Carved teeth and strange jaws: How glyptodonts masticated

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In this paper, the highly peculiar masticatory apparatus of glyptodonts is studied. The general morphology of the skull is analysed using a morphometric procedure, the Resistant Fit Theta Rho Analysis, which allows comparison among different biological forms. Here, a large terminal form, the late Pleistocene genus *Glyptodon*, is compared with the smaller primitive Miocene genus *Propalaehoplophorus*, and with the generalised Recent armadillo *Chaetophractus*. The masticatory musculature of glyptodonts is reconstructed. Their tooth form and wear facets, as well as their mandibular symphysis and jaw joint, are analysed. A model of jaw movement is constructed based on these analyses. It is demonstrated that the masticatory apparatus of glyptodonts had undergone a telescoping process, which was already underway in the most ancient forms whose skull is known. This process created problems in regard to the way stresses produced by mastication were absorbed by the mandible, and therefore it might be regarded as non-adaptive. Some functional explanatory hypotheses are discussed, such as a requirement of keeping the moment of the weight of the cranium small enough to be counterbalanced by the neck muscles, or fitting the head into the armour.

Key words: Biomechanics, Xenarthra, South America, palaeobiology, jaw mechanics.

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Introduction

Glyptodonts (etymologically, carved teeth) are highly peculiar New World mammals, known abundantly from the South American Cenozoic (Hoffstetter 1982). They died out in the great extinction event of continental mammals that took place at the end of the Pleistocene (Lessa & Fariña 1996; Lessa *et al.* 1997). They have been traditionally considered the closest relatives to armadillos, although the phylogenetic relationships

among cingulates have not been satisfactorily resolved. This traditional point of view has been championed by several authors (e.g., Hoffstetter 1958; Robertson 1976; Cartelle & Bohórquez 1985), but pampatheres have also been considered the sister group of glyptodonts (e.g., Patterson & Pascual 1968, 1972; Engelmann 1985; Carlini & Scillato-Yané 1993). It is clear, however, that the dasypodid, glyptodont, and pampatheriid lineages have followed independent histories at least since the middle Eocene Mustersan Age (Scillato-Yané 1986), some 45–48 million years ago (Flynn & Swisher 1995).

Among their many peculiarities, glyptodonts were fully armoured beasts that reached masses of up to two tonnes. Their palaeobiology has recently attracted some attention (Fariña 1995; Alexander *et al.* 1999). The geometry of their peculiar jaws is unique among mammals (Fariña & Parietti 1983; Fariña 1985, 1988). Gillette & Ray (1981) proposed that glyptodonts were probably browsers and belong to Turnbull's (1970) 'rodent-gnawing' type. However, biomechanical analysis by Fariña (1985, 1988) suggested that masticatory movement in glyptodonts resembled more that of ruminants, based on the limitations imposed by the craniomandibular joint (CMJ), as occurs in eutatines (Vizcaíno & Bargo 1998) and pampatheres (Vizcaíno *et al.* 1998; De Iuliis *et al.* 2000). Our preliminary observations suggest that the stout architecture of the masticatory apparatus and the very hypsodont teeth with ridges of hard dentine on the occlusal surface indicate that glyptodonts were probably grazers.

In this paper, we will try to improve our understanding on how these peculiar jaws functioned. In so doing, we will analyse the general morphology of the skull using morphometric methods, reconstruct the masticatory musculature, and analyse tooth form and wear facets, as well as the mandibular symphysis and jaw joint. A model of jaw movement will be constructed based on the results of these analyses.

Material and methods

Material. — The landmarks used for the method described below were taken from the following specimens: *Chaetophractus villosus*, Museo de la Plata, Departamento de Paleontología Vertebrados (hereafter, MLP-DPV) unnumbered, *Propalaehoplophorus australis* MLP-DPV 16–15, and *Glyptodon* cf. *G. clavipes* MLP-DPV 18. The wear facets were observed in an incomplete jaw of *Glyptodon* sp. in the Departamento de Paleontología of the Facultad de Ciencias, Montevideo, Uruguay, FC-DPV 557. The measurements and bone properties of the descending process were observed in the Lujanian (late Pleistocene–early Holocene) glyptodonts *Panochthus tuberculatus* MLP-DPV 16–29 and *Doedicurus clavicaudatus* MLP-DPV 16–24, respectively.

Shape analysis. — For comparisons of skull shape, a method developed in the early '80s was used (Benson *et al.* 1982). This method is known as RFTRA ('Resistant Fit Theta Rho Analysis'), which is considered appropriate for dealing with the problem of localised deformation. The fundamental methodology has its basis in the fact that, given two set of homologous points or landmarks, it is possible to superimpose them as closely as possible using a scale vector (T), a rotation vector (θ), and two translation vectors (α and β), whenever two dimensions are analysed. The theoretical basis is provided in Siegel & Benson (1982); for updated information see Chapman (1990a, b) and

references therein. It should be noted that a similar method, that of the least-squares analysis (LSTRA, Sneath 1967), has the disadvantage of averaging the differences among all the landmarks. In contrast, RFTRA stresses the differences, which makes it a particularly appropriate methodology for dealing with evolutionary transformations. Software for performing RFTRA analyses was developed by Chapman (1989).

