Rostral reconstruction of South American hippidiform equids: New anatomical and ecomorphological inferences

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Bernardes, C., Sicuro, F.L., Avilla, L.S., and Pinheiro, A.E.P. 2013. Rostral reconstruction of South American hippidiform equids: New anatomical and ecomorphological inferences. *Acta Palaeontologica Polonica* 58 (4): 669–678.

The Pleistocene *Equus* (*Amerhippus*) and hippidiforms frequently occur together in the South American fossil record, suggesting a possible case of sympatry and syntopy. Although resembling each other in their overall morphology, their rostra show distinct differences. While *Equus* (*Amerhippus*) resembles extant horses, hippidiforms are characterised by slender nasal bones, a retracted nasal notch at the level of M2–M3 or posterior to M3, and the presence of dorsal preorbital fossae of variable depth. Here we present an anatomical reconstruction of the muzzle of hippidiforms based on homologous patterns in the extant horse *Equus caballus*, together with a morphofunctional analysis of their rostra and a comparative analysis of premaxillary shape. The rostral morphology of hippidiforms suggests the presence of a developed upper lip with prehensile function, as occurs in extant black rhinoceros. This prehensile structure could be ecomorphologically related to browsing, thus reducing niche overlap with *Equus* (*Amerhippus*), and hence competitive pressure.

Key words: Mammalia, Perissodactyla, Equidae, hippidiforms, anatomical reconstruction, ecomorphology, Pleistocene, South America.

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Received 3 September 2011, accepted 4 April 2012, available online 20 April 2012.

Introduction

Equids first arrived in South America as a result of the Great American Biotic Interchange (GABI) ca. 3 million years ago (Webb 1978; Marshall 1988), and subsequently occupied both lowland and highland environments from subequatorial to subtropical latitudes (Alberdi and Prado 1992). The systematics of the South American equids is still a matter of debate, especially as regards the number of valid genera of hippidiforms. While MacFadden (1997) argued that both *Hippidion* and *Onohippidium* originated in North America as descendants of *Pliohippus*, Alberdi and Prado (2004) recognised just one hippidiform genus, *Hippidion*, which is endemic to South America.

These issues notwithstanding, it is clear that the Pleistocene South American equids can be grouped into two distinct cranial morphologies: *Equus* (*Amerhippus*), resembling extant horses (Fig. 1A, B); and the hippidiforms *Hippidion* and *Onohippidium* (Fig. 1C), possessing a rostral anatomy similar to the North American equid *Onohippidium galushai*. The oldest record of a South American hippidiform, *Hippidion devillei*, dates from the Late Pliocene or Early Pleistocene of Uquia, Argentina (Prado et al. 1998), while the oldest reported occurrence of South American *Equus* (*Amerhippus*) comes from the Early Pleistocene (Ensenadan) of Tarija, Bolivia (Prado and Alberdi 1994). Both forms persisted until the Late Pleistocene or early Holocene, with the possibility of sympatric coexistence (Alberdi and Prado 2004). Indeed, at several fossil localities, such as Lagoa Santa caves in Minas Gerais, Brazil (Cartelle 1999) and Taguata, Chile (Alberdi and Frassinetti 2000), the remains of both types of equids are found together, indicating a potential case of syntopy (MacFadden 1997; Alberdi and Prado 2004).

