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Skull Shape, Masticatory Apparatus, and Diet of *Vassallia* and *Holmesina* (Mammalia: Xenarthra: Pampatheriidae): When Anatomy Constrains Destiny

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The form and function of the masticatory apparatus of the fossil genera *Vassallia* and *Holmesina* are analyzed so that the possible dietary behaviors of these pampathere xenarthrans might be inferred. Analysis is based on comparisons of dental morphology and skeletal features (through RFTRA) associated with the masticatory musculature among the pampatheres, the extant dasypodids *Euphractus* and *Dasypus*, and the glyptodont *Propalaeohoplophorus*. A method is proposed for generating a moment arm of the massetericus independently of the muscle's line of action, which allows direct comparison among extant and fossil mammals. The masticatory apparatus of the pampatheres strongly resembles that of *Euphractus* among extant forms, but the development of muscular attachment sites indicates a more powerful musculature, particularly the massetericus; the taxa differ most markedly in dental morphology. Long moment arms about the jaw joint and large ratios of muscle to bite moments indicate forceful rather than quick movements. The various skeletal and dental features analyzed suggest that the masticatory apparatus of the pampatheres was more powerful and efficient in transverse chewing than in dasypodids and that they were primarily grazers consuming mainly coarse vegetation. These features, some shared with herbivorous ungulates, include wide, relatively flat mandibular condyles; condyles well dorsal to muscular insertion sites; expanded angular processes; unfused symphysis; a posteriorly extended tooth row; open-rooted teeth; mesial teeth that bear mainly transverse striations; distal teeth that are mesiodistally elongated, bear basined occlusal surfaces, and in *Vassallia* possess a central island of resistant dentine that acted as a functional analogue of an ectoloph; and teeth with a stepwise arrangement. The results of this study indicate that detailed analysis and comparison of morphology lead to useful predictions of behavior.

KEY WORDS: Xenarthra; pampatheres; biomechanics; mastication; diet.

INTRODUCTION

Pampatheres formed a conservative lineage of cingulates, or armored xenarthrans, between the Late Miocene and the Late Pleistocene of South and North America (Scillato-

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Yané, 1980; Hulbert and Morgan, 1993). Their relationship to other cingulates has not been satisfactorily resolved, and they have alternately been considered to be more closely related to dasypodids (e.g., Hoffstetter, 1958; Robertson, 1976; Cartelle and Bohorquez, 1985) or glyptodonts (e.g., Patterson and Pascual, 1968, 1972; Engelmann, 1985; Carlini and Scillato-Yané, 1993). It is clear, however, that the dasypodid, glyptodont, and pampatheriid lineages have followed independent histories since the middle Eocene Mustersan Age (Scillato-Yané, 1986), some 45–48 million years ago (Flynn and Swisher, 1995). We follow the recent tendency, as by Edmund (1987) and Downing and White (1995), to regard pampatheres as a separate family, pending a comprehensive phylogenetic review of cingulates.

Pampatheres bear a strong general resemblance to dasypodids but never achieved their diversity and abundance. Traditionally, they are distinguished from dasypodids primarily on their larger size [estimated to have reached nearly 200 kg in *Pampatherium* (Fariña and Vizcaíno, unpublished data)], the presence of only three movable transverse bands of imbricating scutes between the pectoral and the pelvic bucklers (dasypodids usually have more than three) and osteoderms that each bear a single keratinized scute (more than one scute contributes to the osteoderms in dasypodids) (De Iuliis and Edmund, in press). However, the results of this study emphasize that the main differences between these groups are in the form of the masticatory apparatus, with that of pampatheres being more derived.

Pampatheres have traditionally been considered as essentially herbivorous (Winge, 1941, p. 345). Edmund (1985) proposed that they, along with glyptodonts, were browsers or grazers, rather than omnivores or insectivores as are armadillos.

This study describes and analyzes the skeletal and dental morphologies associated with the masticatory apparatus of *Vassallia* and *Holmesina* and investigates the jaw mechanics of these pampatheres. The results are compared with the musculature and mechanics of the extant dasypodids *Dasypus* and *Euphractus* so that the possible behavior and diet of pampatheres may be inferred. Some comparisons are made to the primitive glyptodont *Propalaeohoplophorus australis* from the Miocene of Patagonia. Other pampatheres, such as *Pampatherium*, are similar to those discussed here. Study of the masticatory apparatus of this genus is in progress by the authors, as there are various specific differences, as well as taxonomic aspects, that cannot be adequately covered in this report.

MATERIALS AND METHODS

Acronyms and Abbreviations

AMNH—American Museum of Natural History, New York, USA.
FMNH—Field Museum of Natural History, Chicago, USA.
MLP (DCPV)—Museo de La Plata, Departamento Cientifico Paleontología Vertebrados, La Plata, Argentina.
MLP (DCZV)—Museo de La Plata, Departamento Cientifico Zoología Vertebrados, La Plata, Argentina.
ROM—Royal Ontario Museum, Toronto, Canada.
m—Lower molariform

M—Upper molariform
Mm—Moment arm of the massetericus
Mt—Moment arm of the temporalis
Mb—Moment arm at the bite point
RFTRA—Resistant fit theta-rho analysis
D—RFTRA distance

List of Specimens

Pampatheriidae

Holmesina cf. *H. occidentalis* Hoffstetter, 1952, 1953. Pleistocene, Corralito, Santa Elena Peninsula, Ecuador.

ROM 3881—Well-preserved, nearly complete, and undistorted skull, missing small portions and left m9.

ROM 4954—Nearly complete right and partial left dentaries. Left and right m2 and right m3 preserved; right and left m1 and left m4–m6 missing; other molariforms partially preserved.

ROM 4955—Right dentary and symphyseal portion of left, missing anterior tips, m1, m3, and m4; m5–m9 incomplete.

ROM 4956—Posterior half of right dentary, missing tip of coronoid process. m7–m9 partially preserved.

ROM 4964—Partial right horizontal ramus, m2–m9 completely or partially preserved, m1 missing.

Vassallia maxima Castellanos, 1946. Late Miocene–Early Pliocene, Corral Quemado, Catamarca, Argentina.

FMNH 14424—Nearly complete and well-preserved skull and right dentary, with slight dorsoventral compression of left cranium. Right M6, and m2, m6–m9 preserved; left M8 and M9 broken at alveolar border; other molariforms missing. See also De Iuliis and Edmund (in press).

Dasypodidae

Euphractus sexcinctus Linné, 1758

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

MLP (DCZV) 1236. Skull without mandible. Provenance: Misiones, Argentina.

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

ROM R2019—Skull and mandible. Provenance: Argentina

Dasypus novemcinctus Linné, 1758.

MLP (DCZV) 1750. Skull and mandible. Provenance: Esteros de Ituzaingó, Corrientes, Argentina.

MLP (DCPV) 66, 77, 78 and 80- Skulls and mandibles. Provenances unknown.

ROM R676—Skull and mandible. Provenance: Florida?

Glyptodontidae

Propalaeohoplophorus australis (Moreno, 1882). Early Miocene, Santa Cruz, Argentina. MLP (DCPV) 16-15. Complete skeleton (figured by Lydekker, 1894; Scott, 1903–1904).

Methodology

The relationship between form and function of the masticatory apparatus and diet has been the subject of numerous studies, particularly among vertebrate paleontologists, who often must rely only on form to infer function and diet (Turnbull, 1976; Finch, 1982; Witmer and Rose, 1991; Gambaryan and Kielan-Jaworowska, 1995). Various studies on jaw mechanics have demonstrated correlations among the behavior, diet, and form of the skull, jaws, dentition, and musculature in extant mammals (e.g., Maynard Smith and Savage, 1959; Turnbull, 1970; Moore, 1981; Schumacher, 1985; Smith, 1993). Such studies have been useful in the reconstruction of musculature of fossil mammals and provide a framework for investigation of their diet and behavior. Various authors have used this approach on edentates (e.g., Naples, 1987, 1989; Vizcaíno, 1994; Vizcaíno and Fariña, 1997; Vizcaíno and Bargo, 1998).

Masticatory Musculature

The areas of origin and insertion of the masticatory musculature of the pampatheres were reconstructed based on features of the skeletal elements, following the methods of Turnbull (1976), Finch (1982), and De Iuliis (1988), 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 attachment sites of the masticatory musculature are usually unambiguously indicated in mammals by features of the skull and jaws. Such features include muscular scar lines, ridges, and crests, which suggest the attachment of aponeuroses and tendons, and texture of the attachment surfaces, which indicate fleshy or tendinous origins and insertions. The musculature reconstructed and used for analyses includes the temporalis, massetericus (including the zygomaticomandibularis), and pterygoideus lateralis/medialis.

Jaw Mechanics

The mandible may be considered to represent a lever, with its 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 line of action of the muscles have been used to compare the effective strength of each muscle and the relative bite forces among mammals (e.g., Maynard Smith and Savage, 1959; Turnbull, 1970; Finch, 1982). Application of these concepts to fossil taxa may provide important information on the masticatory apparatus and, in combination with other evidence (e.g., cranial morphology, dentition, paleoclimate, comparison with extant forms), insightful data on the paleobiology of these forms. These methods of inquiry require an interpretation of the form and position of the masticatory musculature. In extinct mammals the position of the muscles is often reasonably clear due to the presence of crests, surface texture, apophyses, and depressions. However, knowledge of the muscular arrangement in the nearest living relatives is essential. Even so, the internal composition or architecture of the musculature of extinct forms cannot be known. Therefore, except possibly in cases of extreme morphological similarity and close phylogenetic relationship, an estimate of a particular muscle's line of action is equivocal and may be open to various interpretations (*vide infra*).

The moment arms of the lines of action of the temporalis and massetericus muscles are estimated so that the mechanics of the masticatory apparatus of pampatheres may be described and compared with those of dasypodids. Total lengths of the skull were standardized to allow the comparisons between forms of different sizes. Modification of the methods of Maynard Smith and Savage (1959) and Smith and Redford (1990) is proposed, as their results are unsuitable for the fossil forms because the authors did not explain clearly how the lines of action of the muscles, particularly of the massetericus, were determined. Alternative interpretations of the origin and inclination of the line of action may result in considerably different moments. Smith and Redford (1990) proposed that the line of action of the massetericus be determined by its most posterior insertion, which in *Euphractus* and *Dasypus* (the taxa studied by these authors) lies nearly at the angular process. It may be inferred from Smith and Redford (1990, Figs. 2b and 3b) that the other end of the line of action lies at the midpoint of the length of the origin of the massetericus on the zygomatic arch. In pampatheres the geometry of the posterior margin of the angular process, which is greatly enlarged (particularly below the angular process), renders the position of the line of action ambiguous.