The skulls of the two glyptodonts, the Lujanian *Glyptodon* and the primitive Miocene *Propalaeohoplophorus australis*, were compared in lateral view, and both were compared separately with the generalised armadillo *Chaetophractus villosus* (Dasypodidae, Euphractini). The landmarks (homologous and geometric points) used in the analysis are presented in Fig. 1.
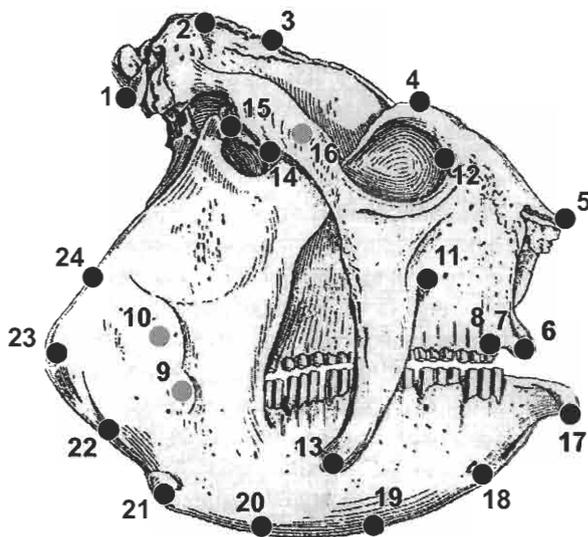
Fig. 1. Landmarks used in the comparisons between the Xenarthran skulls under study, showed in a schematic lateral view of the skull of *Glyptodon asper* (modified from Burmeister 1874): 1, ventral margin of the occipital condyle; 2, parietooccipital suture on the sagittal plane; 3, Parietofrontal suture on the sagittal plane; 4, nasofrontal suture on the sagittal plane; 5, Anterior extremity of the nasal; 6, anterior extremity of the premaxilla; 7, mesial margin of the alveolus of the first upper molariform; 8, Premaxillary-maxillary suture on the ventral margin; 9. distal margin of the alveolus of the last molariform; 10, posterior end of the pterygoid bone; 11, infraorbital foramen; 12, lacrimal foramen; 13, ventralmost level of the zygomatic arch; 14, zygomaticosquamosal suture on the ventral margin of the arch; 15, middle point along the glenoid cavity of the craniomandibular joint; 16, dorsal tip of the coronoid process; 17, anterior symphyseal margin; 18, intersection of the ventral margin of the dentary with the line extending down perpendicularly from the line drawn between landmarks 17 and 24 and at 1/6 the distance between 17 and 24; 19, intersection of the ventral margin of the dentary with the line extending down perpendicularly from the line drawn between landmarks 17 and 24 and at 1/3 the distance between 17 and 24; 20, intersection of the ventral margin of the dentary with the line extending down perpendicularly from the line drawn between landmarks 17 and 24 and at 1/2 the distance between 17 and 24; 21, intersection of the ventral margin of the dentary with the line extending down perpendicularly from the line drawn between landmarks 17 and 24 and at 2/3 the distance between 17 and 24; 22, intersection of the ventral margin of the dentary with the line extending down perpendicularly from the line drawn between landmarks 17 and 24 and at 5/6 the distance between 17 and 24; 23, most distant point in the angle of the mandible from the middle of the distance along the line drawn from points 13 and 14; 24, highest insertion of the masseter muscle on the border of the mandibular angle.

Zygomatic arch. —The loading of the descending process of the zygomatic arch was investigated by measurements on the *Panochthus* skull, on which the process is intact and unrestored. First, a shape tracer was used to draw a section through the base of the process, and its section modulus was determined (see Alexander 1983). Next, the area of origin of the masseter on the process was measured and the bending moment that the muscle would have exerted at the measured section was calculated, with an assumed stress on the muscle of 0.3 MPa, the upper end of the range of isometric stress for vertebrate skeletal muscle (Wells 1965; Josephson 1993). This calculation considers the force as distributed along the entire length of the process, rather than at only one point. In other words, the first moment of area of the area of origin about the measured section was determined and multiplied by the assumed stress. This measure was then divided by the bending moment of the section moduli to produce estimates of the stresses in the descending process.

Results

General description of glyptodont skull and jaw structure. — This description is based on *Glyptodon* spp. but it is essentially valid for all the large, post-Miocene representatives of the family. A complete morphometric comparison of many species of Cingulata is in progress (Vizcaíno 1997; Vizcaíno & Bargo 1998; Vizcaíno *et al.* 1998; De Iuliis *et al.* 2000). As can be seen in Fig. 1, the glyptodont skull (including jaw) has a roughly cubic shape (Vinacci Thul 1945; Gillette & Ray 1981). If this form is compared with that of armadillos (family Dasypodidae), a shortening of the snout is apparent.