http://dx.doi.org/10.4202/app.2011.0107

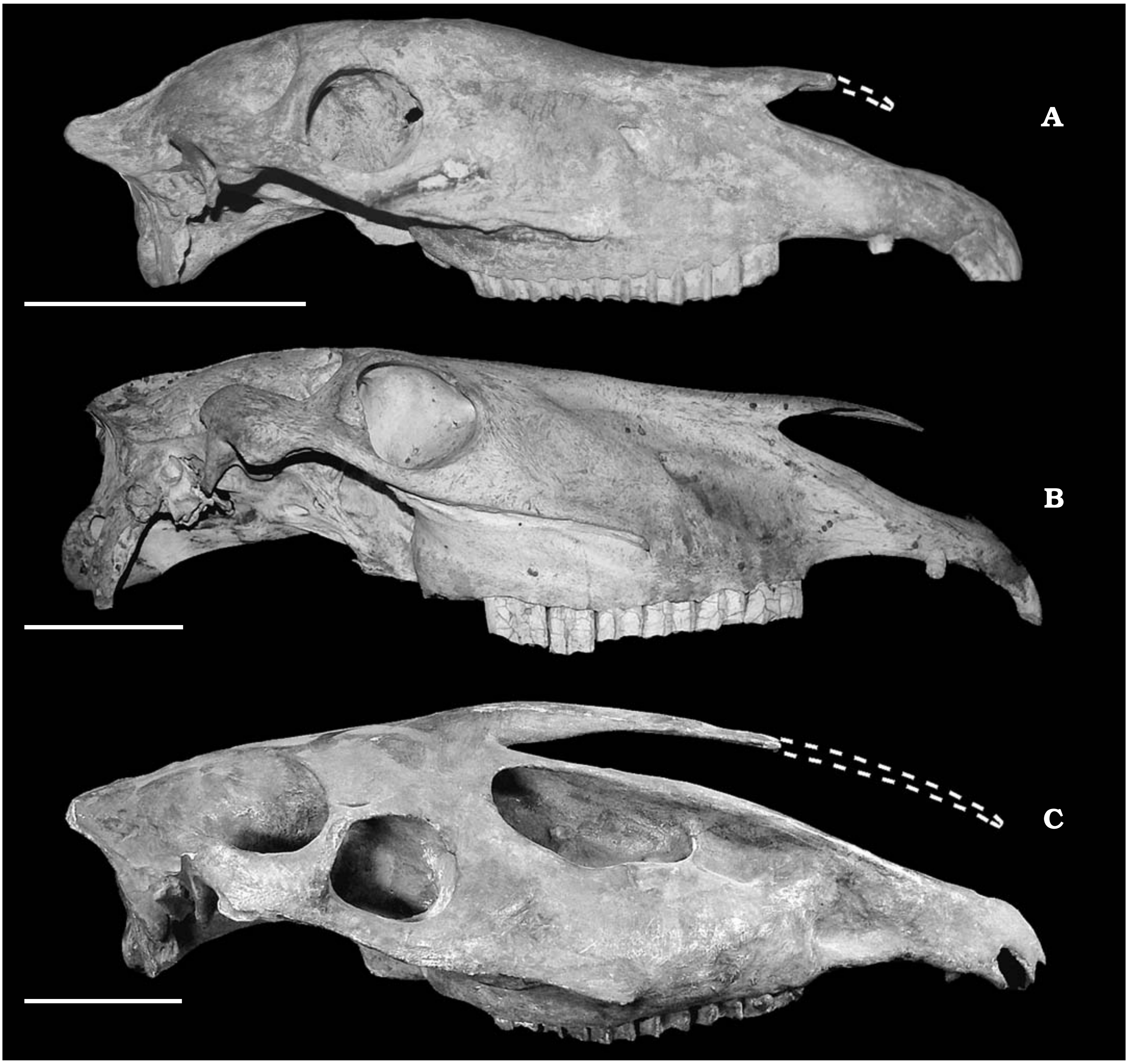

Fig. 1. Comparison of the three equid skull patterns analysed in this study. **A**. The South American horse *Equus* (*Amerhippus*) *andium* Wagner-Branco, 1883 (EPN V-2161 from the Pleistocene of Punin, Ecuador). **B**. The extant horse *Equus caballus* (MN 77320). **C**. The hippidiform *Onohippidium munizi* Moreno, 1891 (MLP 6-2 from the Late Pleistocene of Lobería, Buenos Aires Province, Argentina). Scale bars 10 cm.

Compared to *Equus*, the skull of hippidiforms is large in comparison to their body size (Alberdi and Prado 2004). The nasal notch is retracted posteriorly to a point below M2–M3, or posterior to M3, and the nasal bones are narrow and do not contact the premaxillae and maxillae. Dorsal preorbital fossae (DPOF) are located on either side of the rostrum, below the retracted nasal notch and anterior to the orbit, and vary in shape, size and depth. In some specimens, the DPOF is subdivided and forms a second, smaller fossa towards the anterior portion of the rostrum (MacFadden and Skinner 1979; Alberdi and Prado 2004). Though all of these characters have been extensively discussed in terms of their taxonomic usefulness (Prado and Alberdi 1996; Orlando et al. 2003, 2008; Weinstock et al. 2005), their functional properties have barely been investigated (but see MacFadden 1994).

Palaeoecological inferences about the feeding behaviour of hippidiforms have so far mainly relied on dental characters or isotopic evidence (MacFadden et al. 1999; Sánchez et al. 2006; Prado et al. 2009; Monique Alves Leite unpublished data). Following the approach of Bargo et al. (2006), we compared the rostra of the extant horse *E. caballus* and the South American hippidiforms, using musculoskeletal

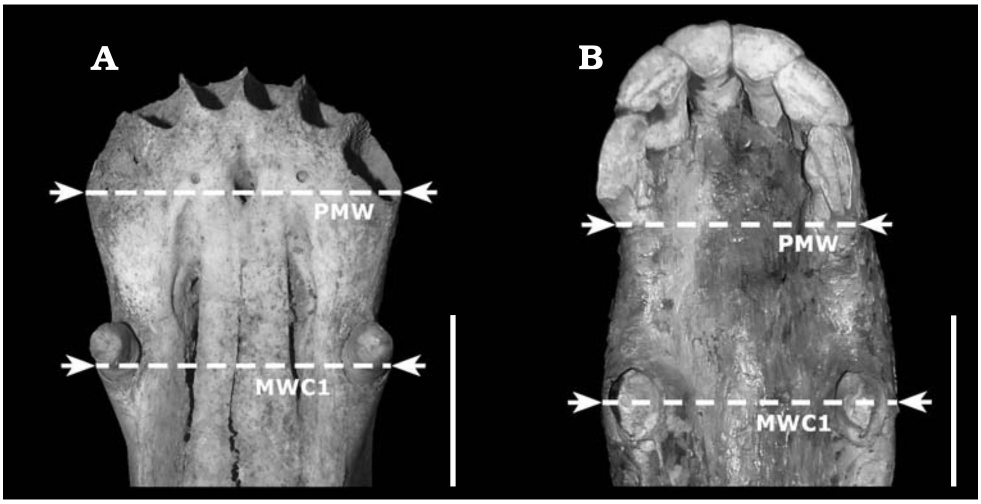

Fig. 2. Palatal view of the premaxillae of extant horse *Equus caballus* Linnaeus, 1758 (**A**) and the hippidiform *Hippidion principale* Lund, 1846 (MLP 6-8 from the Late Pleistocene of San Lorenzo, Santa Fe, Argentina) (**B**), classified according to Solounias and Moelleken (1993). Note the marked palatal concavity on *H. principale*. Scale bars 10 cm. Abbreviations: PMW, premaxillary width; MWC1, maxillary width across C1.

homologues from the former to infer the muscular anatomy and functional morphology of the extinct forms. Based on this, we present a scenario of the ecomorphology of the South American hippidiforms and ancient *Equus*.

