingly large caniniforms. The homodont molariforms of *Euphractus* are subequal in size, except for the smaller first two. They are also beveled, with lingual and buccal margins forming well-defined shearing surfaces, but the beveled surfaces meet to form a sharp peak, which may serve to pierce or puncture. Combined with the great development of the caniniforms in *Macroeuphractus* is the marked diminution of the last molariforms. These features imply that the apparatus is designed for increased effort anteriorly, where the bite tends to be faster, compared with the poste-

TABLE 1. Extended.

<i>Holmesina</i>				<i>Pampatherium</i>				<i>Dasypus</i>			
P	M	A	\bar{x}	P	M	A	\bar{x}	P	M	A	\bar{x}
6	22	24	17.3	7	18	22	15.7	10	16	14	13.3
16.8	30	38	28.3	14	26.3	40.4	27	10	17.2	22.2	16.5
		24				21				46	
0.9	2.1	2.6	1.9	1	2.1	3	2	0.4	0.7	0.8	0.6
		61				55				60	
0.3	0.8	1	0.7	0.4	0.8	1.1	0.8	0.3	0.6	0.6	0.5
		97				90				77	
0.2	0.5	0.6	0.4	0.2	0.5	0.7	0.5	0.3	0.4	0.5	0.4

rior part of the dental series, where bite tends to be stronger.

The masticatory musculatures of the cingulates considered here differ in several aspects. The temporalis in *Macroeufractus* is considerably larger and stronger than in *Euphractus* and pampatheres, and it apparently exceeded the size of the masseter (see "Results"). The masseter, on the other hand, was much larger in pampatheres than in *Euphractus* and *Macroeufractus*, and it greatly exceeded the size of the temporalis. The masseter exceeds the size of the temporalis in *Euphractus*, but not to the same degree as in pampatheres (Vizcaíno et al. 1998).

The more notable differences among the moment arms of the musculature are that although the values of Mm are larger than Mt in all the armadillos and pampatheres, they are much larger in the latter than in the former, and that Mt in *Macroeufractus* is the largest recorded for any armadillo and pampathere. The ratio of muscle moment to bite moment provides a relative measure of the effective bite force generated by the musculature at various positions along the tooth row. The ratio is approximately four times stronger at the most posterior tooth than at the most anterior tooth in pampatheres, 2.6 in the euphractines (including *Macroeufractus*) considered here (Table 1), and 1.75 in *Dasypus* (Vizcaíno et al. 1998).

Long lever arms of the muscles about the jaw joint and large ratios of muscle moment to bite moment indicate forceful rather than fast jaw movements. The masticatory apparatus of pampatheres is constructed for increased bite force at the posterior part of the tooth row, whereas the shorter lever arms of the muscu-

lature and low ratios in *Dasypus* reflect quick rather than forceful movements, which is quite appropriate for an insectivorous form. The ratio for the last tooth in *Macroeufractus* and *Euphractus* falls precisely between the values in pampatheres and *Dasypus*, suggesting a design for a more generalized feeding behavior. The temporalis probably played a more prominent role in *Macroeufractus* than in *Euphractus* and pampatheres, judging from both larger musculature and a longer moment arm, which are features characteristic of carnivorans within epithierians (Maynard Smith and Savage 1959) and carnivorous marsupials (Turnbull 1970). The advanced carnivorous mode of these mammals is also usually accompanied by skeletal adaptations for orthal jaw movements. These similarities are suggestive of, but not necessarily sufficient to indicate, a specialized carnivorous feeding habit for *Macroeufractus*, as it lacks a specialized carnassial dentition and the extreme dominance of the temporalis over the masseter typical of mammalian carnivores.

On the other hand, herbivorous ungulate epithierians, as well as pampatheres (Vizcaíno et al. 1998), are characterized by a masseter that is larger and has a longer moment arm than the temporalis (Turnbull 1970). Further, they are characterized by transverse jaw movements and a variable, though consistent, suite of dental features determined by the type of vegetation consumed.

Macroeufractus possessed a unique suite of features. In large part, these features are strongly characteristic of euphractines, to which *Macroeufractus* is closely related phylogenetically. However, some features tend to converge toward those typical of mammalian

carnivores. The behavioral significance of such a combination must be considered in terms of both functional morphology and phylogeny.

