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Functional and phylogenetic assessment of the masticatory adaptations in Cingulata (Mammalia, Xenarthra)

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Abstract. Cingulata -armadillos, pampatheres and glyptodonts- are among the most representative of South American Cenozoic mammalian groups. Their dental anatomy is characterised by homodonty, hypselodonty, and the absence of enamel in almost all known species. It has been proposed that these peculiarities are related to a primitive adaptation to insectivory and that they represent a strong phylogenetic constraint that restricted, or at least conditioned, adaptations toward other alimentary habits. However, the great diversity of forms recorded suggests a number of adaptive possibilities that range from specialised myrmecophagous species to carrion-eaters or predators among the animalivorous, and from selective browsers to bulk grazers among herbivores, as well as omnivores. Whereas armadillos (Dasypodidae) developed varied habits, mostly animalivorous but also including omnivores and herbivores, pampatheres (Pampatheriidae) and glyptodonts (Glyptodontidae) were herbivores. Morphofunctional and biomechanical studies have permitted a review of previous hypotheses based solely on comparative morphology. While in some cases these were refuted (carnivory in peltephiline armadillos), they were corroborated (carnivory in armadillos of the genus *Macroeuphractus*; herbivory in eutatines, pampatheres and glyptodonts) or refined (different kinds of herbivory in eutatines, pampatheres and glyptodonts) in others. The morphological and adaptive diversity suggests a more extensive cladogenesis than that reflected by current systematic schemes. Analyses have also revealed that some cingulates have evolved mechanical solutions that are neither shared by closely related taxa nor have current analogues that can be used as models to investigate and to interpret adaptations of lineages without living representatives.

Resumen. Evaluación funcional y filogenética de las adaptaciones en Cingulata (Mammalia, Xenarthra). Los Cingulata -armadillos, pampaterios y gliptodontes- se cuentan entre los grupos más representativos de mamíferos cenozoicos sudamericanos. Su batería dentaria se caracteriza por la homodoncia, la hipselodoncia y la ausencia de esmalte en la casi totalidad de las formas conocidas. Se ha propuesto que estas peculiaridades se relacionan con una adaptación primigenia a la insectivoría y representan una fuerte señal filogenética que restringió, o al menos condicionó, la adaptación a otros tipos de hábitos alimentarios. Sin embargo, la gran diversidad de formas registradas sugiere un abanico de posibilidades adaptativas que abarca desde mirmecófagos especializados hasta carroñeros o predadores, entre las formas animalívoras, y desde ramoneadores selectivos hasta pastadores que se alimentan al bulto, entre las herbívoras, e incluye formas omnívoras. Mientras que los armadillos (Dasypodidae) desarrollaron hábitos variados, fundamentalmente animalívoros pero también omnívoros y herbívoros, pampaterios (Pampatheriidae) y gliptodontes (Glyptodontidae) habrían sido herbívoros. Estudios morfofuncionales y biomecánicos nos permitieron revisar hipótesis previas basadas fundamentalmente en una morfología comparada. Mientras que en algunos casos éstas fueron rebatidas (carnivoría en armadillos peltefilinos), en otros resultaron reafirmadas (carnivoría en armadillos del género *Macroeuphractus*; herbivoría en eutatinos, pampaterios y gliptodontes) o refinadas (tipos de herbivoría en eutatinos, pampaterios y gliptodontes). La diversidad morfológica y adaptativa sugiere una cladogénesis más acusada que la reflejada por los esquemas sistemáticos dominantes. En algunos casos se registran soluciones mecánicas no encontradas en formas relacionadas ni análogas actuales, de manera que podrían servir de modelos para interpretar adaptaciones en formas fósiles pertenecientes a linajes sin representantes vivientes.

Key words. Xenarthra. Cingulata. Morphology. Biomechanics. Diet. Phylogeny.

Palabras clave. Xenarthra. Cingulata. Morfología. Biomecánica. Dieta. Filogenia.

Introduction

Cingulates 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 (Webb and Rancy, 1996). With over 100 genera named (McKenna and Bell, 1997), the fossil cingulates attained a much greater diversity than their living representatives (about 25 species of armadillos [Wetzel, 1985]). Following McKenna and Bell (1997), they comprise the typical armadillos (Dasypodidae), including fossil and living forms, some of which reached sizes of about 50 kg (figure 1.A-C); the peltephilines (Peltephilidae), horned armadillos that ranged from medium size to more than 100 kg (figure 1.D); the pampatheres (Pampatheriidae), giant armadillos that must have reached 200 kg (figure 1.E), and the glyptodonts (Glyptodontidae), whose terminal Pleistocene forms reached body masses varying between 1 and 2 tons (figure 1.F; Fariña, 1995; Fariña *et al.*, 1998). Within Dasypodidae, McKenna and Bell (1997) include Da-

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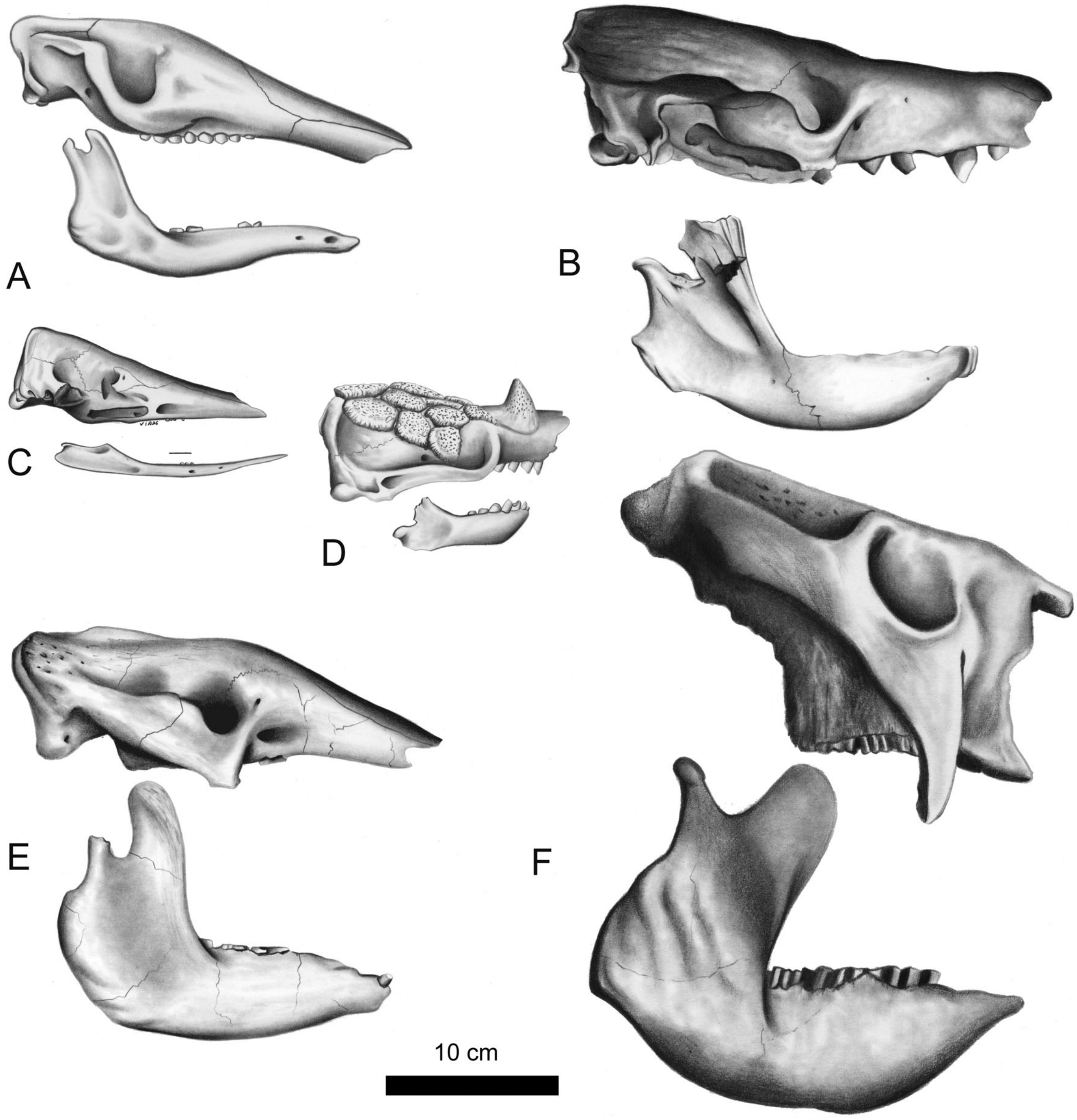