In order to avert this uncertainty we propose a geometric model for the estimation of moment arms for the massetericus that may be compared among fossil and extant mammals. This model requires calculation of averages of the moment arms generated from the most anterior and posterior positions of the massetericus's origin and insertion, as follows.

1. A line of action is drawn from the most anterior insertion on the masseteric fossa to the middle of the origin on the zygomatic arch.
2. A second line of action is drawn between the origin on the zygomatic arch as described above and the most posterior insertion, the latter defined by the most posterior position of the margin of the angular process.
3. The angle between these lines is subdivided into x equal subangles, which generates a total of $x + 1$ lines of action. Any number x may be used, depending on the size of the insertion area, although in practice five lines of action are apparently sufficient because the angular deviations among different taxa are minimal, particularly as the desired quantity is an averaged vector.
4. The moment arms are measured through the temporomandibular joint and at right angles to the lines of action.
5. The arithmetic mean of the moment arms is calculated. This value represents the moments generated by the masseteric musculature on the middle part of its origin on the zygomatic arch.
6. Repeat steps 1–5 for lines of action from additional distinct points of the area of origin. Here, the most anterior and most posterior origins of the massetericus were used.

7. With these data a mean of means for the moment arm of the massetericus is calculated.

In this way values for the moment arm are obtained independently of the actual line of action of the muscle. Values for different species may be compared directly when they are obtained with this method. Further, it renders unnecessary the determination, usually equivocal, of a specific line to describe the action of the muscle and estimation of the muscle's relative force based on the line of action.

The situation for the temporalis is relatively straightforward because most of this muscle's fibers in living mammals usually converge to insert tendinously on the anterior edge of the coronoid process, which thus defines the temporalis's line of action with increased precision. There is no evidence of multiple attachments of this muscle to the cranium of the pampatheres. Thus the resulting analyses on the temporalis in the pampatheres may be compared directly to the results of Smith and Redford (1990). Even so, a procedure analogous to that used with the massetericus was applied in analyses of the temporalis. The lines of action were estimated from the most anterior, middle, and most posterior origins on the skull and from a single insertion on the coronoid process, at the lowest end of the ridge on its anterodorsal part.

Once the moment arms for the temporalis and massetericus have been calculated, comparisons between the pampatheres and the dasypodids are continued following Smith and Redford (1990). Interpretations on the relationships between bite force and velocity are conducted by comparing the proportions of the combined moment arms of the massetericus and temporalis to those based on different tooth positions (i.e., the central point of the anteriormost, middle, and posteriormost teeth).

The occlusal patterns and mandibular movements are determined through study of the temporomandibular joint, the form and arrangement of the dentition, including occlusal wear patterns, and the form and structure of the mandibular symphysis.

Shape Analysis

The shapes of skulls and mandibles are analyzed using the Procrustean method RFTRA. Procrustean methods allow the analysis of form through the superposition of one form onto another using the position of landmark points. RFTRA was developed to identify and measure the 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). Software for performing RFTRA analyses was developed by R. E. Chapman in 1989. This program also generates dendrograms of the unweighted pair-group method using arithmetic average (UPGMA) cluster analysis based on RFTRA distances. The following landmarks (homologous and geometric points) were used.

Skull: 1—ventral margin of the occipital condyle; 2—dorsal margin of the sagittal crest; 3—parietofrontal suture on the sagittal plane; 4—nasofrontal suture on the sagittal plane; 5—anterior end of the nasal; 6—anterior end of the premaxilla; 7—mesial margin of first molariform; 8—premaxillomaxillary suture on the ventral margin; 9—distal margin of the last molariform; 10—posterior end of the pterygoideus; 11—squamosoparietofrontal suture; 12—lacrimomaxillofrontal suture; 13—nasomaxillopremaxillary suture; 14—infraorbital foramen; 15—ventralmost level of the zygomatic arch; 16—ventral end of the mastoid process; 17—zygomaticosquamosal suture on the ventral margin of the arch; 18—mandibular fossa.

Mandible: 1—posterior end of the condyle; 2—junction between the condylar and coronoid processes; 3—dorsal tip of the coronoid process; 4—distal margin of the last molariform; 5—mesial margin of the first molariform; 6—anterior symphyseal margin; 7—intersection of the ventral margin of the dentary with the line extending down perpendicularly from the line drawn between landmark 6 and landmark 10 and at one-quarter the distance between 6 and 10; 8—intersection of the ventral margin of the dentary with the line extending down perpendicularly from the line drawn between landmark 6 and landmark 10 and at one-half the distance between 6 and 10; 9—intersection of the ventral margin of the dentary with the line extending down perpendicularly from the line drawn between landmark 6 and landmark 10 and at three-fourths the distance between 6 and 10; 10—posterior margin of angular process; 11—anterior mental foramen.

RESULTS

Cranial Morphology

Skull

The skull of the pampatheres (Fig. 1) bears a general resemblance to that of the common dasypodid pattern, particularly as the rostrum is elongated, but the latter skull type is lightly built and narrower. In contrast, the pampathere skull is remarkably similar to that of euphractine dasypodids, except for the dentition. The skull of *Euphractus* and the pampatheres is massively built, robust, and wide, particularly across the postorbital processes and the occiput. Although pampatheres are much larger mammals, *Euphractus* has a slightly wider skull, followed by *Vassallia*, in relation to condylonasal length, but the pampathere skulls are deeper in the braincase and frontal regions. The skulls of *Vassallia* and *Holmesina* are clearly similar, with that of the latter being somewhat more gracile and elongated, particularly anteriorly.

The postorbital constriction is prominent in pampatheres and euphractines, in contrast to the condition in dasypodines, and it occurs relatively more anteriorly in *Vassallia* than *Holmesina* and *Euphractus*, so that its braincase is relatively longer. The temporalis lines converge abruptly in *Vassallia*, near the level of the postorbital constriction, to form a prominent sagittal crest. In the other pampatheres the crest is lower and begins slightly further posteriorly, being notably raised only centrally. A crest is absent in the skulls of *Euphractus* examined, although Smith and Redford (1990) stated that a prominent crest was present. The temporalis lines in this genus do not converge at the sagittal midline but continue separately on the parietal.

The zygomatic arches are massive and laterally bowed, particularly in *Euphractus*, and are relatively longer in *Vassallia* and *Holmesina*. The arch is dorsoventrally deeper in the pampatheres, particularly near the zygomaticosquamosal suture, and its medial and ventrolateral surfaces are markedly more rugose. A large muscular origin site, probably for the deep massetericus, is clearly marked on the ventral half of the lateral surface of the arch. Anteroventrally the arch bears a ventrally projecting protuberance in all three genera, being most developed in *Vassallia*. The arch is massively developed in this region and its anteroventral surface is markedly rugose. The protuberance is mediolaterally narrower

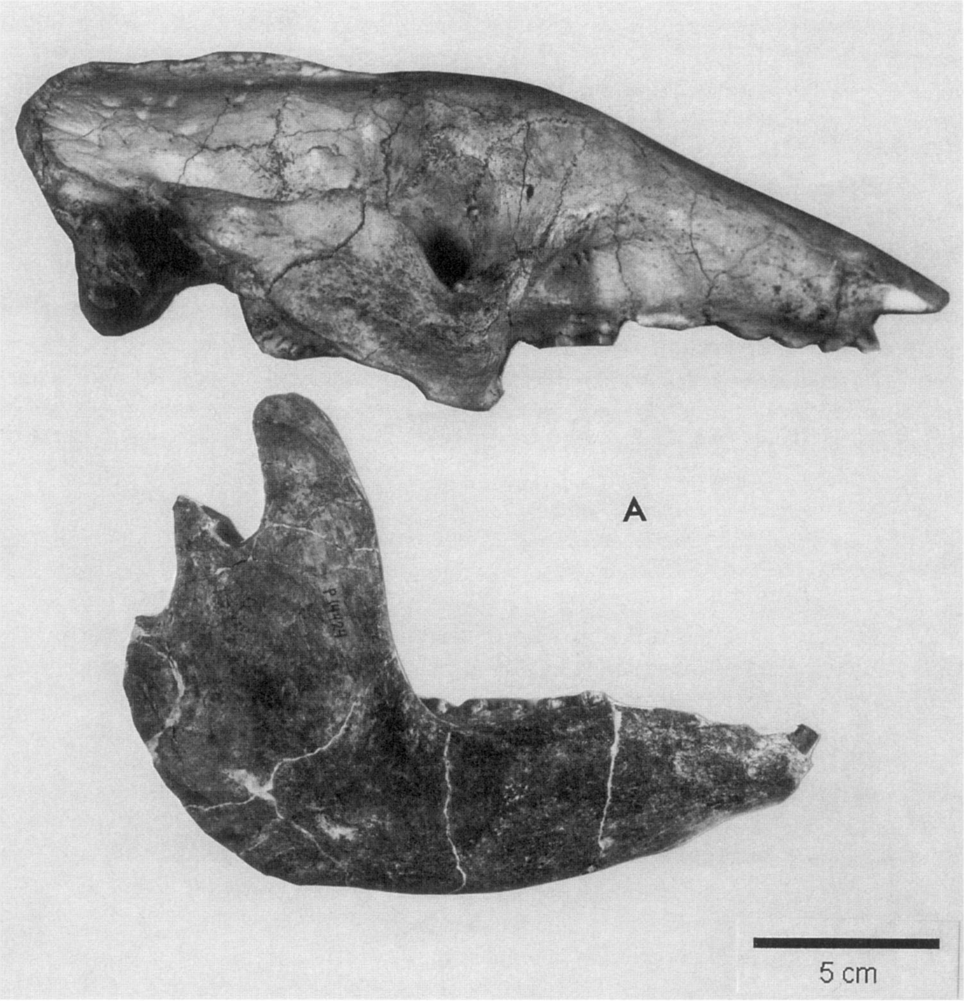


Fig. 1. (A) Skull and mandible of *Vassallia maxima* (FMNH P14424). (B) Skull (ROM 3881) and mandible (ROM 4954) of *Holmesina* cf. *H. occidentalis*.

and less rugose in *Holmesina*, and relatively smooth and less prominent in *Euphractus*. It projects ventrally approximately to the level of the occlusal surfaces of the teeth in this genus, but well beyond this level in the pampatheres. The temporal fossa is rugose, heavily scarred for attachment of the temporalis. In the pampatheres its ventral margin is marked by a low ridge, relatively smooth in *Holmesina* and rugose in *Vassallia*, that extends posteroventrally from the postorbital process approximately to the level of the optic canal. From here the margin is marked by a rugose, almost horizontal and higher ridge, more prominent and nearly crest-like in *Vassallia*, that becomes confluent with the leading edge of the posterior zygomatic root. In *Euphractus* the anteroventral margin runs nearly horizontally to near the ethmoid foramina and is marked by a faint ridge.