To the degree that *Macroeuphractus* resembled euphractines, there is no reason to suspect that it was not already capable of considerable carnivory, at least no less than exists in living euphractines. Moreover, the morphology of *Macroeuphractus* suggests that it was further advanced than any of the latter. For example, the increases in relative (as well as absolute) mass and moment arm of the temporalis are remarkable developments among cingulates (see Vizcaíno et al. 1998, and references therein) and thus represent a marked departure from the cingulate pattern. (They occur as well in peltephilines but see Vizcaíno and Fariña 1997). The same is true of the conspicuous caniniform teeth, the robustness of the dentary, and the larger rostrum. Further, manipulations of the skull and dentary indicate that the development of the postglenoid process and more concave surfaces of the mandibular condyle served to restrict motion at the temporomandibular joint compared with the joint in pampatheres and euphractines.

Macroeuphractus lacks the extreme specializations of carnivorans, but the probability of advanced carnivory is clearly implied by its unique morphology. *Macroeuphractus* may be safely considered a carrion feeder, but there are arguments for predatory carnivory in this genus. It is noteworthy, for example, that scavenging is commonplace in armadillo biology (Redford 1985) but has never resulted in the development of such large caniniforms within the group (see Smith and Redford 1990; Vizcaíno and Fariña 1997). Also, the predental region of the rostrum is considerably shorter than in other armadillos, which suggests that the caniniform, situated very near the front of the mouth, participated in food intake. If the rostrum were as long as in other armadillos, then the caniniforms would have been functional only once the food was in the oral cavity. These teeth appear sufficiently strong to have seized struggling prey. Their conical shape allowed them to resist strong bending stresses, as occurs with proper canines (see

Alexander 1983; Biknevičius and Van Valkenburgh 1996; Vizcaíno and Fariña 1997).

The large body size, presence of the caniniform, and enlarged temporal musculature of *Macroeuphractus* strongly suggest the capacity to catch and kill vertebrate prey larger than that hunted and eaten by living euphractines. Among the latter, *Chaetophractus villosus* has been recorded to prey on nestling birds and eggs, amphibians and smaller reptiles, in addition to invertebrates (Redford 1985). The postcranial skeleton of *Macroeuphractus* is not completely known, but the vertebrae, sacrum, and isolated limb bones are clearly of an armadillo type. This morphology, while not typical of most mammalian predators, does not prevent living euphractines from catching and killing vertebrate prey.

A proposal of predatory carnivory for *Macroeuphractus* does not necessarily imply that they were ferocious animals that fed only on other vertebrates, as Ameghino (1910) proposed for the peltephilines (but see Vizcaíno and Fariña 1997). It simply means that this huge carnivorous-omnivorous armadillo could have played a role among the secondary consumers of their time, preying on small to medium-size mammals. During the Montehermosan and Chapadmalalan SALMA several mammals were potentially suitable prey for *Macroeuphractus*. For instance, the fossorial caviomorph rodent *Lagostomopsis* is quite frequent (Vucetich and Verzi 1995). Also, *Paedotherium*, a hare-sized notoungulate that is one of the most abundant mammals of the Pampean Region (Bond et al. 1995), has been found in association with burrows (Genise 1989). With its typically armadilloid postcranial morphology, the fossorial abilities of *Macroeuphractus* would have allowed it easy access to the burrows of *Lagostomopsis* and *Paedotherium* (Fig. 9).

Macroeuphractus apparently represents the most advanced "essay" in carnivory within the armadillos. Even so, it was not an advanced carnivore in the conventional sense. The absence in *Macroeuphractus* (and probably most other cingulates) of many specializations characteristic of advanced epithierian carnivores is most probably due to phylogenetic constraint. Significantly, several authors (Winge 1941; Hirschfeld and