Another conspicuous feature of the glyptodont skull is the huge descending process of the zygomatic arch, formed by the maxillary and jugal bones. Its extremity reaches downward to a point below the tooth row (for further descriptions see Gillette & Ray 1981). This descending process is particularly important in connection with the origin area of the masseter complex. Its great size reflects the enormous development of both maxillary and mandibular cheek tooth hypsodonty.

As can be observed in the figures in Burmeister (1874), the sinuses in the glyptodont skulls are greatly expanded. It is likely that they play an important part in one aspect of biomechanical function, namely in the distribution of stresses produced during mastication, as is also observed in modern species (Thomason 1995).

The jaw also has the distinctive feature of a highly developed angle. This large angle is associated with insertion areas of the masseter and pterygoid muscle complexes. It is connected to the ascending process, which takes root from the external side of the horizontal ramus.

Symphysis, mandibular section and craniomandibular joint (CMJ). — The symphysis is completely fused in all species of the family for which it is known. The section of the horizontal ramus of the lower jaw is generally elliptical, with the major axis directed vertically (Vinacci Thul 1945; Hoffstetter 1958; Gillette & Ray 1981). The glenoid fossa, limited posteriorly by the paroccipital process, is transversely elliptical and rather flat, directed backward, and slightly downward and outward. In addition, the jaw joint lies well above the tooth row, reaching the highest ratio of CMJ height:skull length recorded for mammals (Fig. 2). The distances of condyle-lower
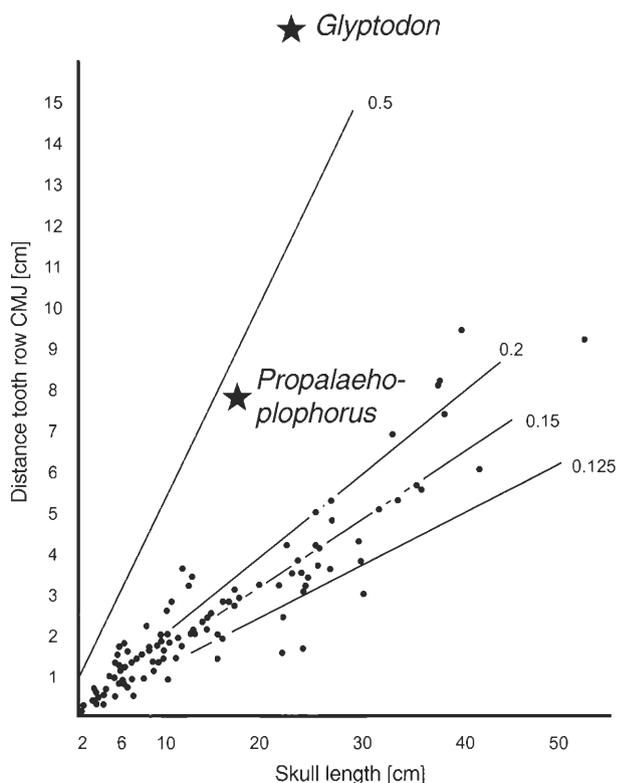
Fig. 2. Diagram graphing craniomandibular joint-tooth row distance against skull length in mammals. Both measurements in cm. Slopes were added to highlight scattering of data (modified from Greaves 1974).

tooth row, and fossa-upper tooth row are generally equal, implying simultaneous occlusion (Greaves 1974, but see below). The jaw condyle in this family is transversely elongated and dorsoventrally convex. Its articular facet is directed forward, articulating loosely with the glenoid fossa, which corresponds with a ruminant-like CMJ structure (Storch 1968), although it is in glyptodonts nearly at a right angle with respect to the arrangement normally observed in mammalian herbivores. Indeed, in lateral view, the tangent of the contact surfaces runs horizontally in most herbivores, but almost vertically in glyptodonts.

Dental morphology. — Glyptodonts have a bizarre dental morphology. The teeth have a curious design not shared with any other mammal (Fig. 3), although they are rather similar to those of pampatheres (see De Iuliis & Edmund in press; Vizcaíno *et al.* 1998; De Iuliis *et al.* 2000). The teeth lack the tribosphenic pattern generally present in therian mammals, and do not posses the conical, reptile-like shape typical of Dasypodidae. With the exception of the first two teeth, which are usually reduced, they are three-lobed. The lobe histology is as follows: a surrounding layer of cement, a matrix of orthodentine, and a central axis of harder, often branching, osteodentine (Ferigolo 1985). True enamel is entirely absent in glyptodont teeth (and in most if not all other xenarthrans), but osteodentine has the same function.
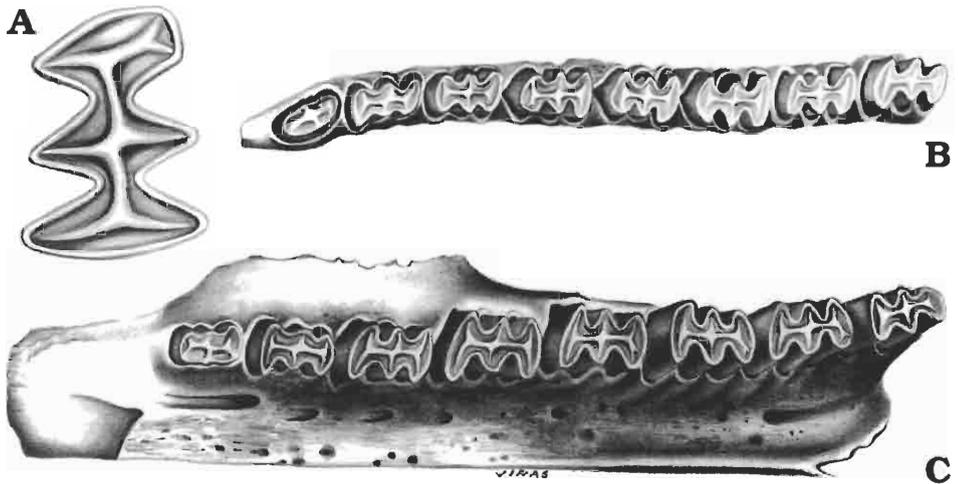
Fig. 3. Glyptodont dentition. **A**. Tooth in occlusal view (anterior is down). **B**. Lower tooth row (anterior is to the left). **C**. Upper tooth row (anterior is to the left). Modified from Burmeister (1874).