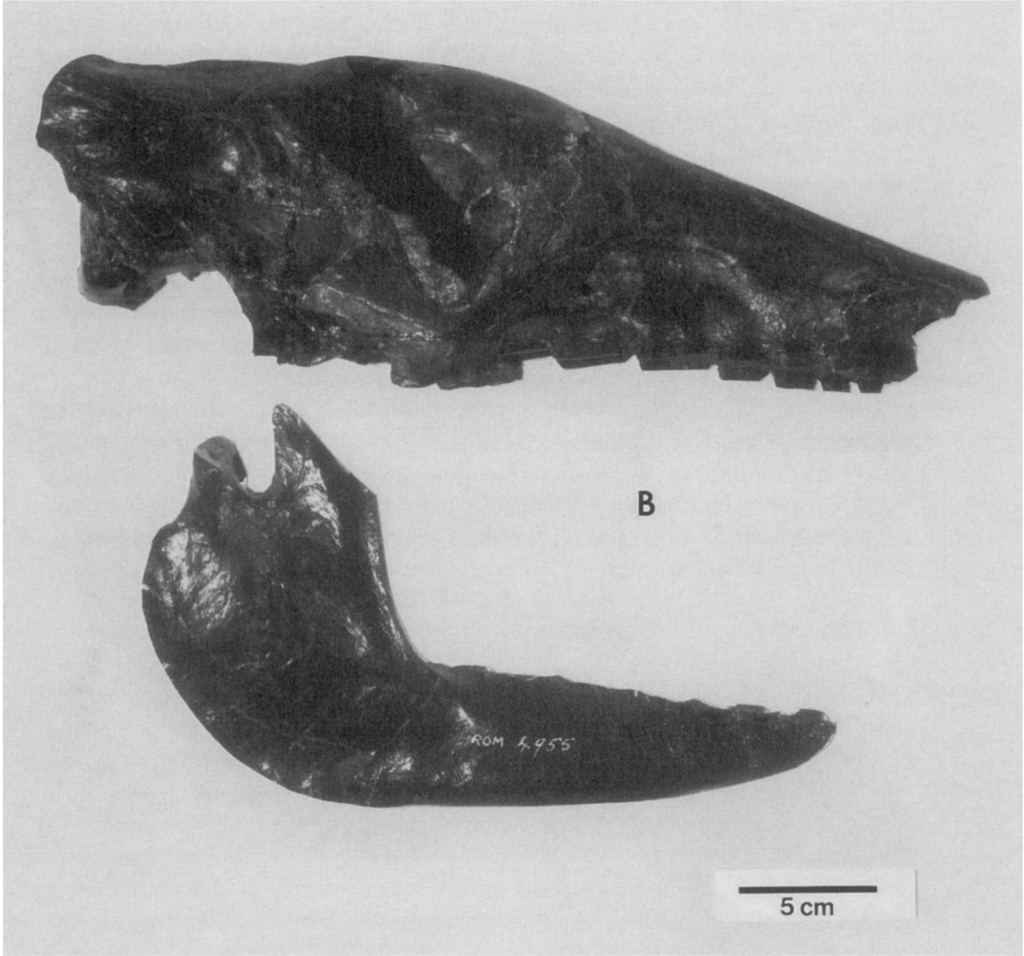


Fig. 1. Continued.

Posteriorly, however, the margin is marked by a crest-like flange of the squamosal that is longer than that in pampatheres. It becomes confluent with the triangular, bony ledge that forms most of the dorsal surface of the posterior zygomatic root, and supports, on its ventral surface, the mandibular fossa. A similar ledge is present in *Vassallia*, but absent in *Holmesina*. The mandibular fossa is transversely elongated, approximately elliptical in pampatheres and reniform in *Euphractus*. It is nearly flat, but slightly convex transversely and anteroposteriorly. The pterygoid flanges are extremely stout and rugose. They do not project far ventrally in pampatheres, but their wide ventral surface faces ventrolaterally. In *Euphractus* they are relatively delicate, smaller, smooth, and project ventrally. The surface of the pterygoid and alisphenoid between the sphenopalatine foramen and the foramen ovale is rugose and bears prominent ridges in *Holmesina*. This region in *Vassallia* and *Euphractus* is also rugose but less prominently scarred.

In *Dasypus* and *Euphactus* the anterior surface of the zygomatic arch and the maxillary rostral wall anterior to it bear a large fossa for the nasiolabialis muscles (Smith and Redford, 1990). A similar fossa is present in pampatheres and strongly resembles that of *Euphractus* in form and relative size. The fossa is relatively largest in *Dasypus*.

Pampatheres have been included together with glyptodonts by Engelmann (1985), even though there seem to be considerable differences between these groups of cingulates. While differences are strongly marked between the large Pleistocene glyptodonts, such as the familiar *Glyptodon*, and pampatheres, there is more similarity between the earlier glyptodonts and pampatheres. For example, the skull of *Vassallia* is remarkably reminiscent of those of earlier glyptodonts, although the nature of the similarity is unclear (see Introduction). The skull of *Propalaeohoplophorus* (Fig. 2) is higher and deeper, with a more strongly inclined dorsal cranial profile, and less elongated, with a relatively abbreviated rostrum. In dorsal view the rostrum is relatively narrower than in pampatheres. The zygomatic arch is of nearly uniform dorsoventral height and thus lacks the pronounced dorsoventral expansion at the zygomaticosquamosal suture present in pampatheres and euphractines. However, the anterior zygomatic buttress is considerably more robust than in these cingulates, and its anteroventral portion is extended into a conspicuously elongated and transversely widened descending process.

Mandible

The mandible of pampatheres resembles but is more robust than that of *Euphractus*, which differs markedly from the thin and elongated mandible of *Dasypus* (Smith and Redford, 1990). The horizontal ramus is deeper in pampatheres, especially in *Vassallia* (Fig. 1a). The symphysis is unfused in *Euphractus* and *Dasypus* and nearly all the pampathere specimens, except ROM 4955, which is a large and probably older individual.

In the pampatheres and *Euphractus* the coronoid process is high, flat, rises steeply, and bears laterodorsally a curved crest that extends anteroventrally into the leading edge of the coronoid process. The mandibular condyle, relatively wider in pampatheres, is approximately rectangular, with the long axis transverse, and faces anterodorsally. It is concave transversely in all three genera and slightly concave anteroposteriorly in *Vassallia*. Its medial surface bears a large rugose surface for insertion of the pterygoideus medialis. It is clearly larger in *Vassallia* than *Holmesina*, despite the considerably smaller size of the former species. It is less rugose and approximately similar in size in *Holmesina* and *Euphractus*.

A prominent ridge lies on the anteroventral part of the medial surface of the coronoid process in pampatheres. It is particularly raised in *Vassallia*, in which it begins near the anterodorsal edge of the process and curves toward the distal alveolar margin of m9. It is weaker in *Holmesina* and its dorsal part is barely perceptible. This ridge apparently marks the anterior margin of the temporalis's insertion. The ventral margin is indicated in *Vassallia* by a low ridge running anteroventrally from the medial buttress of the mandibular condyle. A similar, though much lower ridge, occurs in *Holmesina*.

The area of insertion of the massetericus is relatively larger in the pampatheres. However, the base of the coronoid process bears a shallow masseteric fossa in *Holmesina* and *Euphractus*, whereas this surface is nearly flat in *Vassallia*. The dorsal margin of

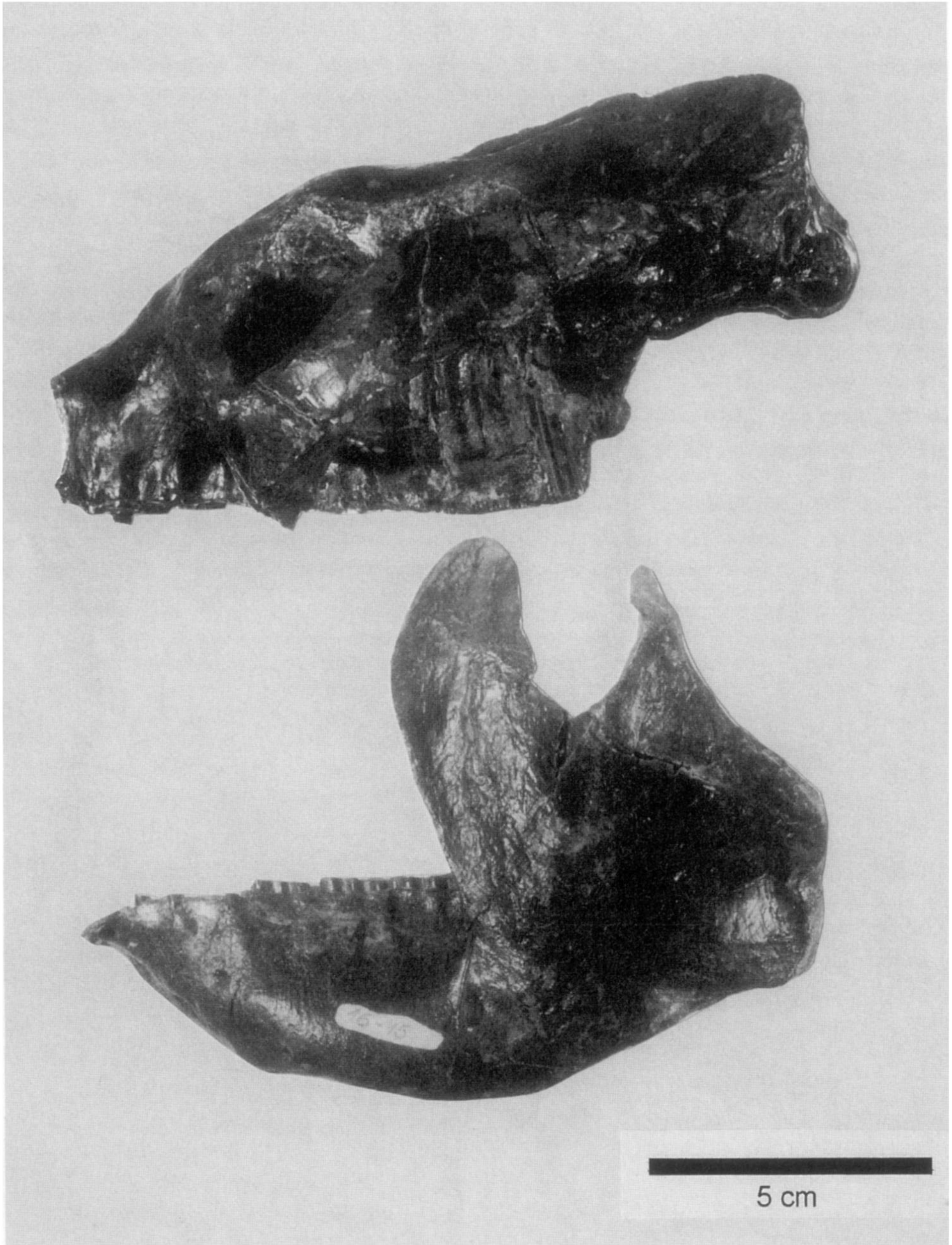


Fig. 2. Skull and mandible of *Propalaeohoplophorus australis* (MLP 16-15).

the insertion coincides approximately with the dorsal margin of the fossa in *Holmesina* and a low ridge in *Vassallia*. In both genera the margin follows the anterior edge of the coronoid process and extends onto the horizontal ramus. In *Euphractus* the dentary bears a concave region ventral to the intersection of the horizontal and ascending rami, and the curved anterior margin of this shallow depression marks the anteroventral insertion of the massetericus (Smith and Redford, 1990). The insertion, indicated by a similar depression, extends considerably further forward in the pampatheres, approximately to the level of the middle part of m7. From here the margin of the massetericus largely follows the ventral and posterior edges of the angular process.