Institutional abbreviations.—EPN, Museo de Historia Natural "Gustavo Orcés V." de la Escuela Politécnica Nacional, Quito, Ecuador; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MN, Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MPH, Museo Municipal "Punta Hermengo" de Miramar, Buenos Aires, Argentina; UC-MG, Museu de Ciências Naturais, Pontificia Universidade Católica de Minas Gerais, Minas Gerais, Brazil; UFF, Departamento de Morfologia, Universidade Federal Fluminense, Rio de Janeiro, Brazil; UFRJ, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; UNIRIO, Universidade Federal do Estado do Rio de Janeiro, Rio de Janeiro, Brazil.

Other abbrviations.—DPOF, dorsal preorbital fossae; GABI, Great American Biotic Interchange; m., musculus; MWC1, maxillary width across C1; PMW, premaxillary width.

Material and methods

Our study was based on six complete skulls, including mandibles, of *Equus caballus* (UFRJ/DG 92; MN 77320, 77321; UNIRIO-CD 1001, 1002, 1003. Two preserved heads of *E. caballus* (held at UFF) were used for studies of anatomical correlation (see below). Fossil specimens included the complete or fragmented skulls and mandibles of *Onohippidium munizi* (MLP 6-2), *Hippidion* sp. (MLP 6-8), *Hippidion bonaerensis* (MACN Pv401), *Hippidion principale* (MPH-P067), and *Hippidion* sp. (MCL- 6277/01), as well as two skulls of *Equus* (*Amerhippus*) (MN 3784-V and EPN V-2161).

The fossil material was photographed in different views. One preserved head of *E. caballus* (formaldehyde 3%) was completely dissected, the muscular groups isolated, and placed directly over a plasticised photograph, in original size and in lateral view, of *Onohippidium munizi*. This procedure provided a rough, but insightful tool to correlate the origins and insertion areas of rostral muscles between extant horses and hippidiforms. Anatomical correlation was used as the basis for a topographic reconstruction of muscle groups on the hippidiform skull. Muscular descriptions follow Budras et al. (2003) and Getty (2008), while muscle terminology is in accordance with the Nomina Anatomica Veterinaria (2005 available at http://www.wava-amav.org /Downloads/nav_2005.pdf).

According to Solounias et al. (1988) and Solounias and Moelleken (1993), there is a strong correlation between the shape of the premaxilla and feeding style in herbivorous ungulates, with browsers generally being characterised by a pointed premaxilla, grazers by a wide premaxilla, and mixed-feeders occupying an intermediate state. Although the scarcity of the material hindered a more complex morphometric approach as performed by Solounias et al. (1988) and Solounias and Moelleken (1993), we quantified the relative width of the premaxilla as the ratio of the maximum anterior width of the premaxilla (PMW; Fig. 2) and the width of the rostrum across the upper canines (MWC1; Fig. 2): a ratio higher than 1.0 reflects a relatively broad anterior portion of the premaxilla, and vice versa.

The anatomy and feeding behaviour of the extant horse, as well as the marked differences in premaxillary morphology and foraging habits observed in black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceroses (Groves 1972; Hillman-Smith and Groves 1994), were used as present-day models to make inferences regarding the possibly distinct feeding strategies of hippidiforms and *Equus* (*Amerhippus*).

http://dx.doi.org/10.4202/app.2011.0107

Table 1. Anatomical description of the rostral muscles present in *Equus caballus*, and inferred correspondences on the hippidiform skull.

Muscles	*Equus*		Hippidiforms	
	origin	insertion	origin	insertion
caninus	border of rostral portion of facial crest	lateral portion of nostrils	border of rostral portion of facial crest	lateral portion of nostrils
levator nasolabialis	lateral border of nasal and part of frontal	superior angle of upper lip and lateral border of nostrils	dorsal surface of nasal and frontal	superior angle of upper lip and lateral border of nostrils
levator labii maxillaris	junction of lacrimal, jugal and maxilla	upper lip	DPOF and its subdivision (when present)	upper lip and above the m. orbicularis oris fascia
orbicularis oris	anterior portion of rostrum, beneath the nostrils, forming the lips; upper and lower lips have approximately same thickness		anterior portion of rostrum, beneath the nostrils, forming the lips; upper portion more robust than in *Equus*	
buccinatoris	maxillary portion of buccinator fossa	angle of the mouth, uniting with m. orbicularis oris	maxillary portion of buccinator fossa	angle of the mouth, uniting with m. orbicularis oris
zygomaticus	beneath facial crest, under the fascia covering the m. masseteris	angle of the mouth, uniting with m. buccinatoris	beneath facial crest, under the fascia covering the m. masseteris	angle of the mouth, uniting with m. buccinatoris
masseteris	facial crest and a tendon of the zygomatic arch	lateral border of angular process of mandible	facial crest and a tendon of the zygomatic arch	lateral border of angular process of mandible

Results

Our comparisons show that *Equus* (*Amerhippus*) differs from *E. caballus* in having a wider angle of the nasal notch, a narrower posterior portion of the maxilla located below the zygomatic arch, and, in some specimens, a shallow depression on the maxilla located posterior to the infraorbital foramen (Fig. 1A). Nevertheless, both species are similar in their overall skull morphology, thus indicating that general statements regarding the rostral muscular anatomy of *E. caballus* (Fig. 3) may also be valid for *E.* (*Amerhippus*).