There are eight cheek teeth in each hemimandible lying almost perfectly parallel to the sagittal plane, and sinusoidal in lateral view. The last upper and lower teeth lie in the transverse plane of the CMJ or even behind it. The position of these teeth makes the models of the distance from the CMJ (Greaves 1978) and the one-third rule (Greaves 1982) unsuitable to explain the jaw system in glyptodonts, as will be discussed below. A close occlusion is possible throughout the tooth row. In the first teeth the crests tend to be arranged more longitudinally. As they are farthest from the jaw joint and favoured by the peculiar anatomy of the glyptodont's jaws, they are the teeth that can exert a significantly lateral power stroke. The last teeth have lobes that are almost completely transverse.

Shape analysis. — The generalised armadillo *Chaetophractus villosus* was compared with the Miocene glyptodont *Propalaehoplophorus australis* (among the earliest forms whose skull and jaws are known) and with *Glyptodon clavipes*, a large Pleistocene species

As seen in Fig. 4A, the main differences between the armadillo and the primitive glyptodont occur in landmarks 4 (nasofrontal suture on the sagittal plane), 5 (anterior extremity of the nasal), 6 (anterior extremity of the premaxilla), 12 (lacrimal foramen) and 13 (ventralmost level of the zygomatic arch). The changes in landmarks 4, 5 and 6 imply a shortening of the edentulous portion of the rostrum, represented by the premaxilla, and a posterior- and dorsalward displacement of the nasals. The lacrimal foramen is displaced anteriorly; various other landmarks in that region (i.e., 14, zygomaticosquamosal suture on the ventral margin of the arch, 15, middle point along the glenoid cavity of the craniomandibular joint, and 16, dorsal tip of the coronoid process) followed this trend, but to a lesser degree. The most remarkable change is the anterior and ventralward migration of landmark 13, which has functional implications that are discussed below. The remaining landmarks are more conservative in their dif-
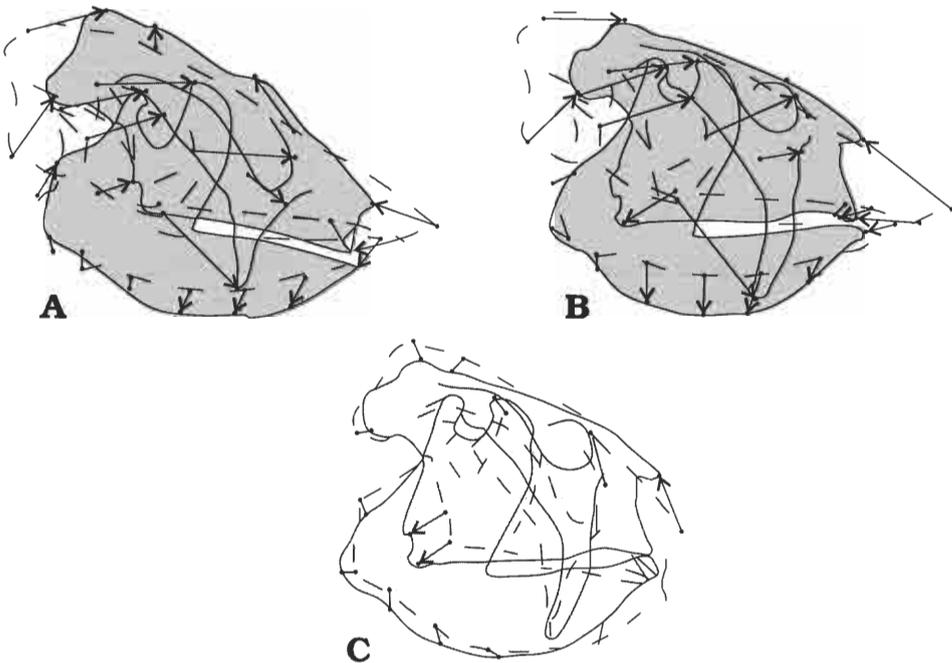
Fig. 4. Comparisons among edentate skulls and jaws using RFTRA. Broken lines indicate base specimens; target specimens are shadowed. **A**. Comparison between *Chaetophractus* (base specimen) and *Propalaehoplophorus* (target). **B**. Comparison between *Chaetophractus* (base specimen) and *Glyptodon clavipes* (target). **C**. Comparison between *Propalaehoplophorus* (base specimen) and *Glyptodon clavipes* (target).

ferences, although landmarks 18 to 23 (ventral margin of the mandible) show a tendency to be more ventral in position.