Figure 1. Skulls and mandibles of various cingulates. Drawings by A. Viñas. **A,** *Eutatus*; **B,** *Macroeuphractus*; **C,** *Stegotherium*; **D,** *Peltephilus*; **E,** *Vassallia*; **F,** *Doedicurus* / *Cráneos y mandíbulas de varios Cingulata.* Dibujos de A. Viñas.

sypodinae (Dasypodini and Stegotheriini), Euphractinae (Euphractini, Eutatini, Utaetini and Chlamyphorini) and Tolypeutinae (Tolypeutini and Priodontini).

Previous authors have proposed either insectivory (*e.g.*, Patterson and Pascual, 1972; Webb, 1985) or omnivory (Smith and Redford, 1990) as the primitive feeding pattern of armadillos. Several clades, such as the eutatines and pampatheres, have been traditionally recognized as herbivores (Winge, 1941; Edmund, 1985). Peltephilines were traditionally considered carnivorous but a herbivorous diet was proposed some years ago (Vizcaíno and Fariña, 1997). This leaves *Macroeuphractus* Ameghino, which includes the largest armadillos as the only probable member of the Cingulata (and possibly all armoured mammals) specialized for carnivory.

The dentition of cingulates, and of all other xenarthrans, is strongly reduced: armadillos (except for the peculiar living *Priodontes maximus* Kerr) and glyptodonts usually have nine or ten teeth in each jaw quadrant. Enamel is absent in the adult and deciduous teeth of all extant and possibly all extinct xenarthrans (with the only proposed exception of the utaetine *Utaetus* Simpson, 1931). The cuspal patterns present in other mammals is also absent. The teeth, composed of osteodentine (Ferigolo, 1985) are always hypselodont. They may be lobated, but are usually simple and separated by short diastemata (figure 2).

These peculiarities of the dentition must have imposed severe functional and biomechanical constraints as lineages adapted to different diets. Nevertheless, the great diversity of the cingulates suggests a wide range of adaptive types, ranging from specialized myrmecophagy to carrion feeding and predation among animalivorous forms, and from selective browsing to grazing among herbivorous and omnivorous forms. While armadillos developed a variety of dietary habits, including animalivory as well as omnivory and herbivory, pampatheres and glyptodonts were mainly herbivorous.

Recent years have witnessed an increasing number of morphofunctional, biomechanical and morphogeometrical studies of Cenozoic xenarthrans, mainly on cingulates, but also on ground sloths (*e.g.*, Naples, 1987, 1989; Vizcaíno, 1994, 1997; Fariña and Blanco, 1996; Vizcaíno and Fariña, 1997; Vizcaíno and Bargo, 1998; Vizcaíno *et al.*, 1998; De Iuliis *et al.*, 2000, Bargo, 2001a and b; Fariña and Vizcaíno, 2001; Vizcaíno and De Iuliis, 2003). Many of these studies have provided new insight on long accepted hypotheses that were based mainly on relatively elementary analyses of comparative morphology. These new studies have, *e.g.*, allowed for the assessment of bite forces, and hence generated insightful new conclusions regarding dietary preferences. The lack of living analogues usually imposes problems on attempts to interpret the ways of life of extinct fauna. However, studies as those mentioned have helped circumvent this static impression. They provide answers to the question of what an animal is well designed for. When coupled with palaeoenvironmental data (geology, palaeoclimatology and palaeovegetation), these results can provide insightful information on palaeocology. In this review we wish to summarize that information and to assess it in a phylogenetic context.

An integrated methodology

This section provides an overview of the various methods employed by the studies on fossil taxa cited above. Although studies on the biomechanics of the masticatory apparatus of living armadillos are almost non-existent, the work of Smith and Redford (1990), who compared the mechanical and functional significance of the differences in the jaw morphology of *Dasypus novemcinctus* Linné and *Euphractus sexcinctus* (Linné), must be noted. These researchers used cineradiography, a standard procedure in the analysis of mastication of living species, but also calculated the moment arms of the masticatory musculature to infer the relative bite forces and velocity. Although they cautioned against using morphology to predict diet, a concept that was revisited by Vizcaíno *et al.* (1998) and summarised below, their article provided a comparative standard among living armadillos and became the basis for a methodological tool that triggered a series of studies on fossil cingulates.

The correlation between diet and the form and function of the masticatory apparatus has been investigated mainly by vertebrate palaeontologists, who must usually rely solely on form to infer function and diet (*e.g.*, Turnbull, 1976; Finch, 1982; Witmer and Rose, 1991, Gambaryan and Kielan-Jaworowska, 1995). Several studies on jaw mechanics have revealed relationships among the behaviour, diet, and form of the masticatory apparatus (including the skull, jaws, dentition, and musculature) of extant mammals (*e.g.*, Maynard Smith and Savage, 1959; Turnbull, 1970; Moore, 1981; Schumacher, 1985; Smith, 1993). These studies have been useful for the reconstruction of musculature of fossil mammals and provide a framework for investigation of their diet and behaviour.

As mentioned above, various authors have included the form and function approach in their investigations on cingulates (Vizcaíno, 1994; Vizcaíno and Fariña, 1997; Vizcaíno and Bargo, 1998; Vizcaíno *et al.*, 1998; De Iuliis *et al.*, 2000; Fariña and Vizcaíno, 2001; Vizcaíno and De Iuliis, 2003), generating new understanding of bite forces and hence dietary preferences of the taxa under consideration. Several methods were incorporated or modified, and integrated to accomplish these analyses. They include a geometric model for the analysis of jaw mechanics and a Procrustean method for analysing skull shape (see below).

The origin and insertion areas of the masticatory musculature (involving mainly the temporalis and massetericus muscles; see Vizcaíno *et al.*, 1998) are reconstructed from features of the skeletal elements, following Turnbull (1976), Finch (1982), Vizcaíno *et al.* (1998), and De Iuliis *et al.* (2000), and the patterns of musculature in modern mammals (Maynard Smith and Savage, 1959; Turnbull, 1970), particularly those in armadillos (Macalister 1869; Smith and Redford, 1990).