By contrast, we found that, in addition to the features mentioned above (MacFadden and Skinner 1979; Alberdi and Prado 2004), hippidiforms differ from *Equus* in a relatively more posteriorly positioned orbit located well ventral to, and directly below, the nasal suture. Unlike *Equus*, hippidiforms also present a less flexed occipital bone, and a flat and low braincase (Fig. 1C). Other features of their rostrum suggesting differences in the proportion, shape, and/or positioning of rostral muscles are discussed below.

According to our anatomical correlations (Table 1), the posterior position of the nasal notch in hippidiforms seems to reflect a caudally displaced m. levator nasolabialis, whose origin is above the nasal and frontal bones in *E. caballus*. In addition, hippidiforms possess a deeper fossa for the origin of the m. buccinator above the maxillary diastema (Fig. 4), implying a more robust development of this muscle than in the living horse. Similarly, the DPOF can also be regarded as an expansion of a muscular origin site. The fossa is located at the junction of the lacrimal, jugal and maxilla, which gives rise to the m. levator labii superioris (Fig. 4). The DPOF is a variable character among hippidiforms, showing different stages of development depending on the individual; a clear subdivision of the fossa into two distinct proximal and distal areas is seen in some cases, as in MLP 6-2 (Fig. 1C). We agree with Alberdi and Prado (2004) that this feature is not a valid character to distinguish the genera *Onohippidium* and *Hippidion*, since it is highly polymorphic. Nevertheless, the location of the DPOF indicates that it may be a specialised area for the attachment of a bipartite origin of the m. levator labii superioris. In comparison with the anatomy of extant horses, the portion of the muscle originating from the proximal part of the DPOF would follow each side of the rostrum and join the opposite muscle at the rostral end of the nasal bone, before descending anteriorly to insert at the upper lip commissure. By contrast, the anterior portion of the m. levator labii superioris, originating from the distal part of the DPOF, would function in a similar way to that found in *Alces alces* (Clifford and Witmer 2004a), with each muscle running along the side of the rostrum before branching out as aponeuroses at the premaxilla, spreading anterodorsally to insert at the dorsal part of the m. orbicularis oris and part of the lateral portion of the m. lateralis nasi. Moreover, considering the slenderness of the nasal bones of hippidiforms, it is possible that the m. levator labii superioris ran partially upon a rigid cartilage that formed most of the narial cavity, as otherwise the nasals would easily be broken, especially among foals.

The ratio of PMW and MWC1 in *E. caballus* and *E.* (*Amerhippus*) is 1.11 and 1.12, respectively, compared to 0.84 in *Hippidion*. These values are reflected in the enlarged and squared anterior part of the rostrum of *Equus*, as opposed to the narrow and U-shaped rostrum of hippidiforms. In addition, both *E. caballus* and *E. (Amerhippus)* have a flattened palate (Fig. 2A), while in hippidiforms the palate is concave (Fig. 2B).

Discussion

Rostral anatomy and function.—The function of the DPOF in hippidiforms has not been widely discussed. Gregory (1920) refuted several earlier suggestions by other authors attempting to interpret the DPOF of hippidiforms as an