The angular process is considerably larger in pampatheres than in *Euphractus*, due largely to posterodorsal expansion, and lies very near the mandibular condyle. Its lateral posteroventral surface bears prominent ridges and scar lines. These are less prominent in *Holmesina*, and less so still in *Euphractus*. The medial surface of the process is heavily and similarly scarred in all three genera, especially along a crescentic area adjacent and parallel to its posterior and ventral margins.

The horizontal ramus of the dentary of *Propalaeohoplophrous* (Fig. 2) resembles that of *Vassallia* in proportions but is higher than that of *Holmesina*. The dentary differs from that of pampatheres in that the dorsal portion of its ascending ramus is displaced markedly forward so that the coronoid process inclines strongly anteriorly and the condyloid process is oriented nearly vertically.

Dentition

The jaws of *Euphractus* are isognathous (Smith and Redford, 1990). As is usual in dasypodids, the homodont dentition of *Euphractus* consists of 9 upper and 10 lower simple, peg-shaped teeth. An external layer of durodentine surrounds the large central portion formed by softer vasodentine (Smith and Redford, 1990). In lateral view the occlusal surfaces are generally beveled, with the mesial wear surface markedly longer in the teeth of the central part of the tooth row. The mesial and distal wear surfaces are nearly equal in more distal teeth. This wear pattern results in sharp buccal and lingual cusps, and a shallow depression of the vasodentine. The two mesial mandibular teeth are distinct. They are smaller than the others and lie mesial to the first upper tooth, which is an incisor because it is implanted in the premaxilla. The first lower tooth occludes against the premaxillary palate, as does the mesial half of the second; its distal half is strongly and obliquely worn against the mesial surface of the upper incisor.

Pampatheres are also isognathous, but their dentition differs considerably from that of *Euphractus*. Indeed, it is in this character that the masticatory apparatuses of these groups differ most markedly. The pampathere dentition is heterodont, consisting of nine upper and lower teeth, arranged in a short mesial series of oval or reniform, peg-like teeth, and a distal set of bilobate teeth (Fig. 3). Pampathere teeth, regardless of shape, are referred to as molariforms because it is difficult to differentiate them into the typical mammalian series. Edmund (1985) stated that the premaxillomaxillary suture presumably occurs between the alveoli of the first two upper teeth and perhaps contributes to the mesial part of the M2 alveolus, although some authors (e.g., Winge, 1915; Castellanos, 1927) believed that M1 and M2 were implanted in the premaxilla (see De Iuliis and Edmund, in press). Pampatheres also differ in that the coronoid process is relatively further

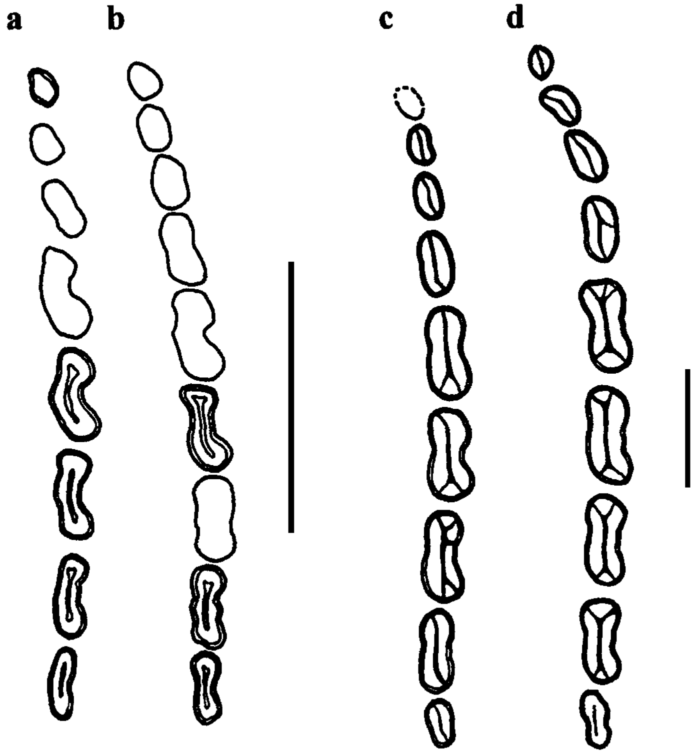


Fig. 3. Diagrammatic tooth rows. (a) *Vassallia maxima* (FMNH P14424), lower right side. (b) *V. maxima* (FMNH P14424), composite upper left side, with M6 reversed from right side. (c) *Holmesina* cf. *H. occidentalis* (ROM 4964), composite lower right side, with m2 from ROM 4955. (d) *H.* cf. *H. occidentalis* (ROM 3881), composite upper left side, with M9 reversed from right side. Scale bar represents 5 cm.

anterior. It usually covers all of m9 and the distal part of m8. In *Euphractus* only the distal part of the last tooth is covered.

In *Holmesina* the teeth of the skull and mandible are set in a step-like arrangement. The presence of such an arrangement in *Vassallia* is ambiguous, as its dentition is incompletely preserved. Apparently, however, the step-like arrangement is present, based on the preserved portions of m6–m9.

The molariforms of *Holmesina* and *Vassallia* are morphologically similar, with only very minor differences (De Iuliis and Edmund, in press). However, there are apparently significant structural differences. Hoffstetter (1958) described the teeth of cingulates as composed of a small central portion of osteodentine surrounded by compact dentine, forming most of the tooth, and finally, by a layer of cementum. In some lineages, particularly glyptodonts, the osteodentine, which structurally resembles vasodentine, is harder. This condition occurs in *Vassallia* (Fig. 3a), at least in the teeth preserving the occlusal surface, as well as in eutatine armadillos. In *Vassallia* the osteodentine is a narrow, elongated, and nearly straight or lingually convex strip, slightly widened mesially and distally, and raised in relief, as is the periphery of the tooth; these areas are less worn than the compact dentine (De Iuliis and Edmund, in press). A similar condition exists in eutatine armadillos, except that the osteodentine is relatively short due to the elliptical form of the molariforms and variable in width. Also, the osteodentine is oriented obliquely following the long axis of the tooth (see Vizcaíno and Bargo, 1998).

In *Holmesina* the osteodentine is not well preserved and usually missing (Figs. 3c and d), suggesting that it was considerably softer. The central part of the tooth bears a narrow longitudinal cavity, along which the tooth tends to split longitudinally, thus dividing the tooth in half. In some teeth multiple fractures radiate from the ends of the cavity toward the periphery of the tooth (De Iuliis and Edmund, in press). The more mesial dentition, m1–m5, is worn nearly flat, whereas the central parts of m7–m9 are more worn than the peripheral margins, which results in a shallow basin. The m6 is intermediate, with a very shallow basin.

The occlusal surfaces of the molariforms of *Holmesina* are variably striated. M1–M5 bear numerous transverse striations, although they are less conspicuous and more nearly rectilinear and parallel than as illustrated by Edmund (1985, Fig. 7). Considerably fewer and usually less prominent mesiodistally oriented striations also occur. In m1–m5 the striations are nearly all transversely oriented; few run mesiodistally or obliquely. The striations on M6 are largely transverse, although a few are variably oriented, but are fewer and finer than on the more mesial molariforms. On m6 striations are similarly oriented and are more prominent than on M6. The striations on molariforms distal to M6 and m6 are very fine and the occlusal surface is almost smooth. The striations may be perceived under low magnification. In M7 and m7 they are largely transverse, although the number of variably oriented striations is increased. In M8 and m8 variably oriented striations are increased, although most are still transversely oriented. M9 is similar. Striations are imperceptible in m9.

The toothrows of *Propalaeohoplophorus* are elongated and extend far distally, as is also the case in pampatheres, but they remain parallel much further mesially in the former and turn gently to form a well-rounded arcade, in contrast to the converging toothrows of pampatheres. The molariforms are distinctly trilobate, with a raised central island of resistant dentine. Lobation begins more mesially than in pampatheres. The molariforms in the latter are more nearly bilobate, although some teeth have what may be described as an incipient middle bulge.

Masticatory Musculature

Temporalis

In the pampatheres the temporalis arose from the scarred surface of the temporalis fossa and a broad aponeurosis covering the temporalis (Fig. 4), as occurs in *Euphractus* (Smith and Redford, 1990) and most other mammals (Turnbull, 1970). It extended anteriorly approximately as in *Euphractus*, but it extended farther posteriorly, nearly to the margins of the nuchal crests, rather than nearly to the level of the posterior zygomatic buttress, as is indicated by Smith and Redford (1990; Fig. 3b). The temporalis was thus probably relatively larger in the pampatheres than in *Euphractus*. The elongated braincase and temporal fossa of *Vassallia* suggest that its temporalis was larger than that of

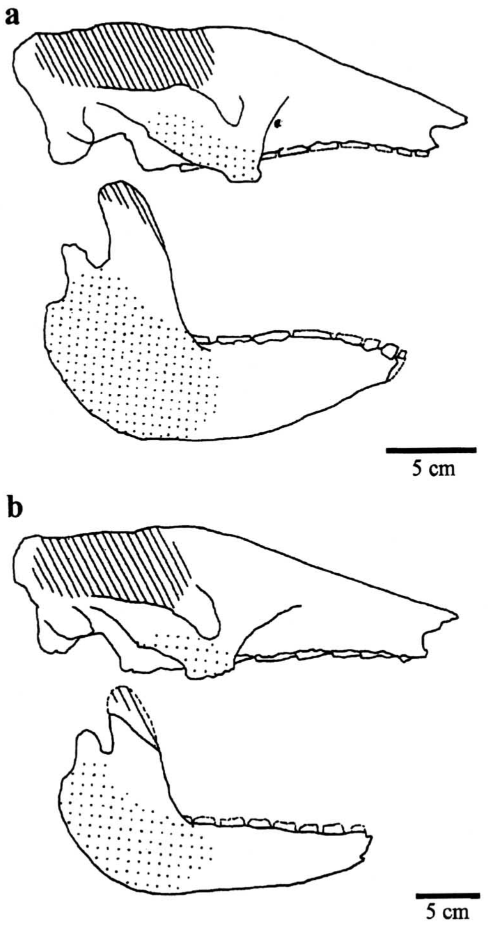


Fig. 4. Reconstruction of areas of origin and insertion of the main masticatory muscles. (a) *Vassallia maxima*. (b) *Holmesina* cf. *H. occidentalis*. Parallel lines represent temporalis; dotted regions represent massetericus.

