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ORIGINAL PAPER

Tracing the Paleobiology of *Paedotherium* and *Tremacyllus* (Pachyrukhinae, Notoungulata), the Latest Sciuromorph South American Native Ungulates – Part I: Snout and Masticatory Apparatus

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Abstract

Inquiring into the paleoecology of extinct forms is always a challenge, particularly when the taxa under study correspond to derived ecomorphs of ancient and completely extinct clades. In this contribution, the configuration of the masticatory apparatus and associated features of the Neogene pachyrukhines *Paedotherium* and *Tremacyllus* are studied in a detailed, mainly qualitative, comparative analysis of 36 specimens. Tooth morphology and the reconstructed muscular configuration of pachyrukhines indicate an important mediolateral component during chewing, and predominant crushing over grinding, as well as anteroposterior movements for the coupling and action of stronger gnawing incisors. These actions are more compatible with hard and brittle or turgid fruit food consumption than specialized folivorous, and particularly grazing, habits. The infraorbital and palatal foramina morphology and other rostral features indicate increased touch sensibility for object recognition and are congruent with the presence of infoldings of the lips protecting the gingiva during gnawing on hard foods. Additionally, there was a morphological gradient between *Tremacyllus* and *P. bonaerense*, from high selection of relatively soft and small food items, to specialized hard item consumption and higher resistance for abrasion and masticatory efforts (e.g., in eventual association with digging habits), respectively. *Paedotherium typicum* presents intermediate characteristics, with incisors designed for better cropping action or poorer selectivity during feeding. This more profound understanding of the feeding habits of pachyrukhines further allows the suggestion of paleoecological factors that could have contributed to niche segregation between these long-term coexisting rodent-like taxa.

Keywords Masticatory apparatus · Functional morphology · Pachyrukhinae · Paleobiology · Rodent-like mammals · Snout anatomy

Introduction

Inquiring into the ecology of extinct forms is always an exciting challenge that requires the application of principles of functional morphology and the careful design of an adequate comparative sample of extant species, particularly when the group under study corresponds to derived ecomorphs of an ancient and

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completely extinct clade, such as the case of Pachyrukhinae.

South American native ungulates (Astrapotheria, Litopterna, Notoungulata, Pyrotheria, Xenungulata, and related groups) were a taxonomically rich and ecologicaly diverse mammalian group, composed of more than 200 genera and with body sizes ranging from less than 1 kg to more than 1000 kg, which lived during almost all of the Cenozoic until their extinction in late Quaternary (Ameghino 1853-1911; Cifelli 1985, 1993; Bond 1986, 1999; Croft 1999, 2016; Croft and Anderson 2008; Barnosky and Lindsey 2010; Giannini and García López 2014; Cione et al. 2015; Croft et al. 2020). Notoungulates include the Suborder Typotheria (late Paleocene to early-middle Pleistocene), a diverse monophyletic group of rodent-like native ungulates, composed of four families: Interatheriidae, "Archaeohyracidae," Mesotheriidae, and Hegetotheriidae; the last three composing the superfamily Typotherioidea (Reguero and Prevosti 2010; Billet 2011). The phylogenetic arrangement of Typotheria and the monophyly of some of their families and subfamilies are still in debate or not supported, but the subfamily Pachyrukhinae is strongly recovered as a monophyletic grouping within the Hegetotheriidae (Croft and Anaya 2006; Billet et al. 2009b; Reguero and Prevosti 2010; Billet 2011). The Typotheria, and particularly the Typotherioidea, became taxonomically and ecologically diverse at the Eocene-Oligocene transition (e.g., Croft et al. 2003; Reguero and Prevosti 2010). The group convergently acquired remarkable rodent-, rabbit-, and wombat-like morphologies, including hypsodont dentition with chisel-like incisors, and enlarged and complex masticatory muscles (Bond 1999; Croft 1999, 2016; Shockey et al. 2007; Reguero and Prevosti 2010; Billet 2011; Gomes Rodrigues et al. 2018; Sosa and García López 2018; Ercoli et al. 2019).

Pachyrukhinae are represented by six genera (*Medistylus*, *Propachyrucos*, *Prosotherium*, *Pachyrukhos*, *Paedotherium*, and *Tremacyllus*; Cerdeño and Bond 1998; Reguero et al. 2007; Reguero and Prevosti 2010; Billet 2011; Seoane et al. 2017, 2019; Ercoli et al. 2018; Seoane and Cerdeño 2019). Their fossil record extends from the early Oligocene (around 30 Mya) to the late Pliocene of Argentina, Bolivia, Chile, and Uruguay (Marshall and Sempere 1991; Reguero 1993; Cerdeño and Bond 1998; Reguero et al. 2007, 2015; Reguero and Prevosti 2010; Croft 2016). All the records of pachyrukhines are from high to, in some cases, middle latitudes, but are currently absent in fossiliferous localities of low latitudes (Marshall and Sempere 1991; Cerdeño and Bond 1998; Croft and Anaya 2006; Reguero et al. 2015). *Paedotherium* and *Tremacyllus* (late Miocene-late Pliocene) are the latest pachyrukhines, and some of the latest notoungulates (Simpson 1945; Zetti 1972a; Cerdeño and Bond 1998). Currently, six species of *Paedotherium* are recognized, including *P. minor*, *P. borrelloi*, *P. dolichognathum*, *P. kakai*, *P. typicum*, and *P. bonaerense* (Zetti 1972b; Cerdeño and Bond 1998; Reguero et al. 2007, 2015; Ercoli et al. 2018; Seoane et al. 2019 and references therein). Regarding *Tremacyllus*, the validity of the different proposed species has not been adequately evaluated, but two species are typically recognized: *T. impressus* and *T. latifrons* [the latter tentatively synonymized with *T. incipiens* by Cerdeño and Bond 1998, see also Vera and Ercoli 2018].