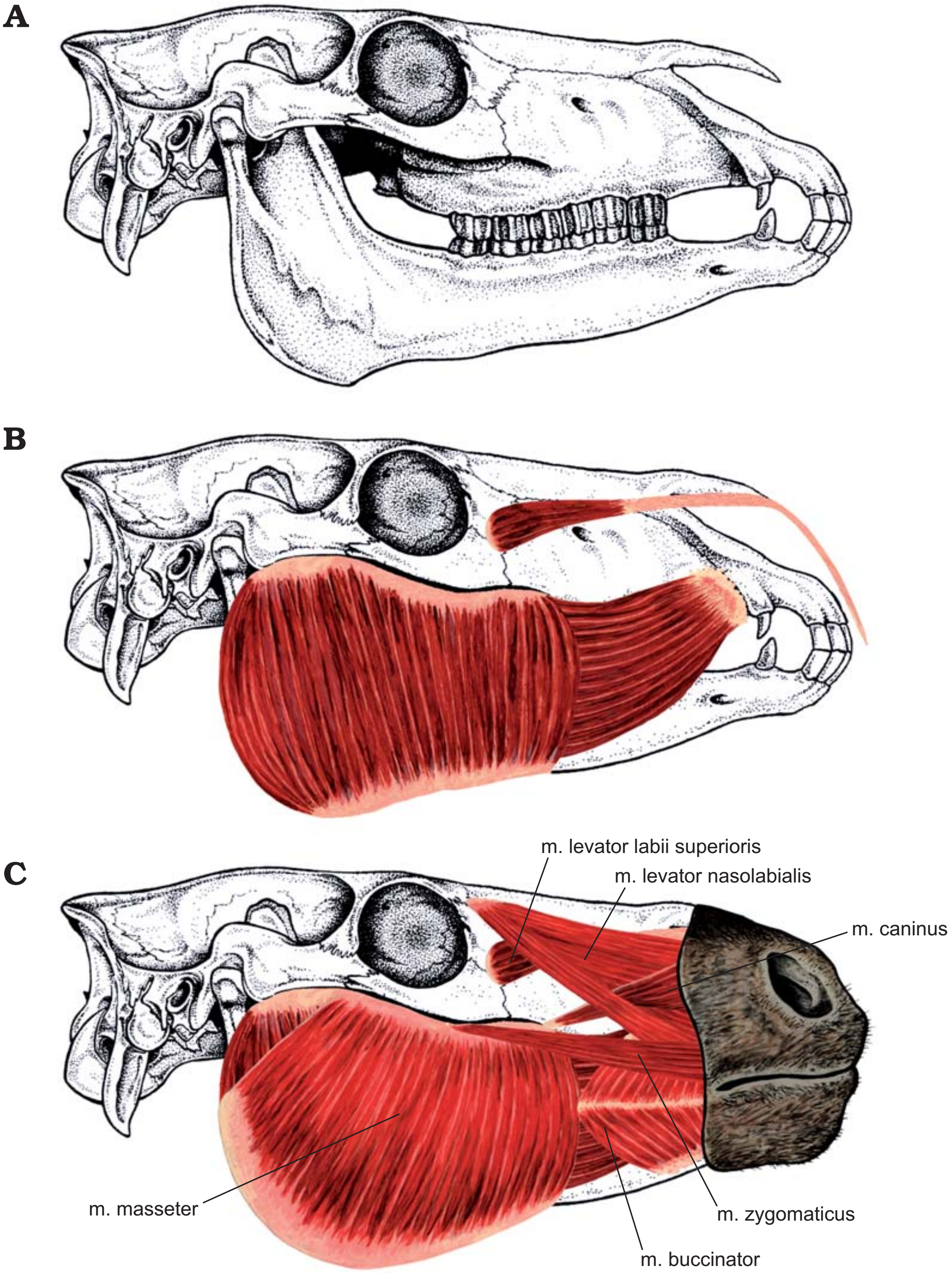

Fig. 3. Anatomical depiction of the rostral musculature of extant horse *Equus caballus* Linnaeus, 1758. Skull (**A**), deeper rostral musculature (**B**), and rostral muscles associated with the mobility of the upper lip (**C**). Note that B excludes the m. levator nasolabialis, so as not to obscure the m. levator labii superioris.

osteological correlate of a facial gland (as can be found in some extant artiodactyls; Gaudry 1862), as the site of attachment of the levator muscles of a proboscis (Studer 1911, apud Gregory 1910), or as the site of attachment for other facial muscles. The author argued that the DPOF were probably sites for nasal diverticula, remnants of which can be seen in extant horses near the anterior part of the lacrimal fossae or on the portion of the maxillae adjacent to the nasal notch. However, Getty (2008) later demonstrated that the m. levator labii superioris originates near the juncture of the lacrimal, jugal and maxilla, which in hippidforms is likely located in the DPOF, thus indicating that the DPOF indeed may serve as an attachment site for rostral musculature.

The functional interpretation of the conspicuous morphological features characterising hippidiforms requires a broad comparative approach including other ungulates. Clifford (2003) discussed the independent acquisition of a proboscis in mammals, especially among ungulates, which he defined as any enlargement of the narial apparatus in a species relative to its outgroup. He argued that a proboscis often arises as