Holmesina. The temporalis inserted mainly and probably tendinously on the anterior edge of the coronoid process, as in *Euphractus*, based on similarity of bony features. Smith and Redford (1990) stated that a few of the temporalis's fibers also inserted on the surface of the coronoid process, presumably through fleshy attachment, but did not indicate the extent of the insertion. The lateral and medial surfaces of the dorsal part of the coronoid process are more prominently scarred in the pampatheres and suggests a larger area of insertion than in *Euphractus*.

Massetericus

The masseteric musculature originates in nearly all mammals from the ventral and ventrolateral surfaces of the zygomatic arch and inserts mainly on the lateral surface of the angular process (Fig. 4). Superficial and deep components are usually recognized, although in some forms, such as ungulates and rodents (see Turnbull, 1970), the massetericus may be further subdivided. A zygomaticomandibularis, originating from the medial surface of the arch and inserting mainly on the masseteric fossa, is also usually recognized (Turnbull, 1970). Smith and Redford (1990, p. 35) stated that the massetericus "of *E. sexcintus* originates from the ventral margin of the zygomatic arch and an external aponeurosis and inserts on the expanded angular process" and "is divisible along connective tissue planes into at least five compartments." This description suggests that these authors did not consider the zygomaticomandibularis. The medial surface of the arch clearly indicates muscular attachment in pampatheres and *Euphractus*, and it is present in nearly all other mammals (Turnbull, 1970). However, Smith and Redford (1990, Fig. 3c) include the masseteric fossa within the insertion of the massetericus. As the divisions of the masseteric musculature cannot be reliably reconstructed in pampatheres, it is recognized as including all the musculature originating from the zygomatic arch and inserting largely on the masseteric fossa and lateral surface of the angular process. Skeletal features indicate that the masseteric musculature of pampatheres was probably similar in form to that of *Euphractus*. However, the expanded angular process and the larger zygomatic arch, including its more robust anteroventral protuberance, of pampatheres suggests larger and more powerful masseteric musculature than in *Euphractus*. The larger protuberance in *Vassallia* possibly indicates a more prominent superficial massetericus than in *Holmesina*.

Pterygoideus

The pterygoideus medialis arises from the lateral surface of the pterygoid and inserts on the medial surface of the angular process. The expanded angular process and large, prominently rugose pterygoid processes of pampatheres suggest a larger, more powerful pterygoideus medialis in pampatheres than in armadillos. The pterygoideus lateralis was probably larger in *Vassallia*, based on the larger insertion site, than in *Holmesina* and *Euphractus*.

Jaw Mechanics

Results of the analyses of moment arms are shown in Fig. 5 (see Methodology for details) and Tables I–III. Compared with the living species, values of Mt for pampatheres are lower than that for *Euphractus* but higher than that for *Dasypus*. On the other hand, values of Mm for pampatheres are higher than that for *Euphractus sexcinctus*, which in turn is higher than that for *Dasypus*. This is true not only for the average values, but also for each of the measurements obtained with the method proposed here, particularly those derived from the most posterior origin.

Also, the ratios of muscle moments to bite moments (combined moment arms of the temporalis and massetericus divided by the moment arms around the anterior, middle, or posterior tooth positions) are calculated. All the posterior values in pampatheres are higher than in the living species, whereas the anterior values are nearly equal in all the species considered.

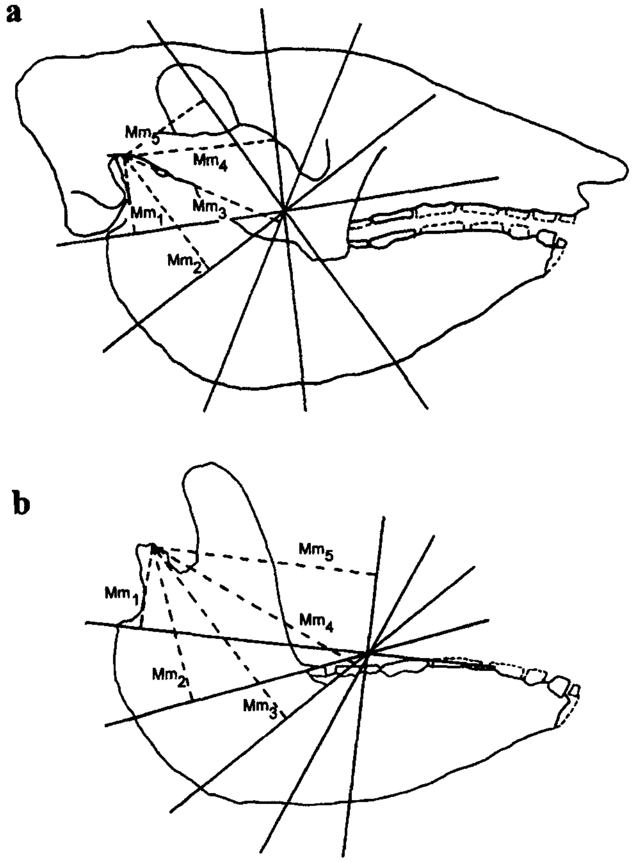


Fig. 5. Moment arms as calculated in *Vassallia maxima*. (a) From the middle position of the massetericus's origin. (b) From the most anterior position of the massetericus's origin. (c) From the posterior position of the massetericus's origin. (d) Moment arms of the temporalis and the bite points. Mm_1–Mm_5, 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. (——) Lines of action of the muscles. (- - - - -) Moment arms of the massetericus and temporalis. (= = = =) Moment arms of the bite point.

Shape Analysis

The pampathere skulls and lower jaws were compared in lateral view with each other, the glyptodont *Propalaeohoplophorus*, and the euphractine *Euphractus sexcinctus*. The landmarks used to perform RFTRA are shown in Fig. 6.

Comparisons between the pampatheres were made using the earliest and probably most primitive of the species studied, *Vassallia maxima*, as the base specimen (Fig. 7). The pampatheres were then compared with *Euphractus sexcinctus* (Figs. 8 and 9), as euphractines possess many primitive cingulate characters (Engelmann, 1985), and with the primitive glyptodont *Propalaeohoplophorus australis* (Figs. 10 and 11). In both cases

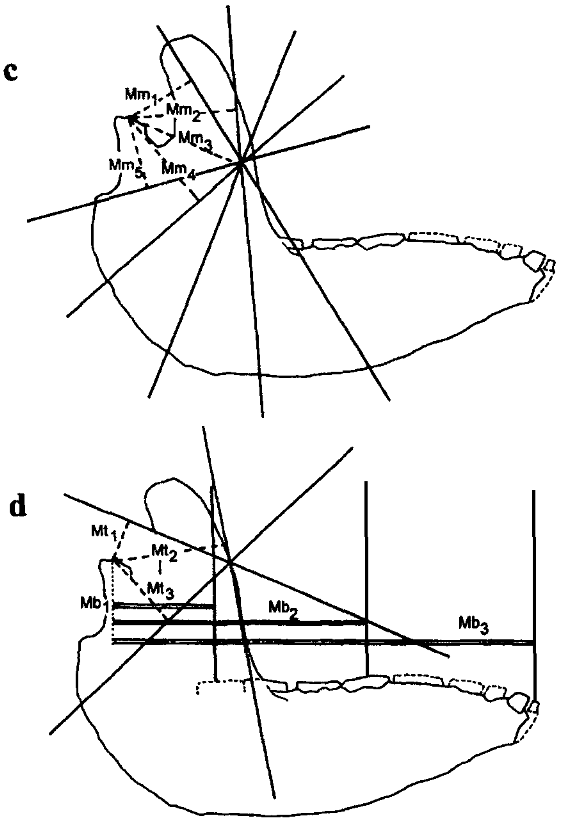


Fig. 5. Continued.

the living species was used as the base specimen. Comparison with glyptodonts is relevant because they were considered sister groups by Engelmann (1985).

The skulls of *Vassallia* and *Holmesina* are remarkably similar, and the latter is essentially an enlarged version of the former. RFTRA confirms many of the observations made from visual analysis, such as the slightly shorter braincase, the longer rostrum, and lower ascending ramus of *Holmesina*, but also shows that the zygomatic arch is slender and the lower tooth row and horizontal ramus of the dentary are longer in this taxon.

The skull shape of *Vassallia* and *Holmesina* differ from that of *Euphractus* in that the dorsal part of the braincase is shorter, the rostrum is elevated, and the zygomatic arch lower in pampatheres. In *Vassallia* the coronoid and angular processes lie more dorsally and the horizontal ramus is deeper than in *Euphractus*. In *Holmesina* the horizontal ramus is also deeper and the angular process is higher than in *Euphractus*, but the condyle lies more ventrally. The tooth row of the pampatheres extends farther distally.

Comparisons with *Propalaeohoplophorus australis* reveal interesting results. This glyptodont has an extremely shortened braincase but a much longer frontal region than *Vassallia*. Its rostrum is markedly shortened dorsally, but less so ventrally. The posterior parts of the palate and tooth rows are anteroventrally displaced, and the zygomatic arch

Table I. Moment Arms of the Massetericus Generated from the Most Posterior, Middle, and Most Anterior Position of the Massetericus's Origin in Selected Xenarthran[a]

Taxon	Angle	Subangle	M_1	M_2	M_3	M_4	M_5	$\sum$	X
			Mm (posterior)						
Vassallia	105	26.25	17	26	30	26	18	117	23.24
Holmesina	120	30	15	22	22	17	8	84	16.8
Euphractus	75	18.75	8	6	9	5	1	29	5.8
Dasypus	90	22.5	7	10	12	12	9	50	10
			Mm (middle)						
Vassallia	120	30	20	35	41	35	22	153	30.6
Holmesina	120	30	18	34	41	35	22	150	30
Euphractus	90	22.5	26	30	31	28	20	135	27
Dasypus	105	26.25	8	17	21	22	18	86	17.2
			Mm (anterior)						
Vassallia	90	22.5	20	39	52	58	54	223	44.6
Holmesina	105	26.25	17	30	42	53	48	190	38
Euphractus	82	20.5	29	39	44	44	32	188	37.6
Dasypus	105	26.25	9	21	28	29	24	111	22.2

[a] M_1–M_5: moment arms of the massetericus measured from the five lines of action.