The mandible may be viewed as a lever, with a fulcrum at the temporomandibular joint, an input force generated by the masticatory musculature, and an output force exerted by the teeth on food. The moment arms of the lines of action of the temporalis and massetericus are estimated so that the effective strength of each muscle and the relative bite forces may be estimated and compared.

Vizcaíno *et al.* (1998) proposed a geometric model that allows comparison of relative bite forces among

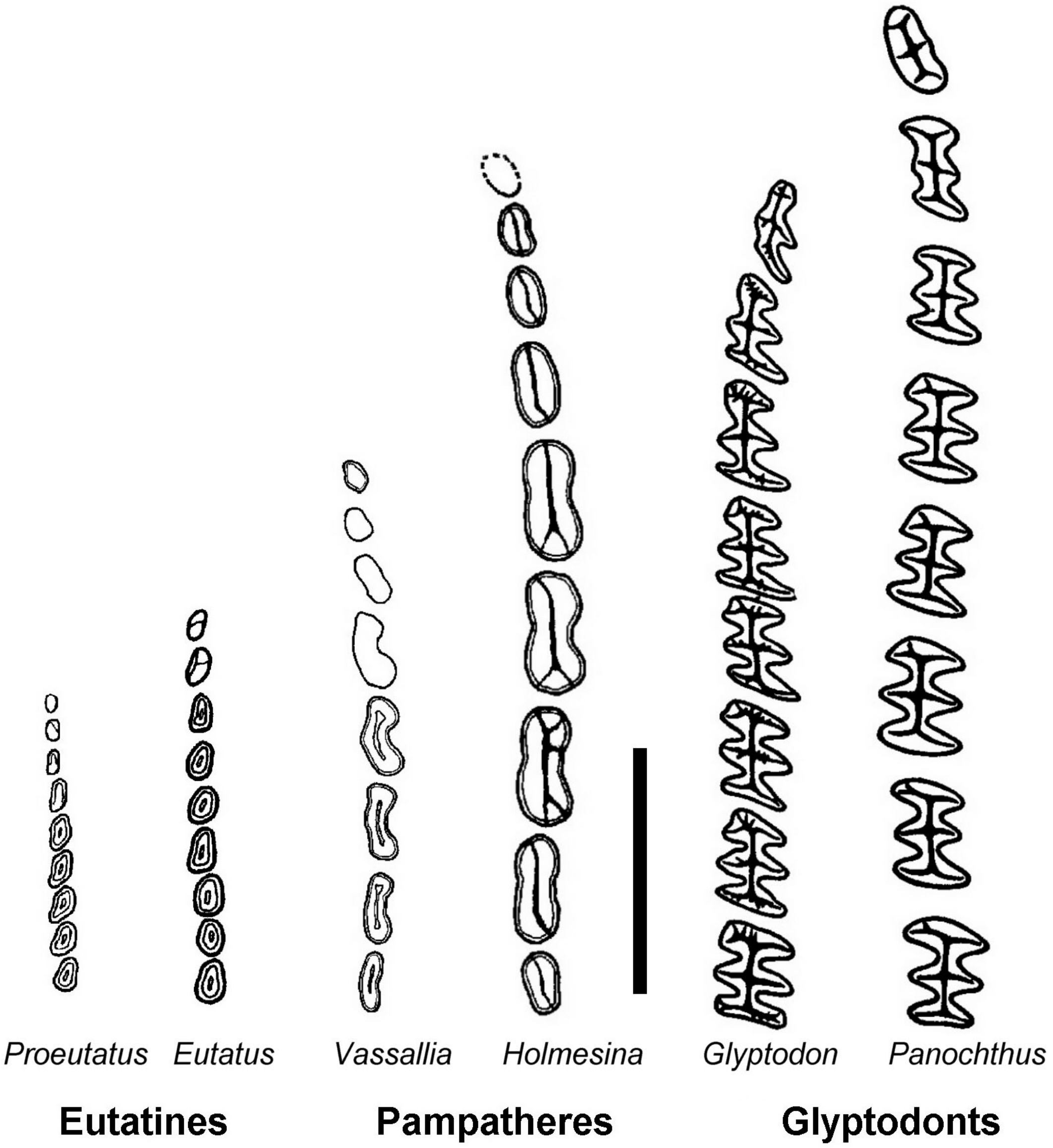

Figure 2. Diagrammatic lower right tooth rows of various cingulates. Scale bar: 5cm / *Esquemas de la hilera dentaria inferior derecha de varios Cingulata. Escala:5 cm.*

different species of fossil and extant mammals (figure 3.A). Differences in skull sizes are standardized to mandible length, following Smith and Redford (1990). The lines of action for the massetericus are estimated from the most anterior and posterior positions of the origin and insertion; and for the temporalis from the most anterior, middle, and most posterior origins on the skull, and from a single insertion on the coronoid process.

The means of the moment arms are calculated. Once the moment arms for the temporalis and massetericus are calculated, different species may be compared following Smith and Redford (1990). Interpretations of the relationships between bite force and velocity may be drawn through comparisons of the proportions of the combined moment arms of the temporalis and massetericus to those based on different tooth positions (i.e., the central point of the anterior most, middle, and posterior most teeth).

Shape analysis based on Procrustean methods was employed in comparisons of skull form. Specifically, Resistant Fit Tetha-Rho Analysis (RFTRA) was the method used. RFTRA is based on the superposition of one form onto another using the position of landmark points (figure 3.B and C). It measures the homologous regions of change in shape by establishing congruence among those that have not changed (Benson *et al.*, 1982; see Chapman, 1990a and b, and references therein, for detailed information). This program also generates dendrograms of un-