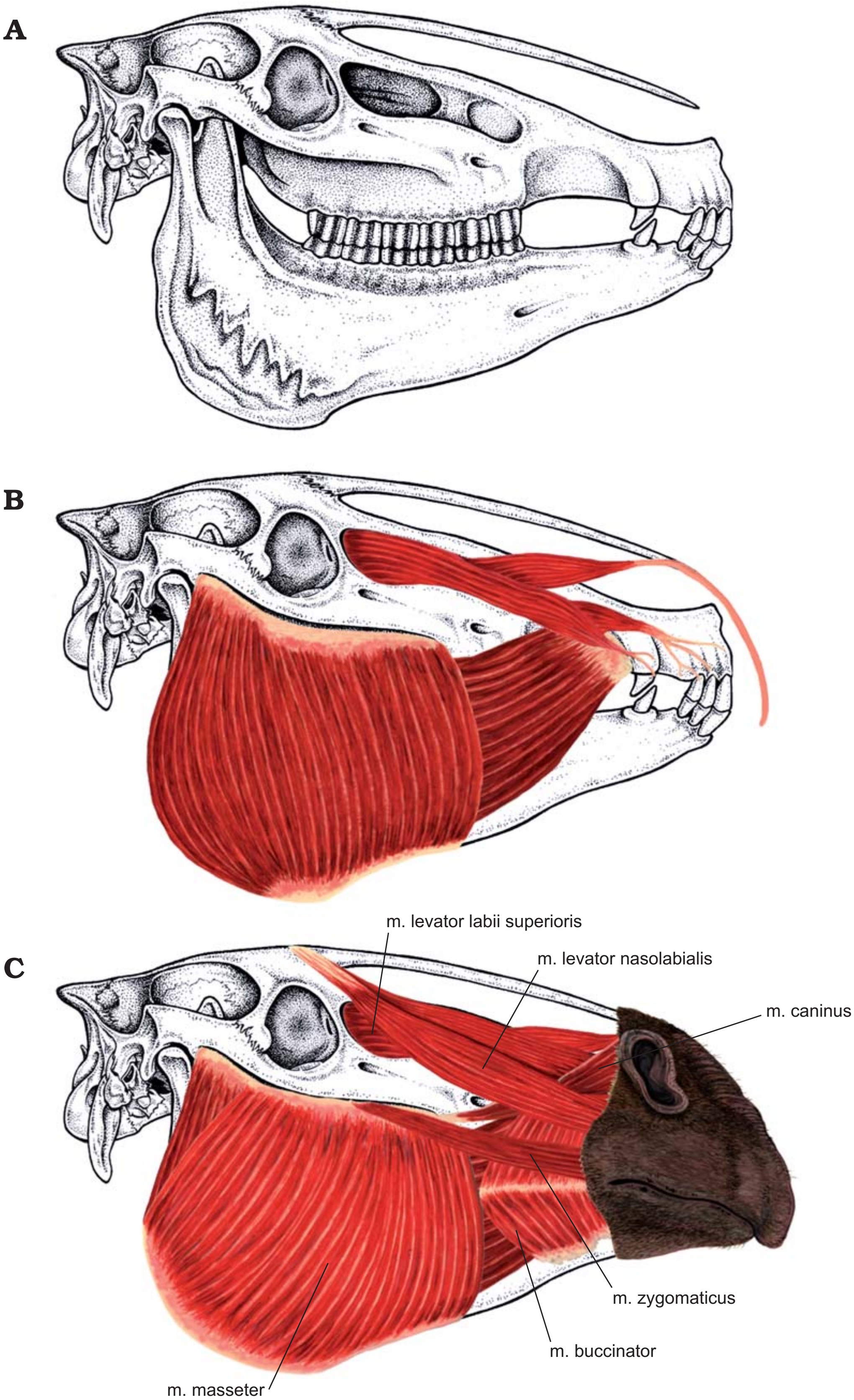

Fig. 4. Anatomical reconstruction of the rostral musculature of hippidiforms based on the homologies with *Equus caballus*. Skull based on specimen MLP 6-2 of *Onohippidium munizi* (**A**), deeper rostral musculature (**B**), and rostral muscles associated with the mobility of the well-developed upper lip (**C**). The cartilaginous buttress that would have held the slender nasal bones is not shown. Note that B excludes the m. levator nasolabialis so as not to obscure the m. levator labii superioris, which is shown with two separate origins at the DPOF.

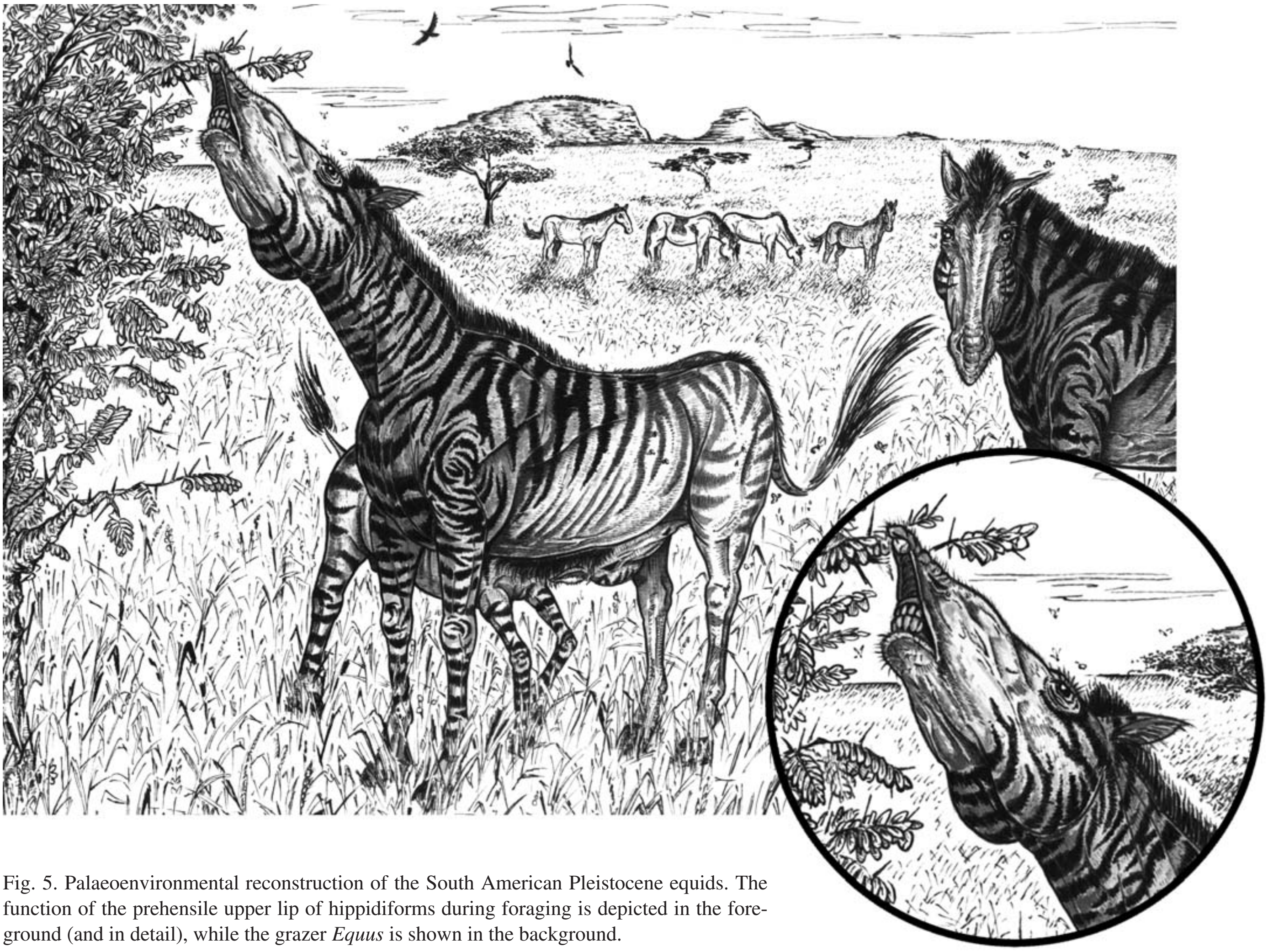

Fig. 5. Palaeoenvironmental reconstruction of the South American Pleistocene equids. The function of the prehensile upper lip of hippidiforms during foraging is depicted in the foreground (and in detail), while the grazer *Equus* is shown in the background.

a result of exaptation of previously existing modifications in rostral anatomy. Hippidiforms show some of the features listed by Clifford (2003) as characteristic of animals that have developed a proboscis through a reorganisation of rostral elements ("vestibular proboscis" sensu Clifford 2003), including a markedly retracted nasal notch, a loss of contact between the nasals and the premaxillae, and the presence of deep buccinator fossae (Fig. 1C). However, hippidiforms also possess greatly elongated nasal bones, thus excluding the possibility of a proboscis in the sense proposed by Clifford (2003).