Table II. Moment Arms of the Temporalis Musculature[a]

	Mt_1	Mt_2	Mt_3
Vassallia	11	28	20
Holmesina	6	22	24
Euphractus	10	27	28
Dasypus	10	16	14

[a] Moment arms generated from the most posterior (Mt_1), middle (Mt_2), and most anterior (Mt_3) positions of the temporalis's origin.

is anteriorly displaced. Both the condylar and the coronoid processes are very markedly displaced anteriorly and the tooth row is displaced distally, whereas the remaining parts of the mandible reveal only minor changes.

The dendrogram grouping skull shapes (Fig. 12) indicates that, as expected, *Vassallia* and *Holmesina* are most similar to each other (D = 0.09), followed by *Euphractus* (D to *Vassallia* = 0.27; to *Holmesina* = 0.26) and, finally, by *Propalaeohoplophorus*. It is clear that pampatheres have an armadillo skull type, but it is remarkable that the glyptodont skull is more similar to that of the pampatheres (D to *Vassallia* = 0.29) than to dasypodids (D to *Euphractus* = 0.35).

The dendrogram of mandibles (Fig. 12) reflects the high degree of similarity among *Holmesina*, *Vassallia*, and *Euphractus*. Although the shorter distance is between

Table III. Comparison of the Moment Arms of the Jaw Muscles and Bite Points in Pampatheres and Living Armadillos[a]

	Vassallia				*Holmesina*				*Euphractus*				*Dasypus*			
	P	M	A	*X*	P	M	A	*X*	P	M	A	*X*	P	M	A	*X*
Mt	11	28	20	19.6	6	22	24	17.3	10	27	28	21.6	10	16	14	13.3
Mm	23.2	30.6	44.6	32.8	16.8	30	38	28.3	5.8	27	37.6	23.5	10	17.2	22.2	16.5
Mb_1		25				24				35				46		
Ratio	1.4	2.3	2.5	2.06	0.9	2.1	2.6	1.9	0.4	1.5	1.9	1.3	0.4	0.7	0.8	0.6
Mb_2		61				61				66				60		
Ratio	0.5	0.9	1.05	0.8	0.3	0.8	1.01	0.7	0.2	0.8	1.0	0.7	0.3	0.6	0.6	0.5
Mb_3		91				97				96				77		
Ratio	0.3	0.6	0.7	0.5	0.2	0.5	0.6	0.4	0.2	0.6	0.7	0.5	0.3	0.4	0.5	0.4

[a] Mt, moment arm of temporalis. Mm, moment arm of massetericus. Mb_1, Mb_2, and Mb_3, 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 Mb_1, Mb_2, and Mb_3. P, posterior; M, middle; A, anterior; *X*, average.

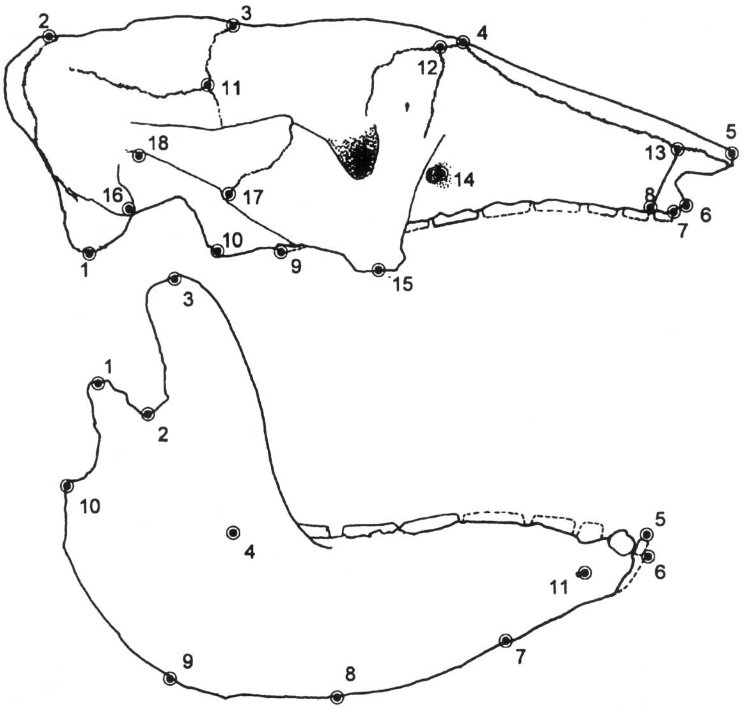


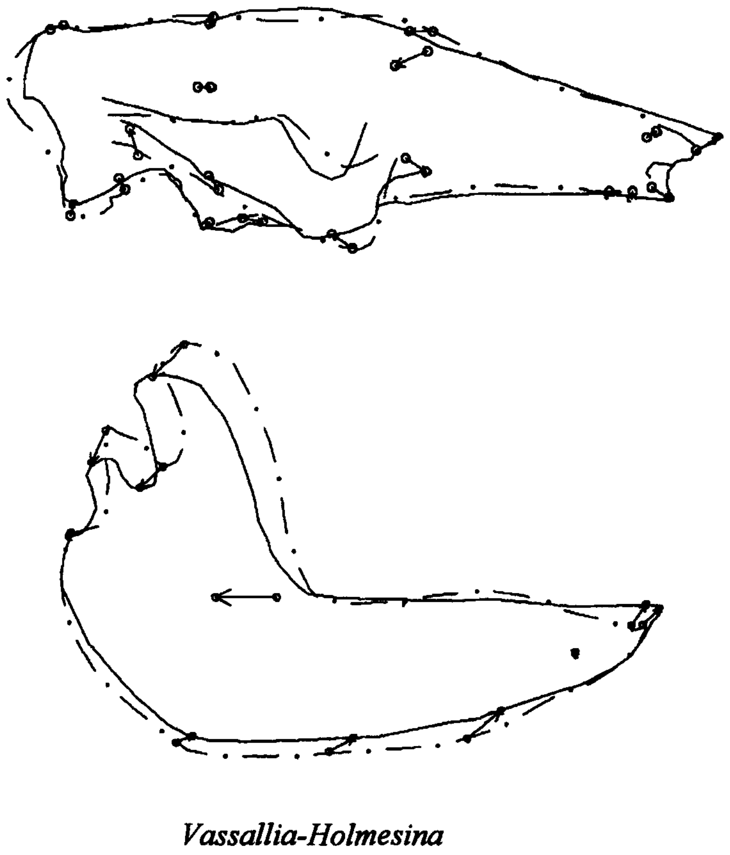
Fig. 6. Skull and mandible of *Vassallia maxima* showing the landmarks used for RFTRA (listed under Materials and Methods).

Holmesina and *Euphractus* ($D = 0.1426$), it is not markedly different from that between *Holmesina* and *Vassallia* ($D = 0.1435$). The analysis of the distances reflects the greater similarity between the mandibles of *Propalaeohaplophorus* and *Vassallia* ($D = 0.25$) than between *Propalaeohoplophorus* and *Euphractus* ($D = 0.36$).

DISCUSSION

The Cingulata includes pampatheres, glyptodonts, and typical armadillos. Patterson and Pascual (1968, 1972) removed pampatheres from the Dasypodidae and considered them more closely allied to the glyptodonts. Engelmann's (1985) phylogenetic analysis of the Xenarthra recognized a primary dichotomy within cingulates. One group, the Glyptodonta, is comprised of eutatine armadillos, glyptodonts, and pampatheres and is based on teeth possessing a central island of compact dentine, more resistant to wear than the surrounding dentine (Hoffstetter, 1958). The other group, the Dasypoda, includes all remaining armadillos, which are characterized by simple teeth that are oval in section.

The Eutatini, including *Proeutatus* and *Eutatus*, and glyptodonts were united in the Glyptodontoidea, 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

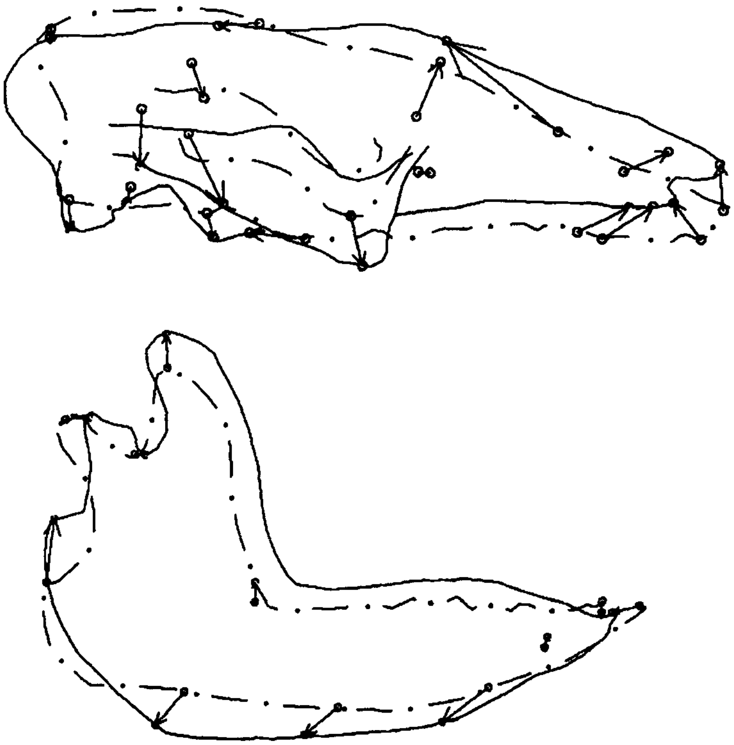


Vassallia-Holmesina

Fig. 7. Results of RFTRA of the skull and mandible of *Vassallia* (base specimen) and *Holmesina*. The figures show landmarks and vectors. Discontinuous line, base specimen; continuous line, target specimen.

tooth (Engelmann, 1985). There are no further recent analyses on the relationships within Cingulata. Gaudin (1995) recognized four unambiguous synapomorphies of the auditory region that diagnose the Cingulata, but relationships within the group were not considered. Fariña (1993, 1995) and Madden *et al.* (submitted) analyzed glyptodonts cladistically but used neither pampatheres nor eutatines as outgroups. Carlini and Scillato-Yané (1993) noted that pampatheres might be the sister group of glyptodonts but did not provide a character analysis. Also, they stated that pampatheres possess cranial, postcranial, dental, and carapace ornamentation characters which are intermediate between those of armadillos and glyptodonts.