Paedotherium remains are more abundant than those of *Tremacyllus* and comprise one of the most common mammalian remains in the localities of the late Miocene-Pliocene of central Argentina, but, in turn, *Paedotherium* is scarcely represented in the western and northwestern localities of Argentina. Conversely, *Tremacyllus* remains are relatively more abundant in late Miocene-Pliocene localities of northwestern and western regions of Argentina than in the central ones (Zetti 1972a; Cerdeño and Bond 1998; Bonini 2014; Vera and Ercoli 2018). Pachyrukhines present a highly modified cranial and postcranial morphology, converging with extant lagomorphs and rodents in their overall small size (~1–4 kg; a reduced body size range compared to other typotherians), and several features of the masticatory apparatus, including hypsodont cheek teeth (a feature shared with other typotherians), reduced dental formula, few, large-sized, ever-growing incisors, and enlarged diastemata (the latter features also shared with other typotherians, except for some basal representatives, such as the trachytheriines) (Sinclair 1909a, b; Kraglievich 1926; Cifelli 1985; Bond 1986, 1999; Elissamburu 2004, 2007, 2012; Reguero and Prevosti 2010; Reguero et al. 2010; Croft 2016; Gomes Rodrigues et al. 2018; Sosa and García López 2018), as well as in several other features related to other cranial and postcranial regions (e.g., Cerdeño and Bond 1998; Elissamburu 2004, 2007; see accompanying contribution, Ercoli et al. in prep.). Moreover, differing from other typotherians, pachyrukhines converge with sciuromorph rodents in having large zygomatic plates and antorbital maxillary processes in relation to a rostral origin of an enlarged masseteric group (Ercoli et al. 2019). With regard to *Tremacyllus* and *Paedotherium* species, beyond the mentioned common pachyrukhine features, some morphological differences were previously suggested, from a taxonomic point of view. For example, *Tremacyllus* stands out by its smaller overall size, large bullae, highly imbricated teeth, and curved tooth rows (Zetti 1972a; Cerdeño and Bond 1998; Ercoli et al. 2018; Vera and Ercoli 2018). *Paedotherium* species differ from each other and from *Tremacyllus* by numerous, sometimes relatively subtle, dental features, including different degree of "molarization" of premolars, presence and degree of differentiation of marginal cusps and sulci, and particular shape changes in the occlusal design (Cerdeño and Bond 1998; Ercoli et al. 2018). The representatives of *Paedotherium* typically present larger size than *Tremacyllus*, especially *P. typicum* and *P. bonaerense*, while *P. borrelloi* and *P. minor* present intermediate sizes, between *Tremacyllus* and the former *Paedotherium* taxa (Cerdeño and Bond 1998; Elissamburu 2012; Ercoli et al. 2018). *Paedotherium typicum* presents the more marked stylized postcranial morphology (interpreted as related to a higher degree of cursorial habits; Elissamburu 2004, 2007; Elissamburu and Vizcaíno 2005; see also Croft 2016), while *P. bonaerense* stands out for its more robust appendicular morphology (interpreted as related to digging habits; Elissamburu 2004, 2007; Elissamburu and Vizcaíno 2005), more marked sciuromorph condition (Ercoli et al. 2019), and "molarization" of premolars (Cerdeño and Bond 1998; Ercoli et al. 2018).

Since the earliest contributions of the beginning of the twentieth century, researchers have mainly focused on the systematics and phylogeny of Pachyrukhinae, while the functional morphology of these notoungulates still remains poorly studied (e.g., Sinclair 1909a, b; Ameghino 1853-1911; Kraglievich 1926). As was stated by Zetti (1972a) for *Paedotherium* and *Tremacyllus*, and more recently by Croft (2016:214–215), and also recognized in a broader sense for typotherians in Gomes Rodrigues et al. (2018), there are no sufficient paleobiological studies to elucidate the niche partitioning and extensive coexistence of these pachyrukhines. Recent contributions on some aspects of the paleobiology of pachyrukhines include the studies of cranial remains of the early Miocene *Pachyrukhos* (Cassini 2011; Cassini et al. 2011, 2012; Cassini and Vizcaíno 2012; McCoy and Norris 2012; Filippo et al. 2020); and the studies of cranial and postcranial morphology of *Paedotherium* and/or *Tremacyllus* (Elissamburu 2004, 2007; Sosa and García López 2018; Ercoli et al. 2019; Filippo et al. 2020).

Features of the masticatory apparatus, and particularly the tooth morphology of pachyrukhines, were interpreted as indicating preference for open habitats and grazing habits (Zetti 1972a; Bond 1986; Reguero et al. 2007; Cassini et al. 2011, 2012; Seoane et al. 2017). However, Reguero et al. (2015), in a similar manner for other ungulates (e.g., Janis 1988, 1995; Janis and Fortelius 1988) and specifically other notoungulates (MacFadden 2005; Croft and Weinstein 2008; Townsend and Croft 2008; Billet et al. 2009b; Croft et al. 2020), suggested that hypsodonty is not necessarily linked to grazing habits in the late Miocene northwestern taxon *P, kakai*, which would have been a mixed feeder of forested and humid habitats. Cassini et al. (2011, 2012) also argued about different factors (e.g., grit consumption and digging) other than grazing habits to explain hypsodonty in the pachyrukhine *Pachyrukhos* and other typotherians, despite interpreting these taxa as grazers (Cassini et al. 2011) or, alternatively, as dicot feeders (Cassini et al. 2012). More recently, the ability of hard-object consumption was proposed for pachyrukhines (Ercoli et al. 2019), and mixed, rodent-like, dietary habits were also suggested for some taxa (e.g., *Paedotherium*; Kraglievich 1926).

Beyond this literature, the dietary habits of some pachyrukhines (including *Paedotherium* and *Tremacyllus*) are still debated, and studies that compare the dietary habits of coexisting pachyrukhines species are necessary to elucidate any niche partitioning. Moreover, there are no exhaustive analyses of the entire craniomandibular complex, and almost all previous contributions focused on specific parts of the masticatory apparatus. Some structures of the rostral anatomy could provide additional information that is frequently overlooked in paleobiological studies (but see De Blieux and Simons 2002; Bargo et al. 2006), and, the same applies to packyrukhines. Muchlinski (2010) indicated that there is a relationship between the development of the infraorbital foramen and the infraorbital nerve that traverses it, and the development of the vibrissae and other mechanoreceptors of the maxillary region in mammals. Many researchers (e.g., Broman 1919; Landry 1970; Frahnert 1999) have studied and supported the association between the development of the gnawing apparatus of rodents and lagomorphs and the presence of infoldings of the lips behind the incisors and the consequent modifications of other structures, such as the incisive foramina and the opening of the nasopalatine ducts, specifically in rodents. These and other structures could allow the reconstruction of some traits of the soft tissues that composed the rostrum of extinct taxa, and give clues about the perception, as well as the type and initial processing of dietary items.

On the other hand, few contributions dealing with the paleobiology of pachyrukhines had considered a numerous and diverse comparative sample of extant representatives, such as rodents and other mammals together (e.g., Croft and Anderson 2008), a shortcoming already pointed out by previous authors (Cassini et al. 2012). In fact, a comparative anatomical analysis in a diverse group of lineages and ecomorphological types of extant herbivores is the most suitable way to understand the paleobiology of completely extinct groups. Even more, these arguments are reinforced when considering taxa that seem to be better understood as a mosaic of traits. This is the case of pachyrukhines, which seem to combine characteristics of their ungulate ancestry with convergences to various rodent-like groups.

In this context, the main goal of this study is to perform a comprehensive morpho-functional analysis of the masticatory apparatus and associated structures of *Paedotherium* and *Tremacyllus*. This is accomplished through a mainly qualitative comparative morphological analysis and the partial reconstruction of oronasal soft tissues. The inference of the feeding habits, including food-item selection abilities and dietary preferences, and mastication modes aims to shed light on the paleobiology and aspects of ecological niche partitioning of these coexisting genera of pachyrukhines.