A similar pattern emerges when *Chaetophractus* is compared with the large Pleistocene species *G. clavipes* (Fig. 4B). However, the landmarks that show the greatest differences are 5 (anterior extreme of the nasal), 13 (ventralmost level of the zygomatic arch), 12 (lacrimal foramen), 14 (zygomaticosquamosal suture on the ventral margin of the arch), 15 (middle point along the glenoid cavity of the craniomandibular joint), and 16 (dorsal tip of the coronoid process). All these landmarks are moved markedly in an anteroposterior direction, though 5 is displaced also dorsally and 13 ventrally. As with *P. australis*, the most dramatic displacement occurs in landmark 13. Again, landmarks 18 to 23 (ventral margin of the mandible) show a tendency to be placed more ventrally, and the last tooth (landmark 9) is placed more posteriorly. The remaining landmarks show lesser differences in their placement.

When the primitive glyptodont *Propalaehoplophorus* is compared with the terminal form *Glyptodon clavipes* (the former being the base specimen, Fig. 4C), differences in migrations of the landmarks are not as marked. The appropriate distance *D* is 0.22 in this case, a lower value than those obtained in the two previous comparisons (0.44 and 0.48, respectively). The nasals are higher in *Glyptodon*, and its last tooth is placed even more posteriorly. The remaining landmarks are much closer to their homologues.

Stress of the descending process. — A range from a maximum compressive stress of 15 MPa for the descending process at its posterior surface to a maximum tensile stress of 20 MPa at its anterior edge was obtained. These stresses are an order of magnitude less than the ultimate compressive and tensile strengths of compact bone.

Discussion

Shape analysis. — As in Fariña & Parietti (1983), the analyses performed indicate that the skull of glyptodonts has undergone a very peculiar process of telescoping, in which the braincase is placed above the posterior half of the tooth row, whereas in their close relatives the armadillos it lies behind the tooth row, as is primitive for mammals. This condition results in a number of differences in regard to the masticatory mechanics, which will be considered below. The most noteworthy is the size of the descending process of the arch. The results obtained in Fariña & Parietti (1983) differ in some respects from those presented here. In particular, they proposed that telescoping was mainly a result of major modifications in the rostral region of the skull combined with relative stasis of the posterior region of the skull. In contrast, the present analyses indicate that the posterior region of the skull is placed more anteriorly and dorsally in glyptodonts, and that the rostrum is shorter than in armadillos, but to a smaller degree. These differences in the results may be due to the fact that Fariña & Parietti (1983) used *Dasypus novemcinctus* as base specimen for their comparisons, and this species shows a rather high degree of specialisation to a myrmecophagous diet. The present analysis was based on comparisons to *Chaetophractus*, a generalised omnivore. Using RFTRA, Vizcaíno (1997) demonstrated the different ways in which the skulls of various myrmecophagous armadillos (the living genera *Dasypus* and *Priodontes* and the highly specialised genus *Stegotherium* from the Miocene of Patagonia) are elongated in comparison to *Chaetophractus*. In the case of *Dasypus*, the elongation takes place mainly in the anterior part of the maxilla and premaxilla.

The results obtained here in the comparison between a generalised armadillo and both glyptodonts are consistent with those obtained by Vizcaíno *et al.* (1998). They compared the pampatheriids *Vassallia* and *Holmesina* and the armadillo *Euphractus* with *Propalaeohoplophorus*, and found that the zygomatic arch of the glyptodont was anteriorly displaced, that both the condylar and coronoid processes were very markedly displaced anteriorly, and that the tooth row was displaced distally, whereas the remaining parts of the mandible revealed only minor changes.

Tooth wear. — There is no direct evidence of the diet of glyptodonts, such as identifiable fossil faeces, but their highly hypsodont teeth suggest grazing. Other morphometric features of their skulls and jaws also tend to place them near the group of grazers in the graphs presented by Janis (1990).

A possible analogue for the dental arrangement of glyptodonts may be seen in the dentition of bovids. Neither glyptodonts nor bovids have upper incisors (and glyptodonts also lack lower incisors) or canines; toothless pads at the front of the mouth are used by cows in conjunction with a powerful tongue to pluck bundles of grass. Although the use of lips (as in both white and black rhinos) cannot be ruled out, it will be

noted below that there is evidence of powerful tongue musculature in *Glyptodon* (Pérez *et al.* 2000). Even so the tongue was apparently more important in the reworking of food in the oral cavity than in food intake (Pérez *et al.* 2000), but the subject remains unresolved. Further back in the mouth, both have long rows of cheek teeth (premolar and molar teeth in bovids and non-homologous cheek teeth in glyptodonts), such as cattle use for grinding grass. In both cases the teeth are highly hypsodont. Therefore, it will be assumed that bovids and glyptodonts shared a diet based primarily on grazing.