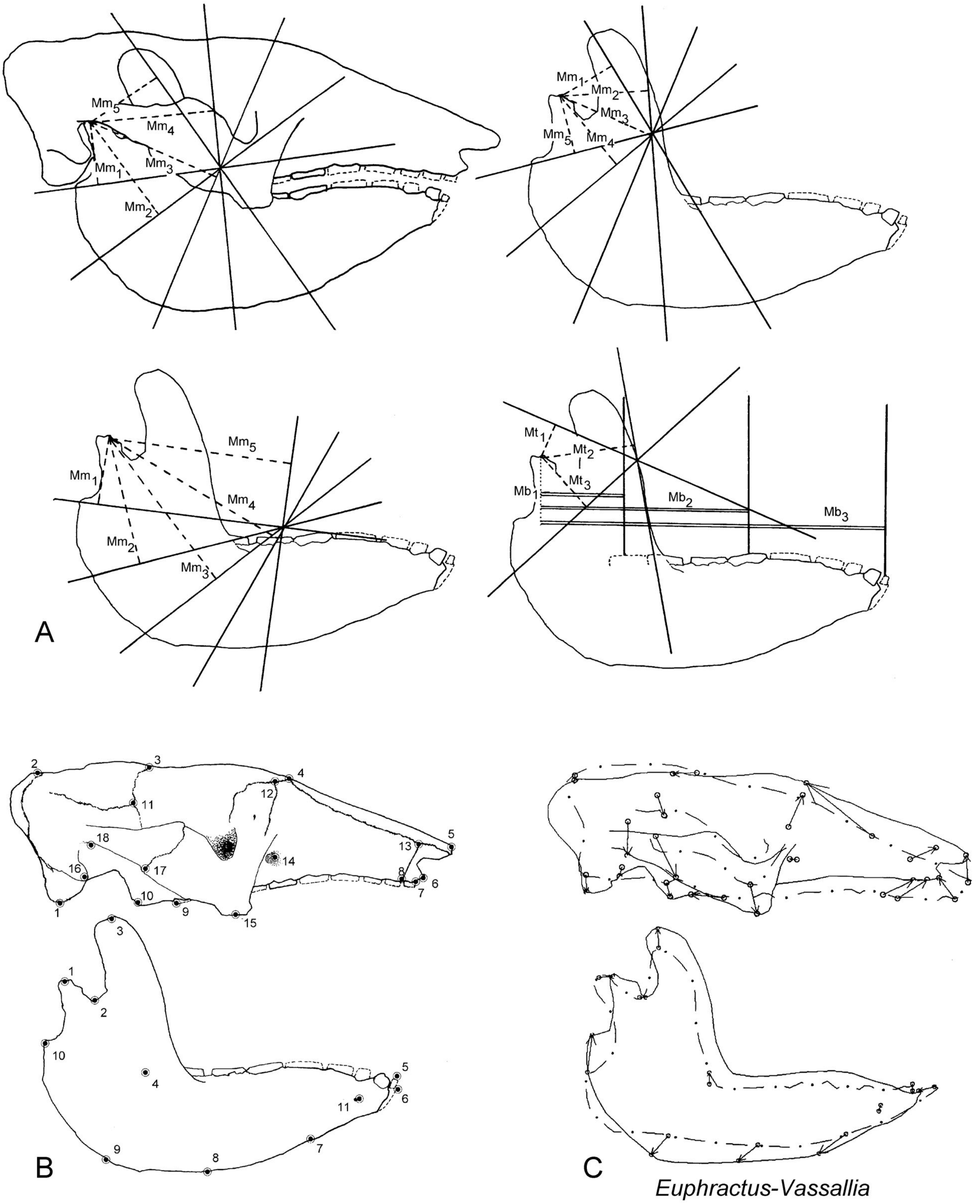

Figure 3. A, Geometric model from Vizcaíno *et al.* (1998). Moment arms as calculated in the pampathere *Vassallia maxima*. Mm_1-Mm_5: moment arms of the massetericus; Mt_1-Mt_3: moment arms of the temporalis; Mb_1-Mb_3: moment arms of the bite points at the distal, middle and mesial teeth respectively / *Modelo geométrico de Vizcaíno* et al. *(1998). Brazos de momento tal como calculados en el pampaterio* Vassallia maxima. *Mm_1-Mm_5: brazo de momento del masetero; Mt_1-Mt_3: brazo de momento del temporal; Mb_1-Mb_3: brazos de momento de los puntos de mordida en los dientas distal, medio y mesial, respectivamente.* **B,** Skull and mandible of *Vassallia maxima* showing the landmarks used for RFTRA analysis / *Cráneo y mandíbula de* Vassallia maxima *mostrando los landmarks usados para el RFTRA.* **C,** Graphic representation of RFTRA, comparing skull and mandible of *Euphractus* and *Vassallia* / *Representación gráfica del RFTRA, comparando cráneo y mandíbula de* Euphractus *y* Vassallia.

weighted pair-group method using arithmetic averages (UPGMA) cluster analysis based on RFTRA distances. This allows analysis of morphological variability within a predefined phylogenetic framework (Chapman, 1990a).

Occlusal patterns and mandibular movements were determined through analysis of the craniomandibular joint (including manipulation), the shape and arrangement of teeth (including occlusal wear patterns), and the morphology of the symphysis.

Animalivores

The literature indicates that all living armadillos consume a considerable amount of animal material (see Redford, 1985, and references therein). Redford (1985: 429) noted that living armadillos "show a range of trophic specialization from the generalised carnivore-omnivore through the generalist insectivore to the specialist insectivore." Several 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. Accordingly, this review begins with the animalivorous cingulates.

Much of the diversity of fossil armadillos is represented by the euphractines, which are known since the Early Eocene. Living euphractines constitute Redford's (1985) carnivore-omnivore group, which is characterized by a diet that includes many types of plant material (*e.g.*, roots and tubers, nuts of a low palm) mixed with a variety of animal matter that ranges from ants and carrion to birds and mice. Smith and Redford (1990) noted features of *Euphractus* Wagler that indicate larger massetericus and pterygoideus muscles and a larger moment arm of the massetericus. These adaptations reflect greater bite forces and more efficient transverse mandibular movements. In a recent study of the late Pliocene euphractine *Macroeuphractus outesi* Ameghino, one of the largest dasypodids known, Vizcaíno and De Iuliis (2003) noted that its skull possesses features that are remarkable for an armadillo. Several features, such as its complete dental arcade and large caniniform teeth had already been singled out in the literature as indicative of scavenging behaviour. The morphological analyses of Vizcaíno and De Iuliis (2003) revealed that the main differences between *M. outesi* and other euphractines include an enlarged cranial region, especially the temporal fossa, which bears more prominent origin scar lines for the temporalis; a rostrum that is expanded, particularly dorsoventrally; a more powerful anterior dentition, with greatly enlarged M2s that are modified as caniniforms; and a deeper, more robust zygomatic arch. Their biomechanical studies indicated that the moment arm of the temporalis musculature is greater than that recorded for other armadillos. These analyses suggest that the temporalis was larger than in other euphractines and played a more important role than the massetericus in *Macroeuphractus*, a pattern that is more typical of carnivorous mammals. Taken together, the complex of features indicate that *Macroeuphractus* occupied an extreme position in the spectrum of carnivorous-omnivorous feeding behaviour of euphractines. Its large size indicates that it could have easily preyed on hare-sized animals.

The peltephilines comprise a group of armadillos traditionally regarded as specialised carnivores (Ameghino, 1910; Winge, 1941; Hoffstetter, 1958; Scillato-Yané, 1977). However, a recent reanalysis by Vizcaíno and Fariña (1997) of the available evidence, including a morphofunctional study suggests a different view of this group (see below).

The highly specialised animalivorous habits of the Early Miocene myrmecophagous dasypodid *Stegotherium tessellatum* Ameghino (Scott, 1913; Patterson and Pascual, 1968; Scillato-Yané, 1982; Vizcaíno, 1994, 1997) provide an example where earlier studies have been corroborated by more comprehensive research. Analysis of both the craniomandibular joint and muscular attachment sites indicates that jaw movements were primarily oriented anterioposteriorly (Vizcaíno, 1994). The great reduction in number and size of the teeth and elongation of the rostrum (though differently than in the living analogues *Dasypus* Linné and *Priodontes* F. Cuvier) clearly suggest a myrmecophagous diet (Vizcaíno, 1994, 1997).