Materials and Methods

For the purposes of the present study, we analyzed the rostrum and masticatory apparatus of 36 fossil specimens belonging to the Pachyrukhinae: *P. typicum*, *P. bonaerense*, *P. minor*, *P. borrelloi*, and *Tremacyllus* spp. (Appendix 1). The descriptive and morpho-funtional analysis was further extended to the available descriptions from the relevant literature (e.g., Kraglievich 1926; Cerdeño and Bond 1998; Ercoli et al. 2018, 2019; Sosa and García López 2018). The decision of considering *Tremacyllus* at the genus level was related to the uncertainty about the systematic arrangement of its species (see Introduction).

The studied material was selected to include some of the best preserved specimens in order to provide as much anatomical information as possible (Fig. 1). For the case of *P. typicum*, *P. bonaerense*, and *Tremacyllus* spp., all the studied anatomical regions were represented by one or more specimens, so almost all the compared structures could be adequately described. In the case of *P. minor*, the entire rostrum and the horizontal ramus of the mandible are preserved, but there are no specimens preserving the posterior region of the zygomatic arch, the posterior extreme of the palate and pterygoid process of palatine, and the mandibular ascending ramus posterior to the base of the coronoid process. For *P. borrelloi*, the available specimens preserved only the teeth, part of the palate, the rostrum, and the horizontal ramus, but there are no specimens preserving the antorbital maxillary process, the zygomatic arch, the pterygoid process of the palatine, cranial structures posterior to the rostrum, the incisive lower arch, and the mandibular ascending ramus posterior to the base of the coronoid process (Fig. 1). *Paedotherium dolichognathum* and *P. kakai* were the only two *Paedotherium* species not extensively described here. The single specimen of *P. kakai* (S. Sal. Scar. Paleo. 2012–045 of the Museum of San Carlos, Salta, Argentina; see Reguero et al. 2015) preserves only the p4, the lower molars, and the associated parts of the horizontal ramus (including the anterior part of the masseteric crest), while *P. dolichognathum* is known by a single badly preserved specimen, including the palate, part of the rostrum and the upper cheek teeth (Zetti 1972b).

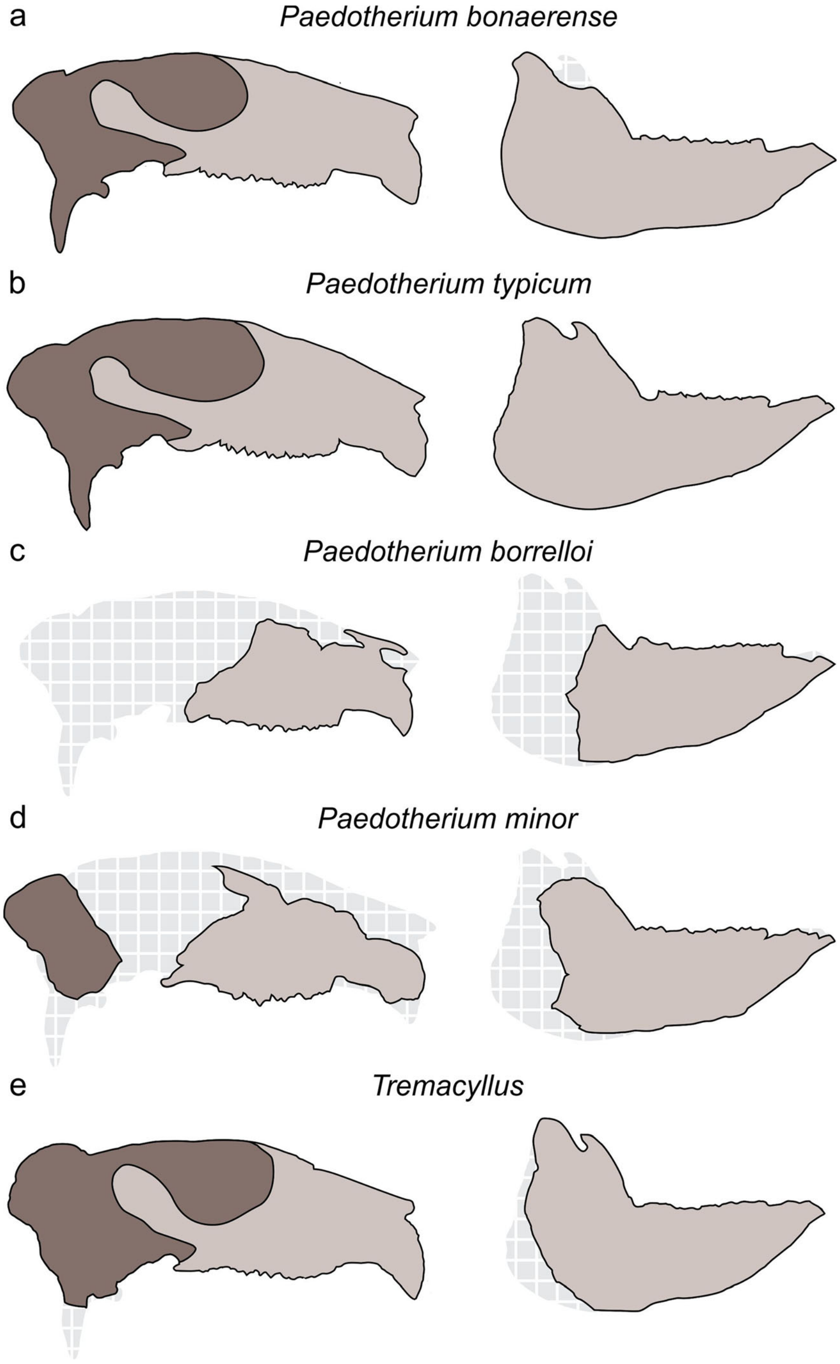
Eight extant small-sized herbivorous mammals representing divergent life habits and diverse clades were analyzed as comparative models (Appendix 1): *Cavia aperea* (Caviidae; Hystricomorpha; Rodentia; body mass (BM) ~ 650 g; Asher et al. 2004), *Chinchilla chinchilla* (Chinchillidae; Hystricomorpha; Rodentia; BM ~ 500 g; Smith et al. 2003), *Ctenomys frater* (Ctenomyidae; Hystricomorpha; Rodentia; BM ~ 250 g; Anderson 1997), *Cynomys ludovicianus* (Sciuridae; Sciuromorpha; Rodentia; BM ~ 800 g; Hoogland 1996), *Ratufa affinis* (Sciuridae; Sciuromorpha; Rodentia; BM ~ 1100 g; Hayssen 2008), *Lepus capensis* (Leporidae; Lagomorpha; BM ~ 4500 g; Begnoche 2002), *Heterohyrax brucei* (Procaviidae; Hyracoidea; BM ~ 2600 g; Barry and Shoshani 2000), and *Tragulus kanchil* (Tragulidae; Artiodactyla; BM ~ 2500 g; Meijaar and Groves 2004). In terms of life style and feeding habits, the Brazilian guinea pig *Ca. aperea* is a generalist feeder that includes a high proportion of grasses and has generalized epigean habits (Seckel and Janis 2008; Rocha-Barbosa et al. 2015; Bernal 2016). The chinchilla *Ch. chinchilla* is a generalist feeder that includes a high proportion of grasses and displays saltatorial and rock-dwelling habits (Mares and Lacher 1987; Seckel and Janis 2008; Tirado et al. 2012). The cape hare *L. capensis* is also a mixed feeder, including grasses in its diet, with cursorial-saltatorial locomotor habits (Seckel and Janis 2008; Johnston et al. 2019). The tuco-tuco *Ct. frater* and the prairie dog *Cy. ludovicianus* both display fossorial habits (scratch- predominating over tooth-digging) and feed on tubers, roots, and grasses (Fagerstone et al. 1981; Ojeda et al. 2015; Morgan et al. 2017; Vivar 2017). The pale giant squirrel *R. affinis* is an arboreal sciurid that feeds mainly on hard fruits (Thorington and Darrow 1996; Seckel and Janis 2008). The yellow-spotted hyrax *H. brucei* is a rock-dwelling browser (Hoeck 1975; Mares and Lacher 1987). Lastly, the lesser mouse-deer *T. kanchil* is a cursorial species that displays folivorous/frugivorous dietary habits (Meijaard 2011; Feldhamer et al. 2015; Timmins and Duckworth 2015).