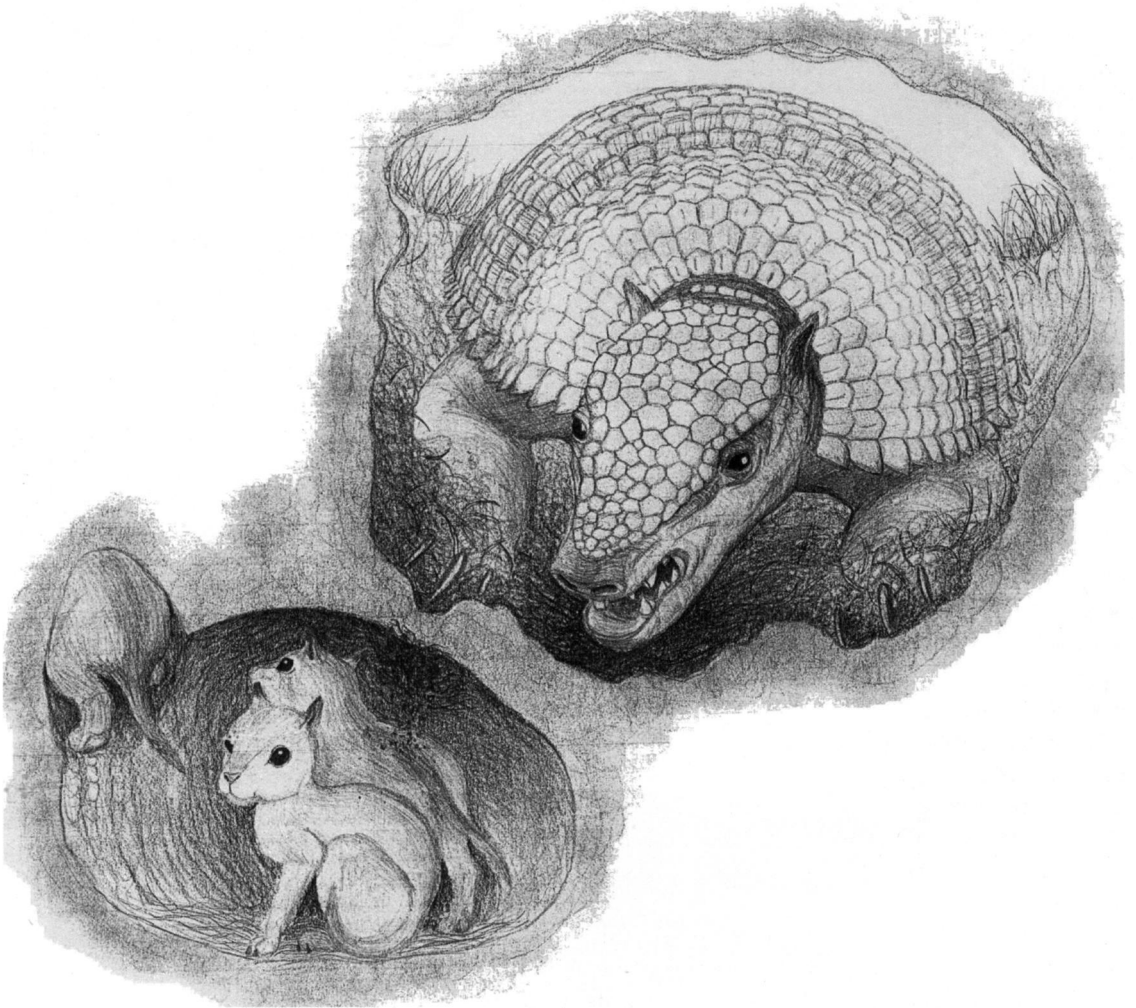


FIGURE 9. A life representation of *Macroeufractus outesi* about to prey on juveniles of the fossorial rodent *Lagostomopsis* sp.

Webb 1968; Patterson and Pascual 1972; Hirschfeld 1976; Webb 1985; Naples 1987) have noted that the specializations for insectivory among early xenarthrans imposed a severe phylogenetic constraint in the subsequent adaptations to different diets among the various clades. However, Smith and Redford (1990: p. 42) suggested that "the general configuration of the masticatory apparatus in *Euphractus* is most likely primitive and may indicate that omnivory was the primitive feeding pattern of armadillos." Despite the differences in some skeletal features noted above, the mechanical design of the masticatory systems of *Macroeufractus* and *Euphractus* is virtually identical and the dentition strongly resembles that of

Euphractus and nearly all other armadillos in general form except those armadillos in which the dentition is very strongly reduced, such as *Stegotherium* (Vizcaíno 1994, 1997), or specialized for herbivory (see above).

Phylogenetic constraint imposed by the dentition may have been the dominant factor in the relatively narrow range of morphological specialization among armadillos (and all the main xenarthran clades, albeit in different directions). Indeed, from their earliest records, armadillos are known to have possessed a homodont, hypselodont dentition that lacked enamel, which would be an extremely specialized condition for epitherians. Thus armadillos, and likely xenarthrans as a

clade, lost very early in their history the generalized cuspal pattern characteristic of the tribosphenic molars of therians. Alternatively, the other possibility, that the ancestor of xenarthrans never passed through a stage characterized by a tribosphenic molar, seems unlikely given that xenarthrans are widely accepted to be eutherians (Delsuc et al. 2001, and references therein). Given the early loss of the typical tribosphenic molar, we should not expect armadillos to have evolved morphological responses convergent on those of many epitharians. The conspicuous anatomical feature of armadillos that might ultimately be responsible for this circumstance is the absence of enamel. In nearly all other mammalian groups enamel plays an important part in the differentiation of the occlusal surfaces of the teeth, and the resulting patterns are well correlated to particular dietary habits. Thus, for example, the differences among many carnivores are clearly reflected in the occlusal patterns of their teeth, and these patterns are correlated with different grades of carnivory: there is no doubt that *Ursus* (bear) is an omnivore, whereas *Mustela* (weasel) is highly carnivorous.