Herbivores

Vizcaíno and Fariña (1997) challenged the traditional view that regarded the Santacrucian (Early Miocene) *Peltephilus* Ameghino (as well as the other peltephilines) as the most cursorial and active hunter armadillo (Ameghino, 1910; Hoffstetter, 1958, Scillato-Yané, 1977). Ameghino (1910) viewed peltephilines as ferocious animals that fed on other mammals based on coprolites and the arrangement of teeth. The presumed coprolites were recently reidentified as plantules belonging to angiosperms (see Vizcaíno and Fariña, 1997). Based on a biomechanical analyses, Vizcaíno and Fariña (1997) concluded that *Peltephilus*, and very likely other peltephilines, are poorly designed as carnivorous, actively cursorial mammals. Their teeth are too slender, with the main masticatory efforts performed in the anterior portion of the tooth row rather than in the cheek region, where a secodont molar is situated in other carnivores. Peltephiline limb anatomy does not suggest more cursorial habits than that of any other armadillo; indeed, it clearly suggests digging behaviour. On the basis of these studies, Vizcaíno and Fariña (1997) proposed an alternative hypothesis that views peltephilines as having fed on soft, tough items, probably plant material of underground origin. As scavenging is commonplace in dasypodid biology (Redford, 1985), it cannot be excluded as a possibility for peltephilines.

The eutatine armadillos have been considered herbivorous based on their singular skull and dental morphologies. Vizcaíno and Bargo (1998) analysed the masticatory apparatus of the Late Pliocene to Early Holocene *Eutatus* Gervais and compared it with that of other Miocene and Pliocene eutatines to test the hypothesis of herbivory and evaluate the presence of an evolutionary pattern of adaptation within the clade. The general shape of eutatine mandible and teeth of the eutatines is markedly similar to that of many herbivorous ungulates. The mandibular condyle is well elevated to improve the mechanical advantage of the massetericus. Its concave to flat morphology allows considerable lateral and anteroposterior mandibular movements. The unfused symphysis may be related to transverse chewing movements, as suggested by Greaves (1978). The teeth of eutatines are better adapted for cutting or shearing than those of living armadillos. They display flat-grinding surfaces in the posterior two thirds of the tooth row. The outer and the inner hard dentine layers, elevated above the level of softer medial dentine, are almost parallel to the long axis of the tooth, which implies a strong lateral component in mastication. The outer layer forms ridges that may have been important in slicing up food.

The jaw apparatus of *Eutatus* apparently optimises a combination of fast closing movements (based on the short temporalis moment arm), and more powerful biting (based on a long massetericus moment arm). Also, the posterior position of the tooth row (which increases relative bite force) and the relatively long snout (which decreases bite force) suggest a compromise between fast and powerful movements. The masticatory apparatus of *Eutatus* is generally more similar to that of browsing ungulates of moderate to small size, such as some deer and antelopes, rather than of cows and horses. Taken together, these comparisons suggest that *Eutatus* was mainly a browser, adapted to feeding on plant material such as leaves and buds, but possibly also ingesting some proportion of grasses. The long snout and the absence of anterior teeth indicate that items such as nuts, twigs roots, and tubers were not part of its diet. As there is no evidence for muscle attachments supporting a powerful lip musculature adapted to gather plant food, a vermiform tongue may have acted as a prehensile organ. Vizcaíno and Bargo (1998) concluded that *Eutatus* and *Proeutatus* Ameghino exhibit the most specialised morphology known for an herbivore with an armadillo-like skull pattern. Additionally, they identified a morphological group passing from the omnivorous, Miocene *Stenotatus* Ameghino to the Pleistocene *Eutatus*, with the Pliocene *Doellotatus* Bordas and *Ringueletia* Reig as intermediate stages. The Miocene *Proeutatus* deviates from this pattern. Also, the shape analysis performed by Vizcaíno and Bargo (1998) demonstrates that the form of the mandible is less conservative than that of the skull, as its morphology is more influenced by dietary adaptations and less constrained by the conflicting demands imposed on the skull by such factors as the origin of neck muscles, attachment of the cephalic shield, participation in burrow or tunnel formation, vision and olfaction, among others.

Studies on the pampatheres *Vassallia* Castellanos, *Holmesina* Simpson and *Pampatherium* Ameghino (Vizcaíno *et al.*, 1998; De Iuliis *et al.*, 2000) have revealed that they were more powerful and efficient in transverse chewing than dasypodids, and were primarily grazers consuming mainly coarse vegetation. Features (some of which are shared with herbivorous ungulates) demonstrating these behaviours include wide, relatively flat mandibular condyles that lie well dorsal to muscular insertion sites; expanded angular processes, posterior extension of the tooth row; mesial teeth with predominantly transverse striations; mesiodistally elongated distal teeth with basined occlusal surfaces and, in *Vassallia*, a central island of resistant dentine that functioned as an ectoloph. The teeth also have a step-wise arrangement. The main differences among pampatheres were associated with the musculature, so that differentiation in masticatory function was due primarily to changes that led to differential input forces. The available evidence suggests that the Plio-Pleistocene paleobiogeographic distribution of pampatheres is correlated with masticatory function and, therefore, diet. *Pampatherium typum* Ameghino, which is best adapted for grinding coarse vegetation, occurs in the more arid Pampean regions of South America. *Holmesina occidentalis* (Hoffstetter) is recorded from deposits near the current Peru-Ecuador border, an area of humid lowlands during glacial maxima, and was the least suited to coarse vegetation. *P. humboldtii* (Lund) and *H. paulacoutoi* Cartelle lie between these extremes, with the former better adapted for abrasive vegetation.

Glyptodonts pose different problems in the design of their masticatory apparatus (Fariña, 1985, 1988; Fariña and Vizcaíno, 2001). They have been considered grazers based on their very high crowned teeth. Also, they seem at first sight to have a short skull. Fariña and Vizcaíno (2001) analysed the general skull morphology of the large Pleistocene *Glyptodon* Owen, and compared it with the smaller and less derived Miocene *Propalaeohoplophorus* Ameghino. They demonstrated that the masticatory apparatus of glyptodonts has undergone a telescoping process that was already underway in the most ancient forms for which the skull is known. As a result, the lower tooth row extends posteriorly medial to the ascending ramus and as far as the craniomandibular joint. Thus, glyptodonts are a clear exception to the one-third rule proposed by Greaves (1982), which suggests that the most stable position for elevators of the jaw is in the posterior third of the distance from tip of the jaw to the craniomandibular joint. The cheek teeth should lie in the middle third of this distance. Fariña (1988) and Fariña and Vizcaíno (2001) proposed that this peculiar glyptodont morphology was the price large glyptodonts had to pay for being so well armoured. Indeed, it would be difficult to retain an armadillo-like (or, more generally, primitive mammalian) position of the masticatory apparatus in combination with extensive armour that covered even the cervical region dorsally. This is due to the fact that the scaling up of the skull implies an allometric increase in strength of the cervical musculature. Indeed, skull weight would be increased in cubed proportions, while muscular strength, which is a function of the cross-sectional area of a muscle, would be increased by squared proportions. In the case of glyptodonts the cervical musculature would increase to the point where its size would be more and more difficult to accommodate beneath the cervical armour. The response to this situation of moving the large, hypselodont teeth closer (posteriorly) to the fulcrum (i.e., the occipital condyles) imparts shorter output arm for the skull. Consequently, its moment about the fulcrum is smaller, and it can thus be balanced by a smaller input force, which allows a relative reduction of the neck musculature. This development, however, gave rise to problems related to absorption by the mandible of stresses produced by mastication, and it could therefore be viewed as an evolutionary oddness.