The studied fossil and extant specimens (Appendix 1) are housed in the mammalogical and paleontological collections of the Instituto Miguel Lillo (CML, PVL, Argentina); Museo Argentino de Ciencias Naturales (MACN A, MACN Ma, MACN Pv; Argentina); Museo de La Plata (MLP; Argentina); Museo de Mar del Plata (MMP, MMP Ma; Argentina); Museo “Saturnino Iglesias” of Instituto de Geología and Minería (IDGYM; Argentina); and Field Museum of Natural History (FMNH, FMNH P; USA).

The anatomical descriptions were organized by anatomical regions (Cranium: upper teeth, rostrum, zygomatic arch, palate, temporal fossa and glenoid cavity; Mandible: lower teeth, horizontal ramus, muscular insertions, and ascending ramus). The anatomical terms used for the descriptions follow Cerdeño and Bond (1998); Pérez (2010); Reguero and Prevosti (2010); Evans and De Lahunta (2013); and Ercoli et al. (2018, 2019), and are illustrated in Fig. 2. Detailed comparative descriptions for each pachyrukhine species are presented, followed by comparisons of specific features with extant models. Different morphologies observed in extant models with distinct life habits were used to functionally explain the comparable osteological features found in the fossil species (e.g., Sargis 2001; Argot 2003).

A set of 20 measures were taken in order to construct 14 indices to quantify morphological differences between pachyrukhines and the extant sample (Online Resource 1). The cranial measures were (i) condylo-basal length (CBL); (ii) maximum cranial height, at the level of alveoli of cheek

Fig. 1 Anatomical regions preserved in the studied sample of pachyrukhines, illustrating *Paedotherium bonaerense* (**a**), *P. typicum* (**b**), *P. borrelloi* (**c**), *P minor* (**d**), and *Tremacyllus* (**e**). Preserved regions are indicated in solid colors: pale gray indicates described structures, while dark brown indicates structures preserved not described in this contribution, but included in the descriptions of the accompaning contribution (Ercoli et al. in prep.). Gray checkered pattern indicates missing structures. See Materials and Methods for descriptions of minor remains preserved and analyzed of *P. dolichognathum* and *P. kakai* and a more detailed description of preserved structures



teeth (MCH); (iii) maximum bizygomatic width (MBW); (iv) maximum breadth between upper molariform rows (MBMR); (v) M1 width, perpendicular to the main axis of tooth row (M1W); (vi) posterior elongation of incisive foramen, distance between posterior end of incisive foramen and anterior end of diastema (PEIF); (vii) rostral length, from the anterior margin of the orbit up to most anterior of rostrum without considering incisors (RL); (viii) length of upper diastema, between alveoli (UDL); (ix) width of upper incisive arch, at the level of the occlusal plane (UIAW); (x) length of upper molariform rows, considering the main axis (UMRL); (xi) minimum lifting of the zygomatic arch, with respect to the level of alveoli (ZL); and (xii) cranial height at the level of the minimum lift up of the zygomatic arch (CHZL). The mandibular measurements were: (xiii) condylar height, with respect to the alveolar level (CH); (xiv) condyle-incisive length, from the anterior end of condyle to the posterior margin of the incisive alveoli (CIL); (xv) length of lower diastema, between alveoli (LDL); (xvi) width of lower incisive arch, at the level of the occlusal plane (LIAW); (xvii) length of lower molariform rows, considering