Among extant perissodactyls, tapirs provide an example of a different style of proboscis. During the course of their evolution, the rostrum of tapirs underwent several changes in shape (Prothero and Schoch 2003), with the development of a proboscis, constructed of connective tissue and muscle, resulting in parts of the bony nares becoming reduced and displaced posteriorly, and several nasal cartilaginous elements being lost (Witmer et al. 1999). While this situation seems to resemble that found in hippidiforms, their elongated nasal bones preclude the presence of a muscular hydrostatic organ analogous to that of tapirs.

The saiga antelope (*Saiga tatarica*) also possesses a proboscis, in this case used to regulate nasal airflow and clean inhaled air of any dust particles (Frey et al. 2007). The nasal cavity of saigas is characterised by an enlarged and greatly altered nasal vestibule, while the bones forming the narial margin are marked by reduced lateral cartilages and a modified attachment site for the buccinator muscle (Clifford and Witmer 2004b). Furthermore, the lateral surface of their maxilla, between the infraorbital foramen and the facial crest, bears an angled tubercle with a sharp rostral margin serving as attachment site for the maxillolabial muscles (Clifford and Witmer 2004b). However, the large nasal vestibule is compressed through the action of the maxillolabial muscles in saigas, whereas the same function in equids is performed by the m. nasalis, thus implying that the saiga may not be the most suitable model to understand the rostral functionality of hippidiforms.

Moose (*Alces alces*) also present apomorphic changes to their nasal and oral vestibules (Clifford and Witmer 2004a), with their lateral nasal cartilage and the m. levator labii superioris performing movements analogous to a small proboscis. In moose, the m. levator labii superioris runs rostrally underneath the m. levator nasolabialis, and halfway along its length branches out into several tendons inserting on the posterodorsal part of the nasal region. Thus, bilateral contraction of the m. levator labii superioris leads to the elevation and eversion (i.e., outward projection) of the upper lip (Witmer et al. 1999). In addition, hypertrophy of the muscles in the muzzle results in great mobility (Clifford 2003).This morphology provides probably the most appropriate model for the conspicuous rostral anatomy of the South American hippidiforms.

Although their elongated nasal bones mean that hippidiforms do not meet all the criteria established by Clifford (2003) for mammals bearing a proboscis, several features of their skull morphology and inferred rostral anatomy are consistent with the hypothesis that hippidiforms possessed a well-developed, prehensile upper lip. Nevertheless, despite the reorganisation of the narial cartilaginous components in tapirs, saigas, and moose, none of them have fossae on their maxillae serving as attachment sites for cartilaginous structures, as suggested by Gregory (1920) for hippidiforms. Rather, all of them show a modified line of action of some muscles related to the functionality of the proboscis (Clifford and Witmer 2004a, b). Indeed, the skull morphology of hippidiforms differs from that of other (proboscis-bearing) ungulates. In extant horses, the nasal notch is the site of attachment of two opposed, comma-shaped alar cartilages united by fibrous tissue, resulting in a certain degree of mobility and, in some cases, an effective articulation of the nostrils (Getty 2008). In hippidiforms, the retraction of the nasal notch and the reduction of the lateral portion of the nasals probably exposed the sinuses, and resulted in the detachment of the posterior portion of the narial cartilages from the nasal bones, thus providing in even greater rostral mobility. This hypothesis is further supported by features indicative of a well-developed m. buccinator, which controls the movements of the nasal and oral vestibules, and is often enlarged in proboscis-bearing mammals (Clifford 2003). Thus, hypertrophy of the m. levator labii superioris and the m. buccinator may have afforded hippidiforms greater mobility of the muzzle than in *E. caballus*, and likely also resulted in the development of a more robust upper lip (Figs. 4C and 5).

Palaeoecological implications.—In addition to a transversally narrow premaxilla and the presence of a circular arcade formed by the incisors (see also MacFadden 1997), our specimens show a concave palate relative to that of *Equus* (Fig. 2B). While the narrow premaxilla may function in effectively selecting food items, the concave palate forms an ellipsoid space between the roof of the mouth and the tongue during occlusion. This may help to maximize food extraction from a plant by pressing the food against the hard palate, while using the incisors to pull it off (Solounias and Moelleken 1993). The rostral morphology of hippidiforms therefore seems to be consistent with browsing, while *E. caballus*, and probably *E.* (*Amehippus*), are mainly grazers.