Discussion

Morphology, function and behaviour

An evident conclusion of this review is that the peculiarities of the masticatory apparatus of cingulates (and other xenarthrans as well) imply the underlying influence of important constraints that must be taken into account in any morphofunctional analysis of variables that might influence dietary behaviours. Some of these variables may be quantified and compared among xenarthrans using the form-function correlation approach elucidated by Radinsky (1987). This approach assumes that a close relationship exists between form and function, so that the latter can be predicted from the former. In other words, in instances where suitable homologies are not available, the tendency among researchers has been to argue for function based usually on biological analogy. When biological analogues are not available, mechanical analogues have often been invoked (see Plotnick and Baumiller, 2000).

As noted above, however, Smith and Redford (1990: 45) cautioned against predicting dietary habits on the basis of morphological form: "comparison of *D. novemcintus* and *E. sexcintus* provides an interesting example of the decoupling of morphological and behavioural specialization. In this case, the morphology of *D. novemcinctus* appears more specialized toward myrmecophagy than the behaviour would suggest." Vizcaíno *et al.* (1998) took issue with this conclusion, arguing instead that strict myrmecophagy is not at all implied by the morphology of *D. novemcinctus*. Such behaviour is, however, implied by the specialised morphology of *Stegotherium tessellatum* and was postulated by Vizcaíno (1994, 1997) on just such clearly specialized morphology. Instead one should use comparative terms: *D. novemcinctus* prefers social insects (in the parts of its range where they are available in sufficient number, i.e., in Central and South America, but not in North America -see Redford, 1985), but is not myrmecophagus to the degree of, for example, *Mymecophaga*; whereas *E. sexcinctus* is considerably less likely than *D. novemcinctus* to display myrmecophagous behaviour. These different behavioural patterns are reflected by the distinctly different morphologies.

Phylogenetic constraint

The previous section serves to highlight a critical component -comparative analysis- of the methodology employed to investigate the living habits of extinct taxa. Of particular relevance here is the question of which groups of mammals are fit or valid comparative subjects for use with cingulates, and indeed all xenarthrans. Cautious or conservative use of living analogues is appropriate given that organisms reflect the duality of adaptation to current environmental demands and the inherited tendency to remain the same, or historical contingency. The latter may be viewed as an inertial resistance that tends to limit the efficacy of selection to produce an adapted phenotype, and is therefore termed evolutionary or phylogenetic constraint (Schwenk, 2001). Thus, if a lineage develops a phenotype in response to a particular environmental demand, the phenotype need not be necessarily identical or even closely similar to a phenotype produced in a distantly related lineage in response to a similar environmental demand. This concept is particularly relevant in attempting to make sense of adaptations in fossil forms that lack clear, unambiguous ecologic equivalents among their living relatives, as is the case for xenarthrans.

As a case in point, Vizcaíno and De Iuliis (2003) pointed out that the absence in *Macroeuphractus* of many specialisations characteristic of advanced epitherian carnivores is most probably due to phylogenetic constraint. The effect of this factor generally in xenarthrans has been noted previously by several authors (Winge, 1941; Hirschfeld and Webb, 1968; Hirschfeld, 1976; Patterson and Pascual, 1972; Webb, 1985; Naples, 1987), who have suggested that the specialisations for insectivory among early xenarthrans imposed a severe phylogenetic constraint in the subsequent adaptations to different diets among the various clades (although Smith and Redford [1990] suggested that omnivory was the primitive feeding pattern of armadillos).

Vizcaíno and De Iuliis (2003) proposed that the general dental characteristics acquired early in xenarthran history may be primarily responsible for the relatively narrow range of morphological responses among armadillos. The dentition of armadillos, from their earliest appearance in the fossil record, is homodont, hypselodont and without enamel, a condition that would be highly specialised for epitherians. Given that xenarthrans are confidently recognized as eutherians (Delsuc *et al.*, 2001, and references therein), their ancestry should have included a tribosphenic stage, so that the Xenarthra, as a clade, lost the generalized tribosphenic cuspal pattern very early in its history. Given the early loss of the typical tribosphenic molar, morphological responses closely convergent on those of many epitherians should not be expected in xenarthrans. One factor that may ultimately be responsible for the main evolutionary pathways of xenarthrans is the lack of enamel, which in nearly all other mammalian clades plays an integral role in the differentiation of occlusal surfaces into patterns that are well correlated with dietary habits.

Clearly, viewing the absence of a similar correspondence between dietary preference and occlusal patterns in xenarthrans as evidence that similar dietary differentiations cannot exist or may not have existed is not the only interpretation. Such absence, based just on the wide degree of dietary specialization that exists among living representatives, merely suggests that diet and occlusal patterns are not as closely correlated in xenarthrans. As a result of phylogenetic constraint, the morphological distinctions among xenarthrans are therefore subtler, rendering interpretation of dietary preferences more difficult. Comprehensive morphofunctional and biomechanical analyses, however, do yield considerable insight on dietary habits. The several recent analyses alluded to above for cingulates, and the work by Bargo (2001a, b) on ground sloths, furnish abundant examples of such success. Clearly, such comprehensive analyses lead to more reliable reconstructions than those restricted to comparison with either closely allied modern taxa or supposed analogues; when unsupported by other lines of evidence, the latter approach can lead to misleading conclusions.

Analyses of the masticatory apparatus reveals that some cingulate species present mechanic solutions to certain functional problems that do not occur in either closely or remotely related living representatives. Therefore, simple, strictly actualistic comparisons are insufficient to generate refined hypotheses on the habits of those species. Such cases might prove to be especially insightful for the investigation of other fossil groups without clear living analogues. For instance, among the related clade of ground sloths, the Pleistocene *Megatherium americanum* was proposed to have been at least an occasional flesh-eater (Fariña, 1996; Fariña and Blanco, 1996). This hypothesis that was initially surprising because of the lack of modern analogues demonstrated to be mechanically possible and congruent with part of the available evidence.

Phylogeny

The wide range of morphological and adaptive diversity evident among cingulates also suggests more extensive cladogenesis than is reflected by the more mainstream systematic schemes. Engelmann's (1985) classic phylogenetic analysis (figure 4) recognized a primary dichotomy within Cingulata: the Glyptodonta and Dasypoda. The former includes eutatine armadillos, glyptodonts, and pampatheres; the latter all remaining armadillos (including peltephilines). Among Glyptodonta Engelmann viewed eutatine armadillos, including *Proeutatus* and *Eutatus* united as the Eutatini, as more closely related to the glyptodonts than to pampatheres. Engelmann (1985: 55) diagnosed the Glyptodonta by teeth with "a central island of compact dentine that is more resistant to wear than the surrounding dentine that comprises most of the tooth". He also assumed that a lobate dentition is primitive for cingulates. The Eutatini and glyptodonts were united in the Glyptodontoidea by Engelmann (1985) based on an anteriorly inclined ascending ramus, elevation of the basicranial axis relative to the palate, a relatively dorsal position of the mandibular condyle above the tooth row, a narrow and triangular promontory of the petrosal, and an outer layer of compact dentine that is more resistant than the dentine comprising most of the tooth.