Grass is an abrasive food, partly because there are silica crystals in the cells and partly because, growing near the ground, it tends to have a dusting of sand grains (Janis 1988; Josephson 1993). Horses living in sandy areas tend to have severely worn teeth. Indeed, and as Janis (1988) noted, dust and sand are more important in determining the degree of hypsodonty than the cellular composition of the plant food, as even those browsers living in open habitats show higher crowns than those living in more forested habitats or feeding on higher branches. On the other hand, grass is a food that not only requires but repays thorough grinding, because most of its nutrient content is cellulose, which can be broken down only slowly in the gut. Grinding increases the exposed surface area, enabling the microbes that ferment it in the gut to break it down at a reasonable rate, and also acts to mechanically disrupt the cell walls.

Cattle, as well as horses, have cheek teeth whose great height makes provision for wear. In horses the teeth continue to grow, albeit for a short time, after they have erupted, allowing for even more wear. This condition seems to have been present in glyptodonts, probably in its most extreme condition. Indeed, they were hypselodont, i.e., had ever-growing teeth (see Janis & Fortelius 1988). In cattle and horses alternating layers of very hard enamel, and less hard dentine and cement, run vertically through the tooth. The enamel, being more resistant to wear than the other materials, always protrudes slightly above the dentine and cement on the occlusal surface of the tooth. Wear does not make the tooth smooth, but preserves the file-like surface. Glyptodonts achieved the same effect with different materials; they had no enamel, but instead employed osteodentine. A branched band of osteodentine extends through the depth of the tooth. Its resistance to wear allowed it to protrude slightly above the grinding surface, giving the same file-like effect as in cattle.

Greaves (1973) observed that in ungulate herbivores the hard material (enamel) at leading edge of the tooth forms a smooth flush transition to the softer material (dentine) immediately adjacent, while the softer material at the trailing edge shows a step in the transition to the edge of the hard material following it. Thus, it is possible to predict the direction of movement of the upper and lower teeth during the power stroke by noting where the continuous and discontinuous interfaces are located.

Striae cannot be observed in glyptodont teeth, as is the case in other xenarthrans (Vizcaíno & Bargo 1998). Wear facets in the first tooth are not observable, while in the remaining teeth different regional variations are seen in each individual tooth, but no leading edge is clearly identifiable as those observed in ungulates by Greaves (1973). This suggests little lateral component in the power stroke direction. The teeth have transverse crests in each lobe, but the osteodentine also forms a longitudinal crest, which does not stand as high above as the enamel in ungulate teeth.

Xenarthran teeth have been studied by previous workers. Naples (1987) applied Greaves' model to tardigrade edentates with proportionally larger teeth and prominent ridges of hard dentine. When the model is applied to armadillos (Vizcaíno & Bargo 1998), the patterns observed in eutatines are very peculiar. The posterior mandibular teeth show a step in the interface between the outer hard dentine and the soft dentine and a smooth transition to the inner hard dentine. These patterns suggest that the 'leading edge' role was played by the inner hard dentine core, and the 'trailing edge' by the external hard dentine ridges.

Shape of the jaws. — The shape of the lower jaw of glyptodonts is in some ways like that of a cow, and in other ways rather different, as described above (Fariña 1985). In both, the tooth row lies well below the joint where the jaw articulates with the main body of the skull, an arrangement that leaves ample room for the hypsodont upper teeth and modifies the moment arm of the masseter muscle. In both, the coronoid process where the temporalis muscle attaches is relatively small, and the angle of the jaw provides a large area of attachment for the masseter muscle. Both animals have a long row of grinding teeth, but the last tooth of the cow is well forward of the jaw joint, at the distance predicted by the one-third rule (Greaves 1982). On the other hand, the last tooth in glyptodonts is vertically below the joint, an arrangement made possible by placing the last few teeth on the inner face of the dentary. The lower jaw has in effect been telescoped to fit a long tooth row into a short jaw. The articulating surfaces of the jaw joint have shallowly convex surfaces in both animals, but these surface are roughly horizontal in cattle and vertical in glyptodonts. It is noteworthy that in glyptodonts the tooth row lies further ventral to the CMJ than in any other mammal; this distance may be interpreted as a measure of hypsodonty (Greaves 1974).

The odd skulls of glyptodonts are rendered even stranger by the descending processes of the zygomatic arches, spikes of bone that look like drooping moustaches. Similar but smaller descending processes are present in sloths and provide part of the area of origin of the masseter muscle. It seems clear that the masseter must also have originated on the descending process in glyptodonts, but in their case it seems that the muscle fibres of the masseter must have extended almost horizontally.