Quantitative analyses of dental macrowear and occlusal surface area of *E.* (*Amerhippus*) and *Hippidion* from Toca dos Ossos (BA), northeastern Brazil, also suggest divergent feeding habits for these genera (Monique Alves Leite unpublished data). While *E.* (*Amerhippus*) shows indications of a more abrasive diet, with the molars and premolars presenting marked rostrocaudal wear and a larger occlusal surface area, hippidiforms are characterised by a more uniform molar and premolar wear pattern, and less complex dental folds compared to *E.* (*Amerhippus*) (Monique Alves Leite unpublished data). Carbon and oxygen isotopic data derived from bone and tooth samples of both genera suggest that, while Middle Pleistocene equids adopted an opportunistic feeding strategy which likely enabled them to adapt to a variety of environments, by the Late Pleistocene their diet had become more selective, resulting in more specialised niches and restricted habitats (Sánchez et al. 2006). Following the hypothesis that nutritional stress in plant communities caused by climatic changes may have contributed to Pleistocene megafaunal extinctions, it has therefore been suggested that *Equus* (*Amerhippus*) and hippidiforms may have been driven to extinction by the disappearance of some plants forming critical components of their respective diets (Sánchez et al. 2006). Recently, further reports of the carbon and oxygen isotope composition of bone and tooth samples from different localities revealed that hippidiforms relied on a diet of C3 and mixed C3–C4 plants, whereas *E.* (*Amerhippus*) included C3, C3–C4, and C4 feeders (Prado et al. 2009, 2011), possibly reflecting differences in latitude and altitude.

Differences in feeding style between hippidiforms and *Equus* are further supported by hippidiform coprolites from two localities in western Argentina (García et al. 2007), which indicate that the animals from these sites were browsing on woody plants, typical of dry and warm environments, and herbaceous plants, typical of a dry and cold climate, respectively.

Studies on extant ungulates show that when two or more related species share the same habitat, ecomorphological adjustments leading to different feeding strategies play an important role in reducing competition (Kiltie 1982; Janis 1995; Sicuro and Oliveira 2002). For instance, Codron et al. (2007) demonstrated how different rostral anatomies reduce niche overlap in the case of the white (*Ceratotherium simum*) and black rhinoceros (*Diceros bicornis*). While the muzzle of the white rhinoceros has a flat upper lip as in extant horses (generally associated with adaptation to grazing), the black rhinoceros has a pointed, prehensile upper lip adapted to browsing (Hillman-Smith and Groves 1994; Groves 1972; Mills and Hes 1997). Moreover, analyses of carbon stable isotopes derived from the faeces of African ungulates have shown *D. bicornis* to cluster with browsers, while *C. simum* fits the profile of a grazer (Codron et al. 2007).

Despite the common ancestry of *E.* (*Amerhippus*) and hippidiforms (MacFadden 1997), each lineage evolved distinctly different rostral morphologies, possibly in response to overlapping ecological niches. Based on the estimated time of arrival of *E.* (*Amerhippus*) in South America, both taxa coexisted for nearly 1.7 Mya in the same areas, probably as syntopic populations (Alberdi and Prado 2004). Hippidiforms have no present-day morphological correlates, and represent an amalgam of functional patterns. According to our study, the anatomical modifications of the hippidiform rostrum are related to an increase in muzzle mobility, and are indicative of the presence of a prehensile upper lip similar in function to the upper lips seen in moose (*Alces alces*) and in the black rhinoceros (*D. bicornis*). Although there are other suggestions regarding the functional significance of the conspicuous DPOF of hippidiforms, the scenario proposed here has ecological and anatomical parallels (albeit to varying degrees) among proboscis-bearing and browsing ungulates.

Nevertheless, stable isotope analyses (Sánchez et al. 2006; Prado et al. 2009, 2011) indicate that hippidiforms varied in their feeding preferences depending on the habitat, with southern individuals living at high altitudes seemingly being able to feed on C3 and C4 grasses (Prado et al. 2011). The foraging preferences of herbivores are dictated not only by individual energetic demands (Du Toit 2005) but also by environmental conditions, which can influence the availability and quality of plants (Shipley et al. 2009). Therefore, the presence of a prehensile upper lip, though indicative of a browsing habit, does not exclude the possibility that other food sources (e.g., grass) formed part of the hippidiform diet.

Conclusions

Our reconstruction of the rostral morphology of South American hippidiforms shows that their anatomy reflects modifications of muscles acting on the oral and nasal vestibules. This not only implies anatomical divergence from *Equus*, but also a difference in feeding strategy: whereas *E.* (*Amerhippus*) appears to have been a grazer, hippidifroms became specialised browsers. Assuming that hippidiforms and *E.* (*Amerhippus*) were both sympatric and syntopic, we suggest that these differences reduced niche overlap, and hence competitive pressure, through ecomorphological means. This hypothesis corroborates previous studies that found differences in the use of resources by these two South American Pleistocene horses.

Acknowledgements

The authors are grateful to Castor Cartelle (Pontifícia Universidade Católica de Minas Gerais, Brazil), Hildebrando G. Benedicto (Universidade Federal Fluminense, Rio de Janeiro, Brazil), Luiz Flamarion B. de Oliveira (MN-UFRJ), Alejandro Kramarz and Laura Chornogubsky (both MACN), and Marcelo Reguero (MLP) for access to collections; Mario Alberto Cozzuol (Universidade Federal de Minas Gerais, Brazil) for relevant suggestions; Debora Gabriel Costa and Frederico Bonissoni Pêgo (Programa de Pós-Graduação em Biodiversidade Neotropical – UNIRIO) for help with data collection; Christine Janis (Brown University, Providence, Rhode Island, USA) and Gary Haynes (University of Nevada, Reno, Nevada, USA) for English revision and relevant comments, and the staff of the Laboratório de Biologia Vascular of the Universidade do Estado do Rio de Janeiro for their support.

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