Engelmann's (1985) analysis united the armadillos (excluding eutatines and pampatheres) in the Dasypoda based on simple, oval-sectioned teeth and the assumption that lobate dentition is primitive for cingulates. Within the Dasypoda the Dasypodidae and the Euphracta were recognized as sister taxa. The latter is nearly identical with the Euphractini of Scillato-Yané (1980, 1986) with the notable difference that it groups the peltephilines with *Macroeuphractus* (figure 4). Engelmann (1985) explained that the Euphracta is a fairly uniform morphological group that shares mainly plesiomorphic similarities, but also an ossified bulla with a characteristic configuration. Based on exoskeletal features, Carlini and Scillato-Yané (1996) proposed that, within the euphractines, *Macroeuphractus* is related to the *Chorobates*, *Macrochorobates*, and *Proeuphractus* clade, and that this group of four genera represents a radiation independent from that of the living genera.

Several of the recent analyses on the masticatory apparatus, though essentially morphofunctional in scope, have yielded information that has relevance for these phylogenetic interpretations. For example, the analysis of *Eutatus* and allied genera by Vizcaíno and Bargo (1998) supports the view that eutatines and typical armadillos are less closely related than was traditionally believed. Although these authors viewed inclusion of eutatines in the Glyptodonta as plausible, but in need of further study as at least one of the characters cited by Engelmann (1985) for the Glyptodontoidea was not corroborated by their work: the ascending ramus inclines anteriorly in *Proeutatus*, but not *Eutatus*. In addition, the basicranial axis and the mandibular condyle are also elevated relative to the palate and tooth row, respectively, in pampatheres. And, although the presence of two compact layers of dentine in eutatines and glyptodonts may be useful in supporting the monophyly of the Glyptodontoidea, De Iuliis and Edmund (2002) noted that a central island of compact dentine is present in *Vassallia*, but apparently absent in *Holmesina*.

Other examples for which the study of the masticatory apparatus provides clues to relationships involves the peltephilines, eutatines and pampatheres. In contrast to the apparent homogeneity of the dasypodids, the peltephilines show many peculiarities and are characterised by a set of shared features that have been related to a high degree of specialisation for herbivory (Vizcaíno and Fariña, 1997), such as the short and broad rostrum, wide nasal openings, short jaw, a fused and expanded mandibular symphysis, low condyle, teeth with chisel-like occlusal surfaces, and a U-shaped tooth row.

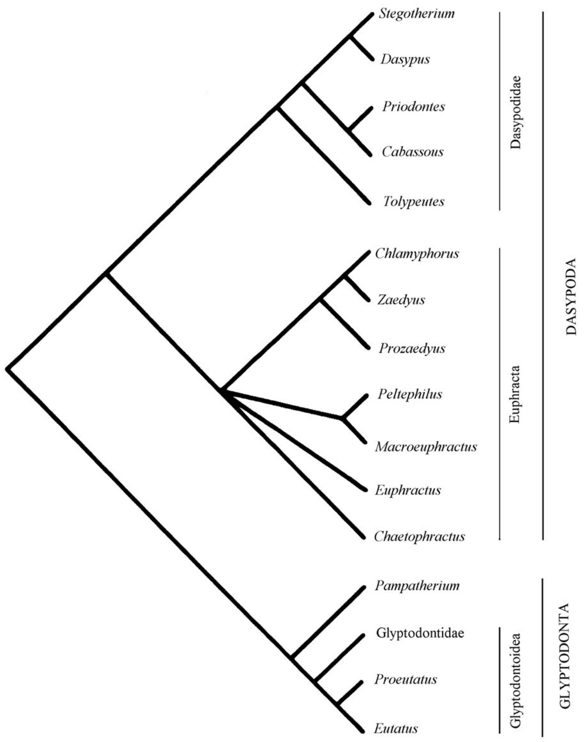

Figure 4. Phylogenetic scheme arrangement of cingulates of Engelmann (1985) / *Esquema de las relaciones filogenéticas de los Cingulata de Engelmann (1985).*

Within eutatines, Vizcaíno and Bargo (1998) identified a morphological group including *Stenotatus*, *Doellotatus*, *Ringueletia*, and *Eutatus* (see above). These are characterized by a gracile mandible with posteriorly inclined ascending ramus, a relatively long predental space, and oval shaped teeth. These authors pointed out that *Proeutatus* departs markedly from this pattern in possessing a more robust mandible, vertical ascending ramus, very short predental space, and cleary bilobate teeth. They stated that this morphological separation might reflect an early dichotomy within the well-defined clade of eutatines.

Pampatheres have been traditionally distinguished from dasypodids primarily on their larger size, the presence of only three bands of imbricating scutes, and osteoderms that bear a single keratinized scute each (see De Iuliis and Edmund, 2002). However, Vizcaíno *et al.* (1998) emphasized that the main differences between these groups occur in the masticatory apparatus, with that of pampatheres being more derived. The mechanical design of the masticatory apparatus among all pampatheres (Vizcaíno *et al.*, 1998, De Iuliis *et al.*, 2000) is nearly identical and has apparently undergone only minor variation since pampatheres first appear the fossil record, suggesting strong phylogenetic constraint in the form of skeletal and dental elements.

Gaudin and Wible (in press; see figure 5) tested traditional groupings with a phylogenetic analysis of 163 craniodental characters sampled across 19 living and extinct cingulates. According to them the most basal cingulate would be the peltephiline *Peltephilus*. The results of their analysis do not support the monophyly of the armadillos, as nested within them is the Miocene glyptodont *Propalaeohoplophorus* and the Pliocene pampathere *Vassallia*. Furthermore, none of the traditional groupings within armadillos are supported. The extinct eutatine armadillos are not monophyletic, with the Miocene *Proeutatus* as the sister taxon to *Propalaeohoplophorus* and *Vassallia*, the Pliocene *Doellotatus* nested within the euphractans (rendering that grouping paraphyletic), and the Pleistocene *Eutatus* even further removed. Relationships among the extant euphractan genera *Chaetophractus* Fitzinger, *Chlamyphorus* Harlan, *Euphractus*, and *Zaedyus* Ameghino are not unambiguously resolved, although they are monophyletic and more closely related to each other than to any fossil euphractans. Gaudin and Wible (in press) claimed that their startling results call for a broader analysis with more taxa and character systems (*e.g.*, postcrania, carapace). Although this is always desirable, we believe that their work actually provides a novel framework that casts new light on various curious aspects of the evolution of the masticatory apparatus of cingulates.

The position of the peltephilines agrees with McKenna and Bell's (1997) systematic arrangement, rather than the more traditional grouping of Scillato-Yané (1980 and references therein) and the first phylogenetic approach by Engelmann (1985). In these arrangements, the peltephilines were shoehorned among the dasypodids, despite, as noted by Vizcaíno and Fariña (1997), a markedly peculiar masticatory morphology for a dasypodid. However, based on the arrangement of Gaudin and Wible (in press) the anteriorly closed and U-shaped dental arcade, rather than the anteriorly edentulous condition in most other xenarthrans (except in the enigmatic Entelopsida), may now be viewed as plesiomorphic features shared with epitherians. This does not, incidentally, invalidate the idea that the masticatory apparatus reflects a derived adaptative type based on other features such as the completely fused and expanded mandibular symphysis, low condyle and teeth with chisel-like occlusal surfaces. This phylogenetic position for peltephilines also has implications for the primitive diet of Cingulata and perhaps all Xenarthra. At very least, it could cast doubt on the traditional hypothesis of insectivory.