There are several curious consequences of the unique geometry of the jaws. Firstly, if the jaw joint acts as a hinge, then each tooth in the lower jaw must move along an arc centred at the joint as the mouth opens and closes. This implies that the front tooth would rise almost vertically to close against the front tooth of the upper jaw, but the hindmost tooth would slide forward almost horizontally to close against its opposite number. Any crushing action of the back teeth would depend on the jaw joint's capacity to slide up and down. Sliding as well as rotation occurs in the jaw joints of rodents, but in rodents sliding is horizontal instead of vertical. Rodents slide the lower jaw back and forth to grind their food. Cows move their jaws from side to side to chew, by forward sliding of the joint on one side of the jaw combined with backward sliding on the other. The articulating surfaces are convex, so these movements can be made without disarticulating the jaw. The vertical articular surfaces of glyptodonts would allow some side-to-side movement of the jaw, as well as up and down sliding. Although, as noted above, no striae were observed on the teeth, the differential wear pattern on the soft dentine of the teeth can be explained by that kind of movement.
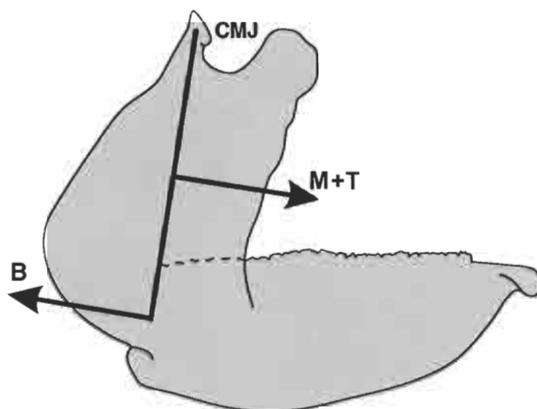
Fig. 5. Diagrams showing forces acting on a glyptodont jaw when food is being bitten. The jaw would be in equilibrium under forces acting as shown; the lengths of the arrows approximately indicate the magnitudes of the forces. The forces are B, the bite force; M, the force of the masseter and lateral pterygoideus muscles; and T, the temporalis muscle.

Another curious feature of glyptodonts is the arrangement of muscles. The space available shows that the masseter and the pterygoideus muscles, on the inner face of the jaw, were much larger than the temporalis. This is the usual situation in herbivores; but in glyptodonts the masseter and pterygoideus were apparently nearly horizontally oriented. It is important to consider how this would have affected the pattern of forces when the animal chewed. Fig. 5 shows the forces that may have acted on the lower jaw when food was bitten by the front teeth. The resultant of the forces M (exerted by the masseters) and T (exerted by the temporalis) have been drawn acting in the directions in which the muscles seem to have pulled, based on the positions of the origin and insertion sites. The food would have exerted a backward force B on the ascending ramus at its junction with the horizontal ramus, as the force was transmitted from the biting tooth. However, the position of the bite is irrelevant to the general mechanical arrangement of the forces, because it is only the ascending ramus that must be considered as a free body, rather than the entire mandible, since only the ascending ramus is the structure that rotates and the horizontal ramus acts as a protruding beam. Hence, the horizontal ramus cannot be approximated to be a prolongation of the ascending ramus, as is assumed in Greaves' (1982) model. Instead, the bite forces are withstood by the horizontal ramus and by the connection between both the horizontal and the ascending rami. Therefore, at any bite point, be it at the first, last or an intermediate tooth, the force transmitted to the ascending ramus is exerted at its ventral extreme (force B in Fig. 5). This, as well as the lack of incisors or canines, renders Greaves' model inappropriate. A more general model that includes the general herbivore pattern and that of glyptodonts (and to a certain extent, that of some proboscideans) will be discussed elsewhere (Blanco & Fariña in preparation).

Another question posed by the strange structure of the masticatory apparatus is the degree of gape. Muscle fibres can exert substantial forces only over a restricted range of lengths (Dimery 1985). Commonly, muscle fibres work over a range of lengths in which the minimum length is 70–75% of the maximum length. The ventralmost bundles of fibres in the masseter of *Panochthus* are 20 cm from the jaw articulation, and would have been 18 cm long when the mouth was closed. If they lengthened by 8 cm to 26 cm, the mouth could have opened by 8/18 radians, or 25° (18 is 70% of 26). It seems
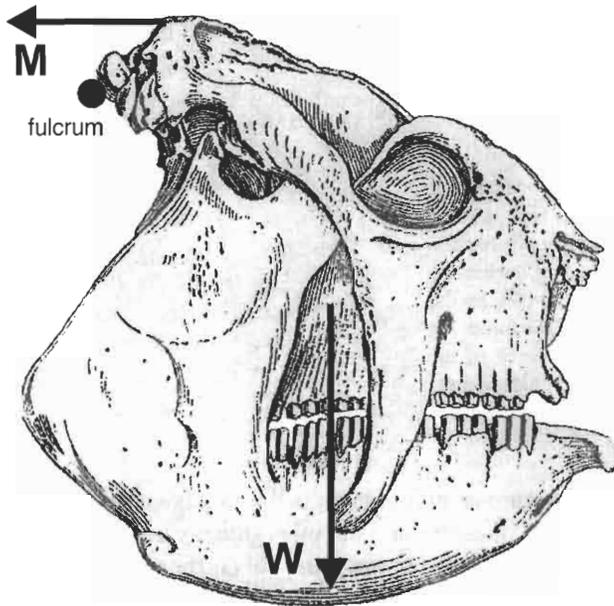
Fig. 6. Forces acting on the head of a glyptodont. *W*, weight of the head; *M*, force exerted by the neck musculature and tendons, and the fulcrum is the atlanto-condylar joint.