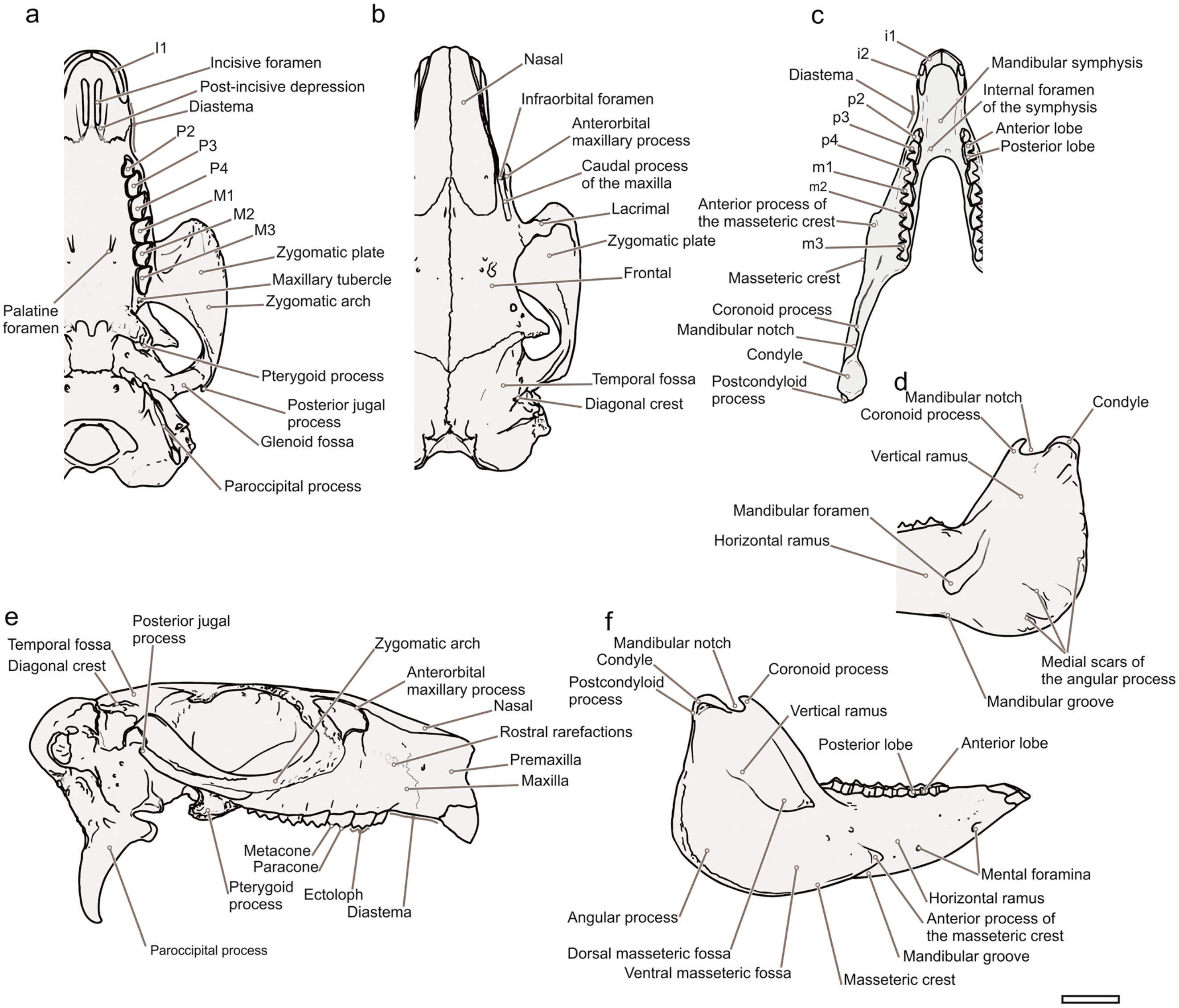


Fig. 2 Anatomical terms used in the descriptions of cranial and mandibular elements of pachyrukhines and the comparative sample. Cranium in ventral (**a**), dorsal (**b**), and lateral (**e**) views, mandible in dorsal (**c**), lateral (**f**), and medial (**d**) views. Scale bar = 10 mm

the main axis (LMRL); (xviii) maximum breadth between lower molariform rows (MBmR); (xix) maximum height of the horizontal ramus (MHRH); and (xx) m1 width, perpendicular to the main axis of tooth row (m1W). All the measurements were taken in oriented and scaled photographs in lateral and ventral views of the cranium, and dorsal and lateral views of the mandible as illustrated in the Online Resource 1. All variables were measured using the measure tool of tpsDig software (Rohlf 2013). The indices constructed from these measurements were: RL/CBL, MBW/MBMR, UIAW/MBMR, PEIF/UDL, CH/CIL, LIAW/MBmR, M1W/m1W, MCH/CBL, MBW/UIAW, (UMRL+UDL)/MBMR, UMRL/CBL, MHRH/(LMRL+LDL), UDL/LDL, and ZL/CHZL (Online Resource 1).

For masticatory muscle reconstructions, we followed the procedure and inferences of Ercoli et al. (2019). In the case of muscles inserted on soft tissues or not preserved structures and the reconstruction of other soft tissues, we relied primarily on analogous anatomies of extant models (e.g., Ike 1990; Frahnert 1999).

All data generated or analyzed during this study are included in this published article.

Results

Cranium

Rostrum, Zygomatic Arch, and Palate

Paedotherium borrelloi and *P. minor* could only be partially described because of the incomplete condition of the studied specimens (see Material and Methods). The studied species of *Paedotherium* and *Tremacyllus* present a low skull (Fig. 3; Table 1, MCH/CBL). In dorsal view, they show a narrow rostrum that makedly widens at the level of the laterally expanded zygomatic arches (see also Table 1, MBW/UIAW, MBW/MBMR). This widening could not be confirmed in *P. borrelloi* (Fig. 3).

In dorsal view, among the extant comparative sample, *Chinchilla*, *Ctenomys*, and *Cynomys*, and secondarily *Heterohyrax*, *Lepus*, and *Cavia*, present an abrupt widening at the level of the zygomatic arches, starting from a relatively narrow rostrum. Conversely, *Tragulus* has a gracile skull, with a smooth widening. Lastly, *Ratufa* has a relatively wide rostrum. Caviomorphs and sciurids possess a markedly low skull and large zygomatic width (see also Table 1, MBW/MBMR) (Figs. 4 and 5). In pachyrukhines, the combination of a low cranium and an abrupt widening at the level of the zygomatic arches are reminiscent of *Chinchilla* and *Ctenomys*, and secondarily of *Cynomys* (Figs. 3 and 5; see also Valladares et al. 2018: fig. 2).

Among pachyrukhines, the rostrum presents variable length and width at the generic and specific levels, being typically larger and longer in *Paedotherium* than in *Tremacyllus* (Table 1, RL/CBL). In *P. bonaerense*, the rostrum is relatively long, in *P. typicum,* it is typically slightly shorter and wider, while an intermediate condition is observed in *P. borrelloi* [Figs. 3 and 6; Table 1, (UMRL+UDL)/MBMR, UIAW/MBMR]. In *P. typicum* and *P. bonaerense*, the rostrum maintains a relatively constant width up to the level of the incisive alveoli. In *P. minor* and *Tremacyllus,* the rostrum narrows progressively toward the anterior sector, where this sector and the incisive arch present the smallest width (Table 1, UIAW/MBMR). The most shortened and more accute rostrum is recorded for *Tremacyllus* (Fig. 6), and in the type specimen of *P. minor*, which is a juvenile [Table 1, (UMRL+UDL)/MBMR, UIAW/MBMR]. In the palatal view of the rostrum, the incisive foramina are elongated, with post-incisive depressions (see Cerdeño and Bond 1998; "impresiones elipticas de los maxilares" of Kraglievich 1926) caudally projected to differing degrees. These depressions are poorly developed in *Paedotherium* (Figs. 3a, g and 6a-c) barely invading the anterior sector of the maxillaries, but depressions lateral to the incisive foramina are well developed. In contrast, the post-incisive depressions are enlarged in *Tremacyllus*, reaching up the level of the P2 or P3, widely invading the maxillary bones (Figs. 3l and 6d; see also Zetti 1972a).