The relevance of this to the dietary habits of armadillos is not that similar differentiation in dietary habits could not have existed, but that differences are not as clearly correlated with dental specializations. As a result of these phylogenetic constraints, the morphological distinctions among armadillos are somewhat subtle, making it more difficult to interpret dietary preferences. Among armadillos, some groups reduced their dentition in response to myrmecophagy (*Stegotherium*, see Vizcaíno 1994, 1997) and some acquired lobate teeth and accentuated differences in hardness of dentine types (*Eutatus*, see Vizcaíno and Bargo 1998; pampatheres, see Vizcaíno et al. 1998; De Iuliis et al. 2000). On the other hand, some took a decidedly different route. For example, *Peltephilus*, which was traditionally considered a carnivore and lacks an analog among epitharians, was reinterpreted as a specialized herbivore by Vizcaíno and Fariña (1997). This line of reasoning may be extended to include other xenarthrans, such as glyptodonts, in which the masticatory apparatus is singularly un-

usual (Fariña and Vizcaíno 2001), and ground sloths (Bargo 2001). Our main point is that when sufficient skeletal and dental remains are available, biomechanical and morphofunctional analyses are entirely appropriate for interpreting the paleobiology of these unusual extinct creatures. Certainly such analyses help provide more accurate reconstructions than mere comparisons with modern closely allied taxa or supposed analogs, which alone can lead to misleading conclusions.

As applied to *Macroeuphractus*, the specializations may not seem sufficient to support a hypothesis of increased carnivory; there are relatively minor departures from the typical armadillo pattern, compared with the changes that occur in other mammalian taxa. However, it is necessary to maintain the proper context when comparing morphologically widely separated taxa (Vizcaíno and Fariña 1999). In light of the severe phylogenetic constraint imposed on these cingulates, these apparently minor changes in *Macroeuphractus* become remarkable. The combination of these features might not be particularly compelling in most mammalian groups, but their presence in an armadillo is strong evidence for carnivorous specialization.

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Appendix 1

Specimens Used

Macroeuphractus outesi

MLP (DCPV) 69-IX-9-3. Skull (Fig. 2), sternum, ribs, pelvis, some caudal vertebrae, and pieces of carapace. Chapaldmalal Formation. Mar del Plata, Buenos Aires Province, Argentina. Chapadmalalan SALMA (late early to early late Pliocene).

Macroeuphractus retusus

MLP (DCPV) 64-VIII-25-1. Left edentulous dentary, missing the anterior tip of the horizontal ramus distal to m2 and the tip of the coronoid process (Fig. 3). Monte Hermoso, Buenos Aires Province, Argentina. Montehermosan SALMA (early Pliocene).

Vassallia maxima

FMNH 14424. Skull and right dentary. Corral Quemado, Catamarca, Argentina. Huayquerian SALMA (late Miocene–early Pliocene).

Pampatherium typum

MACN 11543. Nearly complete, edentulous skull, and MACN 11474 right dentary. Both from Rio Carcaraña, Santa Fe Province, Argentina. Lujanian SALMA (late Pleistocene).

MLP (DCPV) 81-X-30-1. Complete left mandible, preserving molariforms, posterior fragment of the skull, and isolated scutes. Lujanian SALMA (late Pleistocene).

Holmesina occidentalis

ROM 3881, skull; ROM 4954, right and partial left dentaries; ROM 4955, right dentary and symphyseal portion of left; ROM 4956, posterior half of right dentary; ROM 4964, partial right horizontal ramus. All from Corralito, Santa Elena Peninsula, Ecuador (Pleistocene).

Euphractus sexcinctus

MLP (DCZV) 1180. Skull and mandible. Provenance unknown.

MLP (DCZV) 1236. Skull. Provenance: Misiones, Argentina.

MLP (DCPV). Skull and mandible, without catalog number. Provenance unknown.

ROM R2019—Skull and mandible. Provenance: Argentina.