unlikely that the mouth would have opened wider than that, but it would have easily been sufficient for feeding on grass. Humans can open their mouths through an angle of about 25°.

In the preceding argument it was assumed that at least the ventral part of the masseter was parallel-fibred, with fibre bundles running all the way from the angle of the jaw to the descending process of the zygomatic arch. In many mammals the masseter is pinnate, with short fibres converging on tendons. The latter arrangement increases the force that the muscle can exert (because it increases the number of fibres that can be fitted into the muscle), but reduces the range of movement (because the fibres are shorter). If the ventral part of the masseter muscle of glyptodonts were pinnate, gape would be severely restricted.

The large masseter muscle must have exerted strong forces on the descending process of the zygomatic arch. Clearly, the process was strong enough to resist snapping, but how strong was it? An answer to this question may be obtained by following the procedure described in the Material and methods section. Moreover, as stated in the Results, these stresses are an order of magnitude less than the ultimate compressive and tensile strengths of compact bone. However, the process is made of cancellous bone with only a superficial layer of compact bone, as determined by examining a descending process of *Doedicurus*, another large Lujanian glyptodont, that had been broken close to the base. The broken surface showed that the outermost layer of the process was compact bone (about 4 mm thick on the anterior face, 0.5 mm elsewhere), but that the bulk of the process was cancellous. Cancellous bone is weaker than compact bone because of its spongy nature. Its strength varies, depending on the degree of

sponginess, but ranges up to at least 50 MPa (Currey 1984). Various leg bones of mammals (which are known to suffer much higher stresses and are cancellous) have been shown to be between two and five times as strong as is needed to withstand the forces that act on them in strenuous activities such as running and jumping (Alexander 1981). Similarly, it seems likely that the zygomatic process, mainly cancellous bone with an outer compact layer, was designed to be several times as strong as was needed to withstand the forces of biting.

In calculating the force on the process, it was assumed that the masseter muscle was composed of parallel fibres. It has been shown that unless its ventral part was parallel-fibred, gape would have been severely restricted. More dorsal parts may have been pinnate but this would not alter the calculation considerably, because the ventral parts would have had most effect on the bending moment.

All these peculiarities are a consequence of the fact that the masticatory apparatus migrated from a position in front of the braincase to underneath it, making the condyle–lower tooth row and glenoid fossa–upper tooth row distances generally equal, which implies simultaneous occlusion (Greaves 1974).

In our proposed hypothesis glyptodonts do not seem to have been highly efficient at chewing, even though they clearly had an appropriately high food intake. This is congruent with the relatively small grinding area of their dentition, as evidenced by the fact that dental measurements yield underestimates of body mass (Fariña et al. 1998). This is consistent with what Pérez et al. (2000) proposed about the function of the tongue, which in glyptodonts might have had a central function in processing food in contrast to the more complementary function in cattle. These factors suggest a mechanism whereby glyptodonts shunt food to the stomach or perhaps even to a caecum. The idea of incomplete oral processing of food is congruent with McNab's (1989) suggestion of a low metabolic rate for glyptodonts. Fariña (1988) proposed that the peculiar evolution of the masticatory apparatus described above was the evolutionary price paid by large glyptodonts in exchange for being so well armoured. Smaller forms, such as the Miocene *Propalaehoplophorus*, have relatively longer, less telescoped snouts. Indeed, it would be difficult to retain an armadillo-like (or, more generally, a primitive mammalian) position of the masticatory apparatus in conjunction with a complete armour that includes a dorsal covering for the neck. This is due to the fact that the allometric scaling of the skull implies a proportionately stronger neck musculature to keep it in position, as shown in Fig. 6, where W is the weight of the head, M the force exerted by the neck musculature and tendons, and the fulcrum is the atlanto-occipital joint. Indeed, the skull weight would be increased as the cube function of the linear dimensions, while the muscles are as strong as their cross-sections, and therefore their strength grows in the square function. Thus, the neck musculature (assuming it did not change substantially its pennation pattern) and the nuchal ligament would have increased in size to a point in which its covering by the armour would become more and more difficult. In big glyptodonts, the large, ever-growing teeth are more proximal to the fulcrum (i.e., the occipital condyles). Therefore, the skull weight has a shorter output arm, and consequently its moment about the fulcrum is smaller. Hence, it can be stabilised by a smaller input force, which allows a relative reduction of that neck musculature.

Acknowledgements

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