Regarding rostrum length, there is great diversity among the extant forms. It is worth noting that sciurids and *Heterohyrax* display the shortest rostrum in our study sample (Figs. 4-6; Table 1, RL/CBL). *Lepus* presents well-developed incisive foramina, continued posteriorly by palatine vacuities (Fig. 6g; Wible 2007). These vacuities result in very large openings that invade the palatal region between the premolars. Along the middle and posterior region of the diastema, caviomorphs possess elongated incisive foramina that are larger in *Chinchilla* than in *Cavia* and *Ctenomys* (see Valladares et al. 2018: fig. 2 versus Justo et al. 2003: fig. 2). Diverging from Glires (see Frahnert 1999), the remaining extant comparative sample presents incisive foramina located in a middle-to-anterior position along the palate. The posterior extension of the incisive foramina exceeds half of the diastema in rodents, and particularly in caviomorphs, in which the posterior extension surpasses 65% of diastema length in all cases (Table 1, PEIF/UDL). Interestingly, in Glires and pachyrukhines, the distance between the posterior sector of the incisive foramina and the incisors are approximately half or even more of the diastema length (Fig. 6a-e, g; Table 1). This distance is much shorter in *Heterohyrax* and *Tragulus* (e.g., Fig. 6f; Table 1, PEIF/UDL).

In pachyrukhines, the pterygoid processes of the palatine (Sisson and Grossman 1930; see also palatine crests of Billet et al. 2009b), hosting the origin of the pterygoid muscles, are very well developed, broad, and rugose, mainly extended along the longitudinal plane. These processes are remarkably robust in *P. bonaerense* (Figs. 3 and 6).

The palate of pachyrukhines is concave and is projected beyond the M3 (as occurs in other typotherians; Billet 2011). In the case of *Tremacyllus*, this posterior extension is considerably less than in *Paedotherium*. Immediately posterior to the alveolus of the M3 there is a maxillary tuberosity. In *Tremacyllus*, the palatine foramina are located at the level of M1 or at the transition between the M1 and P3 (Figs. 3l and 6d). In *Paedotherium*, these foramina are located at the level of M1 or more posteriorly (Figs. 3a, g and 6a-c).

Within the extant comparative sample, the processes for the origin of the pterygoid muscles are largely developed in *Heterohyrax* and *Lepus* (reaching a similar or slightly lesser development than in pachyrukhines), and secondarily in *Tragulus*, but they are relatively smaller in the other studied species (Figs. 4 and 6). The palate is narrow and short in the studied caviomorphs, with the palatine foramina closer to the midline, in relation to the anterior convergence and proximity of the cheek tooth rows (e.g., Justo et al. 2003: fig. 2). In the rest of the extant comparative sample, the palate is wide and posteriorly elongated, with the palatine foramina located posteriorly, at the level of the last molars. In *Lepus*, the palate is anteroposteriorly narrower (Fig. 6). The configuration of the palate and palatine foramina of pachyrukhines is similar to that of *Tragulus*, and also *Heterohyrax*.

In pachyrukhines, the zygomatic plate (composed by the maxillary and jugal bones) is expanded through the transverse (in dorsal and anterior aspects) and the longitudinal (ventral and posterior aspects) planes. There is a gradient among pachyrukhines in the widening and lifting of the zygomatic

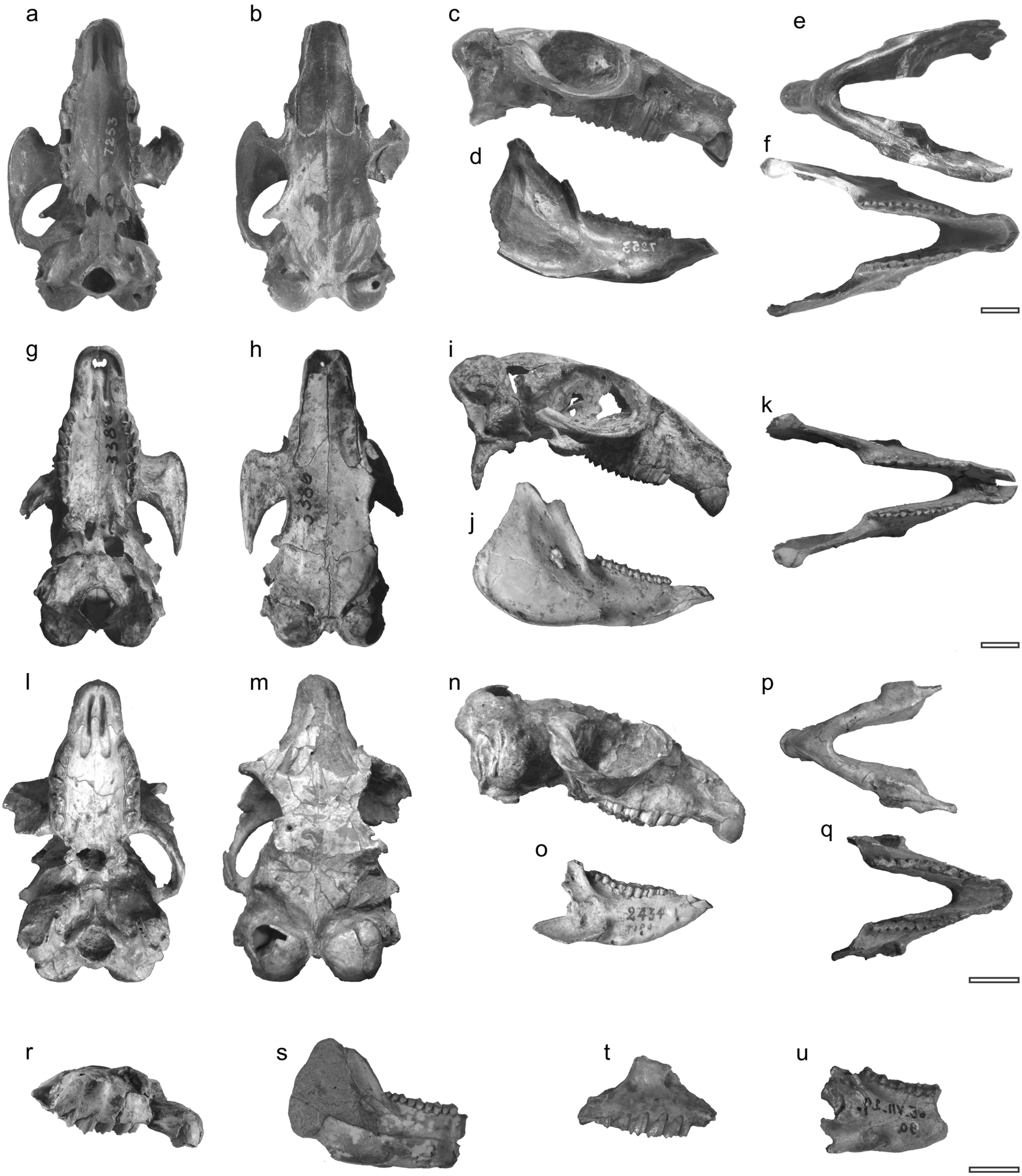


Fig. 3 Representatives of the studied pachyrukhine taxa. *Paedotherium bonaerense* (**a**-**f**), *P. typicum* (**g**-**k**), *Tremacyllus* (**l**-**q**), *P. minor* (**r**-**s**), and *P. borrelloi* (**t**-**u**). Crania are illustrated in ventral (**a**, **g**, l), dorsal (**b**, **h**, **m**), and lateral (**c**, **i**, **n**, **r**, **t**) views; mandibles in lateral (**d**, **j**, **o**, **s**, **u**), ventral (**e**, **p**), and dorsal (**f**, **k**, **q**) views. Scale bars = 10 mm

plate, from *P. bonaerense*, *P. typicum*, and *P. minor* and *Tremacyllus* (Figs. 3, 6, 7; Table 1, MBW/MBMR, ZL/CHZL). In *P. typicum* MMP 1008-M, the lateral projection of the zygomatic arch seems to be larger than the widest *P. bonaerense* specimens, but this condition is the result of an incorrect reconstruction of the original state.