The analysis of the masticatory apparatus of *Eutatus* and allied genera by Vizcaíno and Bargo (1998) lends support to the idea that eutatines and typical armadillos are not as closely related as was traditionally believed. These authors considered inclusion of eutatines in the Glyptodonta to be plausible, but suggested that further study is required to establish relationships within this group, as at least one of the characters cited by Engelmann (1985) for the Glyptodontoidea was not corrobarated by their work: the anteriorly

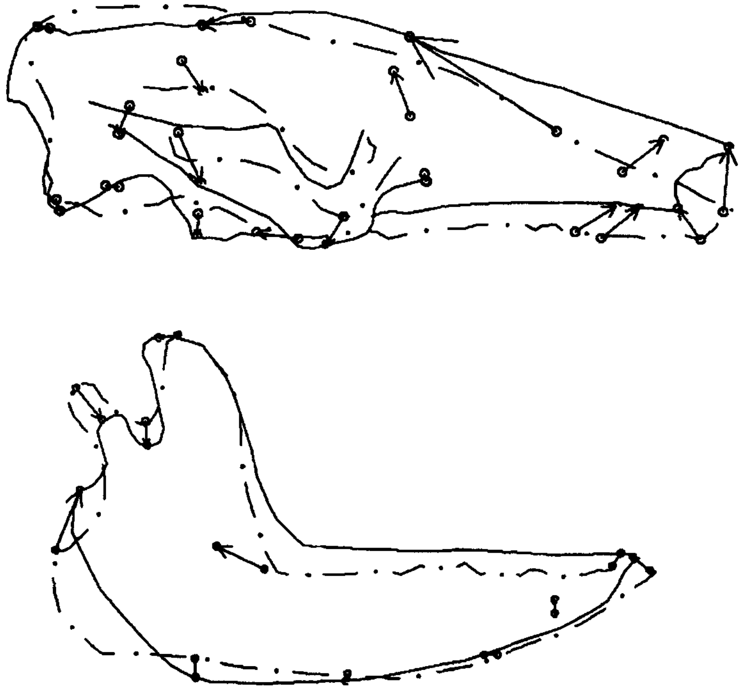


Euphractus-Vassallia

Fig. 8. Results of RFTRA of the skull and mandible of *Euphractus* (base specimen) and *Vassallia*. References as in the legend to Fig. 7.

inclined ascending ramus is present in *Proeutatus* but not in *Eutatus*. Also, the basicranial axis and the mandibular condyle are elevated relative to the palate and tooth row, respectively, in eutatines and pampatheres. The presence of two compact layers of dentine in eutatines and glyptodonts may be a useful character supporting the monophyly of these cingulates. However, detailed analysis of the histology of these layers is required. Furthermore, as has been noted above and by De Iuliis and Edmund (in press), a central island of compact dentine is present in *Vassallia* but is apparently absent in *Holmesina*.

Procrustes methods are not particularly useful in construction of phylogenetic trees due to problems involved with selection of common landmarks between different taxa (Chapman, 1990a, b). However, they allow analysis of morphological variability within a predefined phylogenetic framework (Chapman, 1990a). RFTRA has been shown to be effective in providing information on patterns of morphological variability in dinosaurs (Chapman, 1990b; Chapman and Brett-Surman, 1990). The analysis of pampatheres and glyptodonts was based mainly on homologous landmarks. Only 1 of 18 skull characters and 3 of 11 mandibular characters were strictly geometric, and dendrograms generated from the distance matrices of both skulls and jaws show a similar arrangement. Thus, it is



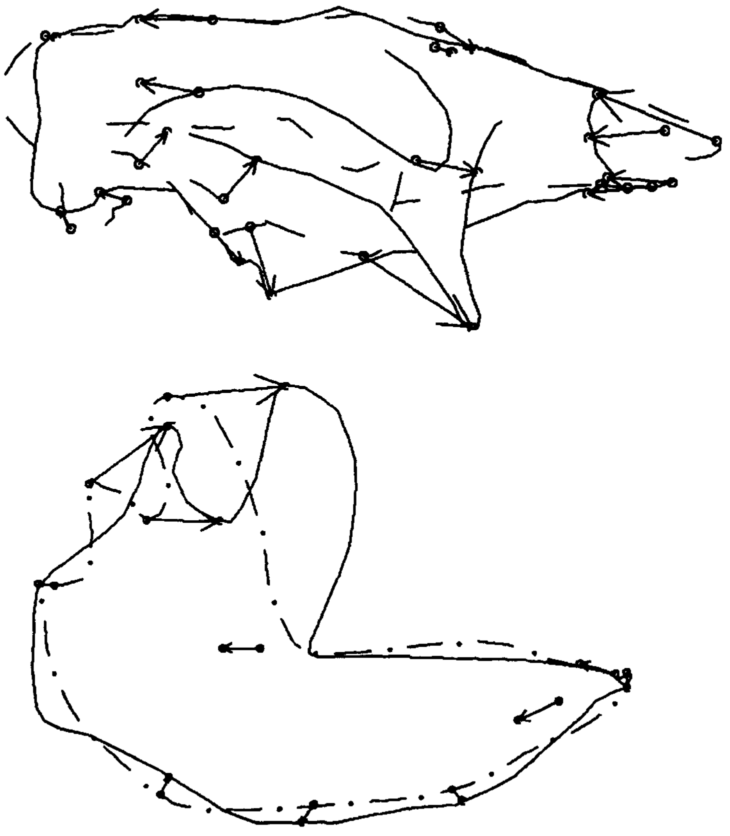
Euphractus-Holmesina

Fig. 9. Results of RFTRA of the skull and mandible of *Euphractus* (base specimen) and *Holmesina*. References as in the legend to Fig. 7.

probable that the dendrograms reflect (but do not recover) phylogenetic relationships. Following Hoffstetter (1958) and Patterson and Pascual (1968, 1972) the general armadillo-like skull shape of pampatheres should be regarded as plesiomorphic. If it could be established that they are not the result of convergences, then some of the shape similarities between glyptodonts and pampatheres revealed by RFTRA might reflect a hypothesized closest relationship between these cingulates. The most notable similarity is concentrated in the mandible, with the enlargement of the angular area and, hence, of the masseteric fossa.

The general form of the pampathere masticatory apparatus, including the temporomandibular joint, mandible, and dentition, strongly resembles that of many herbivorous ungulates, as do those of *Euphractus* (Smith and Redford, 1990) and eutatine armadillos (Vizcaíno and Bargo, 1998). The shape and position of various features of these and other skeletal elements are adaptations that increase the size of the massetericus and pterygoideus muscles and the moment arm of the massetericus, which reflect greater bite forces and efficiency of a mediolateral or transverse component of the mandible.

The temporomandibular joint of these mammals is generally formed by a wide, slightly concave mandibular condyle and a nearly flat mandibular fossa, an arrangement that allows the considerable freedom of motion in the mediolateral and anteroposterior

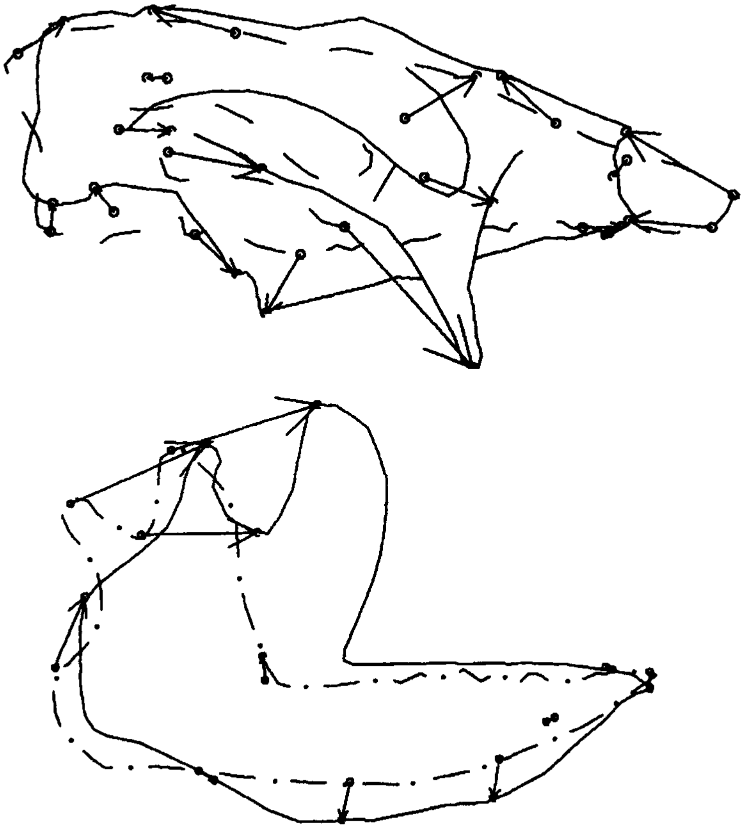


Vassallia-Propalaeohoplophorus

Fig. 10. Results of RFTRA of the skull and mandible of *Vassallia* (base specimen) and *Propalaeohoplophorus*. References as in the legend to Fig. 7.

directions characteristic of grazing ungulates (Maynard Smith and Savage, 1959; Turnbull, 1970). The mandibular condyle lies well dorsal to muscular insertion sites, which increases the moment arm, and thus the mechanical advantage, of the massetericus muscle. A large angular process allows an increase in size of the masseteric musculature, as does the robust zygomatic arch. Turnbull (1970) noted that an increase in the relative size of the masseteric musculature was perhaps the most characteristic feature of the ungulate grinding masticatory apparatus. The angular process is particularly enlarged in pampatheres. Its shape (indeed, the general form of the mandible) resembles that of *Equus*, in which the masseteric musculature is very prominent and complex (Turnbull, 1970).

Greaves (1978) viewed the unfused symphysis of artiodactyls as an adaptation to the action of the pterygoid musculature coupled with transverse lateral chewing. This may also have applied to the pampatheres, in which the symphysis is unfused, except in a single, and probably aged, individual.



Euphractus-Propalaeohoplophorus

Fig. 11. Results of RFTRA of the skull and mandible of *Euphractus* (base specimen) and *Propalaeohoplophorus*. References as in the legend to Fig. 7.