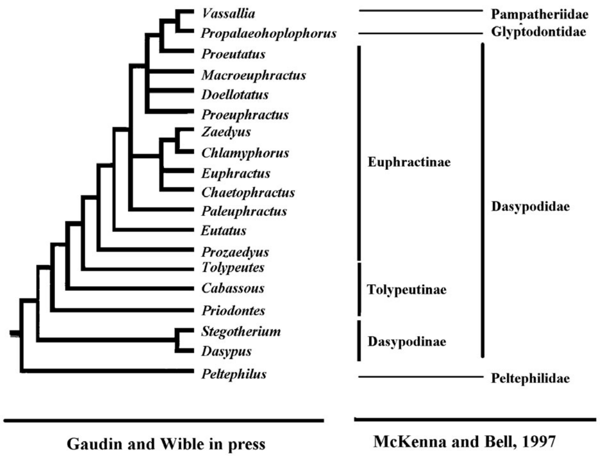

Figure 5. Phylogenetic relationships of cingulates following Gaudin and Wible (in press) and systematic scheme of McKenna and Bell (1997) / *Esquema de las relaciones filogenéticas de los Cingulata de Gaudin y Wible (in press) y esquema clasificatorio de McKenna y Bell (1997).*

Among the most interesting results of Gaudin and Wible's (in press) scheme are the implications suggested by the relationships among typical armadillos. For example, the idea that eutatines do not constitute a natural group is without precedent. Vizcaíno and Bargo (1998) assumed that eutatines had a common origin, even though they recognized considerable diversity in this group by identifying at least three different feeding types: a herbivorous type to include *Eutatus*, an omnivorous type with specializations for herbivory to include *Proeutatus*, and an omnivorous type with specializations for insectivory to include *Stenotatus*. As Gaudin and Wible (in press) noted, this would make eutatines the most trophically diverse of all the cingulate subgroups. Indeed, it is consistent with their findings that these taxa may, in fact, not be closely related to one another, rendering their wide degree of morphological separation from each other less puzzling.

Within the context of Gaudin and Wible's (in press) phylogenetic scheme, these differences no longer need be considered as different adaptations within a single lineage, but as adaptations within a larger clade that includes all Euphractinae (sensu Scillato-Yané, 1980, i.e., Euphractini + Eutatini). It could be argued that many of the craniodental features used by Gaudin and Wible (in press) that result in a phylogenetic arrangement combining taxa traditionally included in different groups (Euphractini and Eutatini *sensu* Scillato-Yané, 1980) might be homoplasies reflecting convergence toward similar dietary behaviour. It is worth noting that traditional systematic arrangements, such as that by Scillato-Yané (1980), are based on a long tradition of primarily relying on carapace characters [a practice against which De Iuliis and Edmund (2002) urged caution].

Thus, for example, the Eutatini were united based on the presence of large perforations along the posterior margin of the osteoderms, which implied abundant hair allowing eutatines to access colder environments than other Dasypodidae (Scillato-Yané, 1980). Given the new phylogentic arrangement of Gaudin and Wible (in press), these perforations may be viewed as independently acquired in the various Euphractinae sensu Scillato-Yané (1980).

Future directions

Morphofunctional studies on cingulates are useful beyond comparisons within the clade itself and generate new models that can be used to investigate and interpret adaptations in lineages without living representatives. An example is the enigmatic Palaeocene *Ernanodon* antelios Ding (figure 6) from eastern and central Asia (see Storch, 2003, and references therein), originally assigned to the order Edentata by Ding (1979). Today, most students of edentate phylogeny consider *Ernanodon* to be an Asian clade of myrmecophagous and/or fossorial mammals, convergent on Xenarthra and Palaeanodonta (*e. g.*, Rose and Emry, 1993). Recently, McKenna and Bell (1997) referred the suborder Ernanodonta to their order Cimolesta, which also includes Pholidota (see Storch 2003 for further discussion). The great development of the temporal and masseteric fossae, sagittal crest and zygomatic arches is indicative of powerful masticatory muscles and is not congruent with a myrmecophagous diet. In addition to a general resemblance with *Peltephilus* (muscle development, short mandible with strong symphysis and the position of the larger teeth in the anterior part of the mouth) preliminary analysis by one of us (SFV, in preparation) indicates the possibility of both important lateral and vertical masticatory movements, which would allow its reinterpretation as a herbivore instead of an animalivore, based on analogy with the approach applied to *Peltephilus* by Vizcaíno and Fariña (1997). This approach, i.e. fossil forms acting as biomechanical analogues for other fossils belonging to different lineages and without living representatives, opens an interesting field of study, not only for cingulates but also for mammals or even for vertebrates in general.

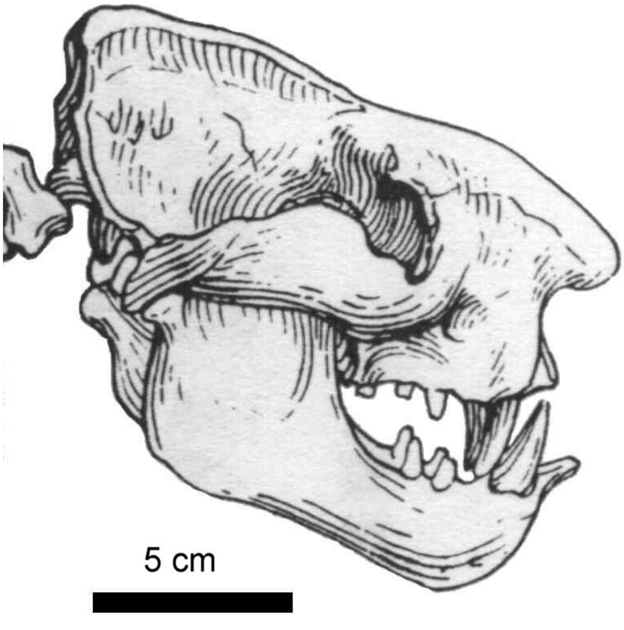

Figure 6. Skull of *Ernanodon antelios,* modified from Caroll,1988 / *Cráneo de* Ernanodon antelios, *modificado de Caroll, 1988.*

There are many fascinating subjects for the study of mastication in the clade. Among them, and due to its bizarre cranial and dental anatomy and to the large size of some of its members, clearly the most intriguing group to keep surprising xenarthrologists is the Glyptodontidae, whose apparent morphological homogeinity hiddens a great diversity in the form of the tooth lobes, the extension and arrangement of crests, etcetera.

Moreover, many opportunities of morphological, morphofunctional and evolutionary research on this fascinating group await to be undertaken. To mention a few, microwear studies, finite element analysis, strain gauge studies of extant taxa, biomechanical studies of the properties of xenarthran teeth *vs.* more standard mammalian teeth. We hope this study and the questions that remain open might prove a stimulus to additional, even more sophisticated studies of the masticatory apparatus of these very unusual animals.

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