Table 1 Morphometrical indices of extant (mean values of specimens listed in Appendix 1) and fossil taxa (values for specimens sufficiently preserved). See Materials and Methods sections for an explanation of the abbreviations, and Online Resource 1 for illustration of measurements

	RL/ CBL	MBW/ MBMR	UIAW/ MBMR	PEIF/ UDL	CH/ CIL	LIAW/ MBmR	M1W/ m1W	MCH/ CBL	MBW/ UIAW	(UMRL+UDL)/ MBMR	UMRL/ CBL	MHRH/ (LMRL+LDL)	UDL/ LDL	ZL/ CHZL
Extant sample														
Cavia aperea	0.456	2.281	0.198	0.807	0.015	0.193	0.926	0.306	0.087	2.093	0.260	0.386	1.497	NA
Chinchilla chinchilla	0.363	2.186	0.328	0.885	0.287	0.306	1.140	0.282	0.151	1.822	0.228	0.393	1.961	NA
Ctenomys frater	0.374	2.776	0.613	0.690	0.253	0.506	0.992	0.313	0.221	2.108	0.219	0.653	1.800	0.154
Cynomys ludovicianus	0.276	2.148	0.274	0.623	0.140	0.366	1.099	0.263	0.128	1.407	0.258	0.515	1.620	0.072
Lepus capensis	0.380	1.650	0.288	0.537	0.329	0.319	1.210	0.399	0.175	1.679	0.174	0.398	1.417	0.074
Ratufa affinis	0.308	2.271	0.286	0.503	0.208	0.291	0.944	0.333	0.126	1.533	0.212	0.483	2.172	NA
Heterohyrax brucei	0.292	1.845	0.502	0.399	0.299	0.658	1.920	0.379	0.271	1.722	0.415	0.500	1.953	0.048
Tragulus kanchil	0.375	1.390	0.450	0.370	0.268	0.414	1.761	0.375	0.324	1.495	0.399	0.229	0.928	0.255
Fossil taxa														
P. bonaerense MACN A 1251/52	0.384	2.189	0.514	0.914	–	0.543	1.200	0.333	0.235	1.435	0.360	0.619	1.563	0.208
P. bonaerense MMP 158-S	–	2.321	–	–	–	–	–	–	–	–		–	–	0.121
P. bonaerense MMP 1655-M	0.427	2.184	0.555	0.711	–	–	–	0.342	0.254	1.530	0.353	–	–	0.255
P. bonaerense MACN Pv 10,513–14	–	2.290	0.551	0.895	0.310	0.574	1.445	–	0.241	1.604	0.364	0.524	1.760	–
P. bonaerense MACN Pv 18,098–100	0.424	2.060	0.532	0.672	–	–	–	0.295	0.258	1.471	0.348	–	–	0.224
P. bonaerense MACN Pv 7214	0.454	2.206	–	0.833	–	–	–	0.316	–	1.541	0.355	–	–	0.125
P. bonaerense MLP 99-X-2-1	0.383	2.335	0.560	0.814	–	–	–	–	0.240	1.503	0.354	–	–	–
P. bonaerense IDGYM s/n	–	2.348	0.543	0.900	–	–	–	–	0.231	1.491		–	–	0.233
P. borrelloi MLP 57-X-10-21	–	–	–	–	–	–	1.556	–	–	–		–	–	–
P. borrelloi MLP 57-X-10-88	–	–	0.578	0.817	–	–	–	–	–	1.591		–	–	–
P. minor MLP 29-IX-2-157	–	–	0.512	0.659	–	–	–	–	–	1.583		–	–	–
P. minor MLP 29-IX-1-116	–	–	0.460	0.778	–	–	–	–	–	1.394		–	–	–
P. minor MLP 55-IV-28-30	–	2.061	0.508	–	–	–	1.462	–	0.247	1.544		–	–	–
P. typicum MACN Pv 5751	–	–	–	–	0.329	0.558	–	–	–	–		0.587	–	–
P. typicum MACN Pv 6436	–	2.168	–	–	–	0.567	1.591	–	–	–		0.540	–	–
P. typicum MLP 12–1782	–	2.148	–	–	–	0.520	1.305	–	–	–		0.554	–	–
P. typicum MLP 52-IX-28-14	0.396	2.236	0.577	0.780	–	–	–	0.330	0.258	1.429	0.327	–	–	0.084
P. typicum PVL 3386	0.413	2.290	0.590	0.794	–	–	–	0.325	0.257	1.508	0.322	–	–	0.098
P. typicum MMP 1008-M	0.439	–	0.518	0.825	0.270	0.558	1.329	0.327	–	1.539	0.321	0.545	1.595	–

Table 1 (continued)

	RL/ CBL	MBW/ MBMR	UIAW/ MBMR	PEIF/ UDL	CH/ CIL	LIAW/ MBmR	M1W/ m1W	MCH/ CBL	MBW/ UIAW	(UMRL+UDL)/ MBMR	UMRL/ CBL	MHRH/ (LMRL+LDL)	UDL/ LDL	ZL/ CHZL
P. typicum MMP 698-S	–	2.266	0.575	0.783	–	0.573	1.247	–	0.254	1.647		0.602	1.941	–
Tremacyllus MACN Pv 2434	0.373	2.174	0.469	0.833	–	0.516	1.479	0.340	0.216	1.395	0.341	0.632	3.437	0.088
Tremacyllus MACN Pv 2913	–	–	–	–	–	–	–	–	–	–		–	–	0.096
Tremacyllus MACN Pv 8157	–	–	–	–	0.344	–	–	–	–	–		–	–	0.035
Tremacyllus MACN Pv 7207	–	–	–	–	–	0.530	–	–	–	–		–	–	–
Tremacyllus FMNH P 14465	0.391	2.059	0.488	0.815	–	–	–	–	0.237	1.329	0.324	–	–	–
Tremacyllus FMNH P 14456	0.384	2.103	0.518	–	–	0.470	1.439	0.318	0.246	1.368	0.320	0.623	1.905	–

Moreover, in pachyrukhines, the anteriorly extended zygomatic plate reaches the rostrum (see Ercoli et al. 2019), on the lateral aspect of the antorbital maxillary process, which bounds laterally the infraorbital foramen (Figs. 3 and 7). The antorbital maxillary process is parallel to the sagittal plane in *Paedotherium*, and more developed in *P. bonaerense* than in *P. typicum* and *P. minor*. In *Tremacyllus*, this process is sharp, somewhat diverging, and smaller than in *P. typicum* and *P. minor* (Fig. 3; see Ercoli et al. 2018).