The occlusal surfaces of pampathere molariforms generally form broad, flattened areas, again characteristic of the pattern of ungulate grazers. In pampatheres the predominance, particularly on the mesial molariforms, of transverse striations also strongly suggests transverse chewing, as does the formation, in the more distal molariforms, of basined occlusal surfaces. The distal molariforms are apparently functionally analogous to the ectolophs, formed by basined dentine between more resistant enamel ridges, of many ungulate grazers. Greaves (1973) noted that the long axis of an ectoloph is oriented perpendicular to the direction of tooth travel. In the pampatheres the bilobate distal molariforms are mesiodistally elongated. *Vassallia* and eutatine armadillos present a closer analogy to the ectoloph function by the presence of an island of harder vasodentine in the center of the molariform. This island, oriented mainly mesiodistally as noted above, served to increase shearing efficiency. The occlusal surfaces lying lingually and buccally between the periphery of the molariform and the central island are basined in a

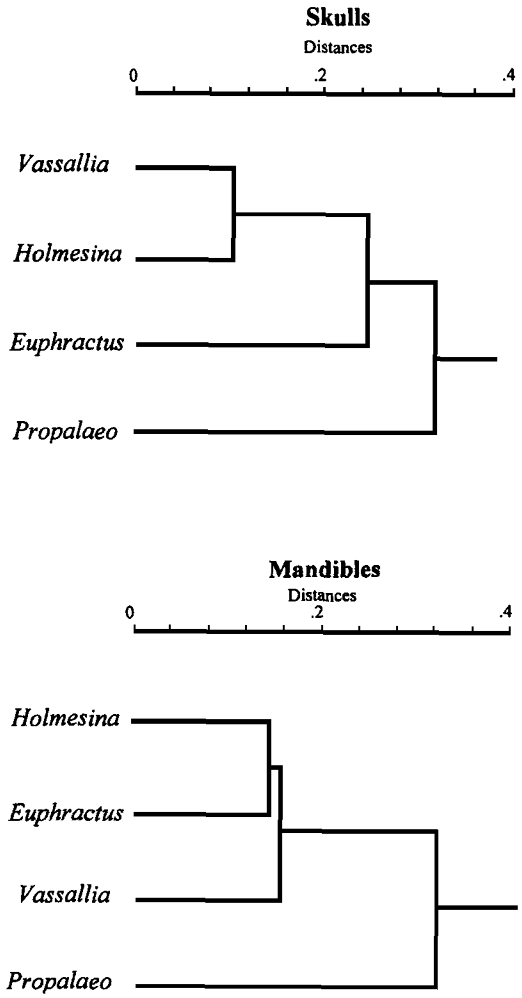


Fig. 12. Dendrograms resulting from UPGMA cluster analysis using RFTRA distances of the skulls and mandibles of pampatheres, the dasypodid *Euphractus*, and the glyptodont *Propalaeohoplophorus* (=Propalaeo).

manner similar to that of the dentine between enamel ridges in an ectoloph (see Greaves, 1973, Fig. 1).

The moment arms of the masticatory musculature were compared among the pampatheres and to those of *Euphractus* and *Dasypus* as recalculated from Smith and Redford (1990) according to the method described here. Values of Mt for the pampatheres fall between those for *Euphractus* and *Dasypus*; *Vassallia* is closer to *Euphractus*, and *Holmesina* to *Dasypus*. The values for Mm are absolutely and relatively higher than Mt in the pampatheres (Table III). In *Euphractus* Mm is 9% larger than Mt, and in *Dasypus* 21% larger, whereas in *Vassallia* and *Holmesina* it is approximately 65% larger. The increase in the pampatheres may be explained by the greater insertion area due to the expanded angular process.

Due to the posterior extension of the tooth row in the pampatheres, the combined moment arms of the temporalis and massetericus are very large relative to the bite force at the most posterior tooth, whereas values for the most anterior tooth are similar to those of the armadillos. 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. It is approximately 4 times stronger at the posterior most tooth than at the anterior most in pampatheres, 2.6 in *Euphractus*, and 1.75 in *Dasypus*.

Long lever arms of the massetericus 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 to increase the bite force at the posterior part of the tooth row, particularly in *Vassallia*. In *Holmesina* a shorter lever arm of the temporalis and longer mandible allowed faster movement than in *Vassallia*.

The analyses of the skeletal elements and action of the masticatory musculature of pampatheres indicate that their masticatory apparatus was capable of producing increased force, particularly at the distal part of the tooth row, and functioned with a more prominent lateral chewing component compared with *Euphractus* and *Dasypus*. Thus, the mandibular condyle is relatively dorsal, the temporomandibular joint allowed considerable freedom of movement, the tooth row is extended posteriorly, the masseteric and pterygoid musculature was greatly increased (reflected by the expanded zygomatic arches, angular processes, and robust pterygoid processes), the symphysis is unfused, the mesial teeth bear mainly transverse striations, and the distal teeth are mesiodistally elongated and bear basined occlusal surfaces. The step-like arrangement of the molariforms in *Holmesina*, at least, perhaps served to restrict mesiodistal movement (Edmund, 1985).

The preceding analysis describes features that largely coincide with adaptations in living herbivores, such as perissodactyls and ruminant artiodactyls, in which the main muscular masticatory effort is performed by the massetericus. This is reflected by the mass and the moment arm of the line of action of the masticatory musculature (Maynard Smith and Savage, 1959; Turnbull, 1970). In ungulates the massetericus is larger than the temporalis, as is the moment arm, but the reverse is true in carnivores. Further, the pterygoideus has approximately the same mass as the temporalis in ungulates, whereas it is much smaller in carnivores.

Smith and Redford (1990) stated that *Euphractus* possesses many skeletal, muscular, and dental features that reflect increased force and shearing, and that it chews with a strong lateral component to the power stroke. These authors related the form of the masticatory apparatus of *Euphractus* with its omnivorous diet, which includes a wide range of foods, such as plant material, hard food items, and carrion; Wetzel (1982, p. 359) stated that "euphractines are generalists with a broad diet that includes small vertebrates, arthropods, carrion, tubers, fruit and seeds." Many of these morphological features (vide supra) are shared by and enhanced in pampatheres. Thus the masticatory apparatus of both mammals promotes force and functions with a strong transverse component.

The main difference between pampatheres and *Euphractus* lies in the form of their dentitions. The homodont molariforms of *Euphractus* are beveled, with lingual and buccal margins forming well-defined shearing surfaces, but the beveled surfaces also meet to form a sharp peak, which may serve to pierce or puncture.

The molariforms of pampatheres are more heterodont. The mesial molariforms are nearly oval and flat, whereas the distal ones are basined and possess well-defined lingual and buccal shearing edges in *Holmesina* and an additional shear surface (formed by the central island of vasodentine) in *Vassallia*. The heterodont dentition suggests different functions for specific areas of the tooth row, as does the greater force produced posteriorly. The form of the distal molariforms suggests that they were adapted for processing resistant vegetal matter. As with the grinding molars of grazing ungulates, the molariforms are flattened (as opposed to beveled), basined, possess well-defined shearing edges, and are open rooted. The mesial dentition may have served in the initial preparation of the food. Alternatively, and possibly simultaneously, they may have served as analogues to the nipping incisors characteristic of grazing ungulates. The mesial molariforms in pampatheres are not at the front of the mouth, but it is probable that pampatheres had an elongated tongue that may have been used to gather long grasses to be cropped or crushed by the molariforms, although these molariforms apparently lack a cutting edge.

Comparisons between *Holmesina* and *Vassallia* indicate variations on a theme. The main differences suggest that *Vassallia* was capable of producing even greater relative bite forces and that it was a more efficient grinder. Thus, the braincase and temporal fossa are relatively longer, the sagittal crest more prominent, the zygomatic and pterygoid processes and the mandible extremely robust, and the molariforms possess a central island of harder dentine. Also, the pterygoideus lateralis was probably larger, which suggests greater mediolateral control of the mandible at the temporomandibular joint.

Smith and Redford (1990, p. 45) cautioned against predicting diet based on morphology: "Comparison of *D. novemcinctus* and *E. sexcinctus* provides an interesting example of the decoupling of morphological and behavioural specialization. In this case, the morphology of *D. novemcinctus* appears more specialized than the behaviour would suggest." The reason behind these comments is that while *D. novemcinctus* possesses some morphological specializations for myrmecophagy, it is one of the most generalized of armadillos. The implication is that one should be careful in predicting a myrmecophagous diet for *D. novemcinctus* based on its morphology. We agree with the general thrust of the last statement, in the sense that *D. novemcinctus* is not strictly myrmecophagous. Clearly, many mammals may subsist on food that is not their preferred diet or that may not normally form the largest component of their diet. What may be more relevant here is that *D. novemcinctus*, at least in a large part of its range, apparently does prefer social insects, whereas *Euphractus* is considerably less likely to display myrmecophagous behavior; the reason for these different behavioral patterns is in large part due to or reflected by their morphologies. It would not be unreasonable to predict that the morphology of *D. novemcinctus* indicates greater myrmecophagy than in *E. sexcinctus*. Certainly, a prediction of strict myrmecophagy for *D. novemcinctus* based on its morphology would be incorrect, the reason being that its morphology does not suggest strict myrmecophagy. A broader comparison would reveal that strict myrmecophagans, such as the anteater *Myrmecophaga* (Vermilingua, Myrmecophagidae), are considerably more specialized. The Early Miocene dasypodid *Stegotherium tessellatum* provides an excellent example of strict myrmecophagy in mammals, and this behavior was postulated by Vizcaíno (1994, 1997) on just such clearly specialized morphology.

As these considerations on the relationship among form, function, and diet apply to pampatheres, we cannot predict that these xenarthrans consumed strictly coarse or resistant vegetation. It is probable that they fed on a variety of other vegetal matter. However, the form of the masticatory apparatus of pampatheres suggests that these cingulates, although not necessarily strict grazers, probably fed largely on coarse vegetation. Further, the flattened molariforms, which lack features facilitating piercing and puncturing, suggest that pampatheres, unlike euphractines, were probably not adept at consuming relatively large arthropods, vertebrates, or carrion and, thus, that they were not generalized omnivores.

Finally, pampatheres are one of the four lineages of herbivorous, armored xenarthrans, together with the peltephiline and eutatine armadillos and the glyptodonts. The very peculiar masticatory apparatus of peltephilines suggests a specialization for feeding on tubers or some other tough, subterranean vegetable matter (Vizcaíno and Fariña, 1997). Vizcaíno and Bargo (1998) considered eutatines to be mainly browsers and glyptodonts probable grazers. They found that eutatines are similar to small antelopes in general shape of the mandible, and hence, feeding style. Jarman (1974) clearly established a relationship between body size and feeding style in antelopes (taken as Bovidae excluding the Caprinae). Small species are predominantly browsers and tend to be highly selective feeders, relying on specific plants or plant parts. These species utilize very diverse diets. On the other hand, the larger species are relatively unselective grazers and rely on a wide range of grasses, but they may graze and browse. Vizcaíno and Bargo (1998) proposed that, although feeding strategies among antelopes cannot be applied strictly to armadillos, they provide insight on general dietary style. This scheme could be extended to other armored herbivores (Vizcaíno and Bargo, submitted): while the eutatines (up to 50 kg) are mainly browsers, the larger pampatheres (up to 200 kg) and glyptodonts (between 1 and 2 tons) represent increasing degrees of grazing.

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