Pachyrukhines possess a broad and rugged lateral margin of the zygomatic plate. In its ventrolateral aspect, it presents a marked anteroposteriorly oriented scar that overlaps with the maxillo-jugal suture. In ventral view, in the anterior sector of the plate, there is a concave, wide, and smooth surface that posteriorly reaches the level of the M2-M3 (Fig. 3a–l). In dorsal view, the anterior margin of the zygomatic plate and the lateral margin of the antorbital maxillary process form a concavity of variable degree. The concavity is deep in *P. bonaerense*, shallower in *P. typicum* and *P. minor* (being somewhat deeper in the former), and it is barely marked (and tilts laterally) in *Tremacyllus*. More particularly in *P. bonaerense*, this concavity exceeds posteriorly the level of the contact between the nasal and frontal bones (Fig. 3b). In this species, this variation is related to a markedly reduced surface of the lacrimal bone in its middle sector (see also Cerdeño and Bond 1998; Billet 2011). The posterior sector of the zygomatic arch is narrower than its anterior region (where the zygomatic plate develops) (Fig. 3).

Among our extant sample, the variation of the development of muscular scars in the rostrum suggests different configurations of the masseteric musculature, especially for m. masseter superficialis. In *Lepus* and caviomorphs, the origin of this muscle is restricted to a small, depressed scar (Woods 1972; Figs. 4 and 6). In most sciurids and artiodactyls, the m. masseter superficialis originates from a tubercle on the lateral rostrum [a convergent condition; see Druzinsky et al. 2011] (Figs. 4 and 6). In *Ratufa,* it attaches onto an oblique crest on the rostrum (Thorington and Darrow 1996). In *Heterohyrax*, this muscle presents a different and plesiomorphic condition (shared with perissodactyls, carnivorans, etc.; Janis 1983; Barone 1987; Druzinsky et al. 2011) with an origin from a wide surface on the ventrolateral aspect of the zygomatic arch, largely overlapping with the origins of the other masseteric muscles.

Pachyrukhines possess a marked rugged zone in the horizontal aspect of the ventral margin of the zygomatic arch. This zone continues anteriorly, after a change of slope, through the dorsal margin of the anterior root of the zygomatic arch and the dorsal margin and anterior end of the antorbital maxillary process (Figs. 3 and 7; see also Ercoli et al. 2019: fig. 2). The presence of this broad margin and the absence of a distinct mark in the lateral surface of the maxillary bone or the zygomatic arch root would suggest a m. masseter superficialis with

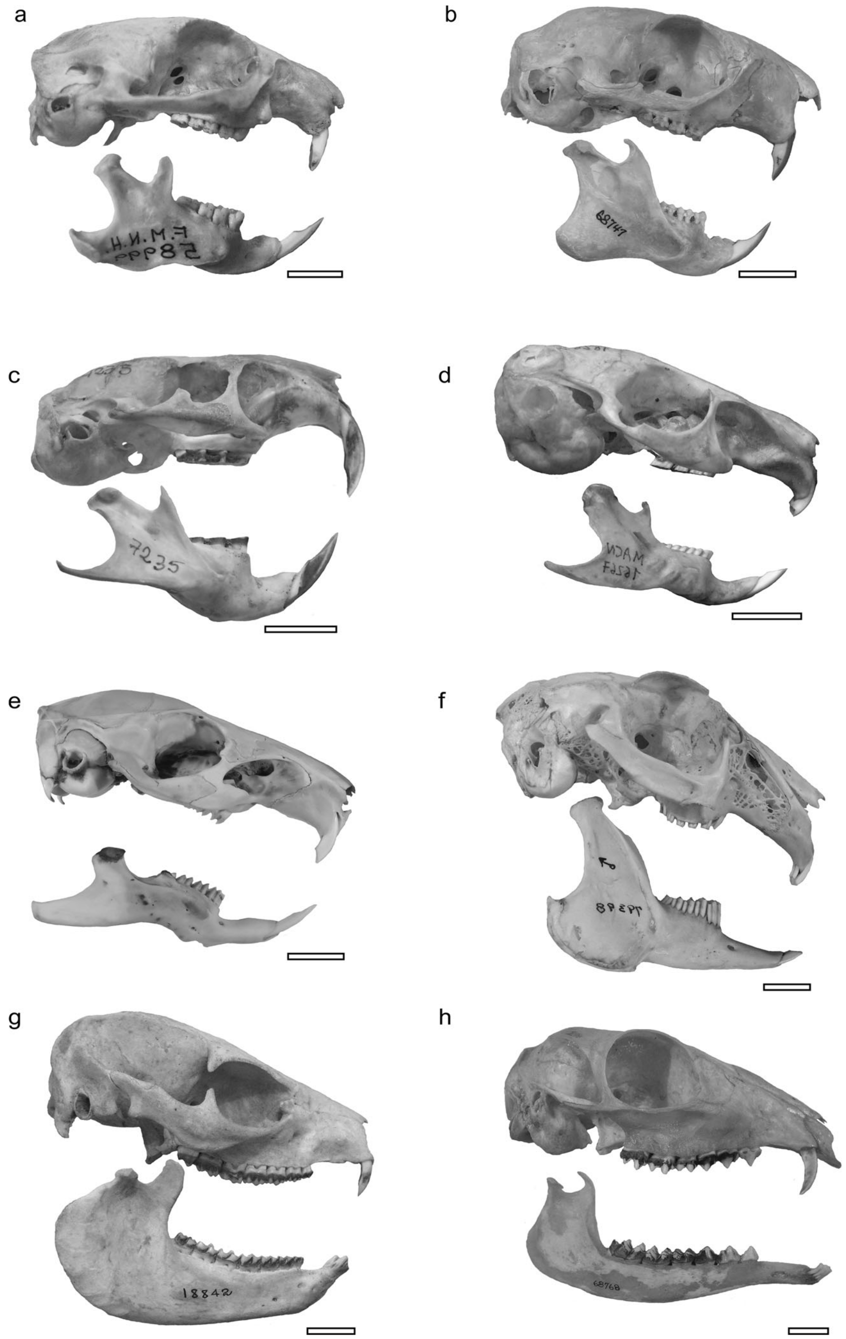


Fig. 4 Representatives of extant taxa used as comparative sample. *Cynomys ludovicianus* (**a**), *Ratufa bicolor* (**b**), *Ctenomys frater* (**c**), *Chinchilla chinchilla* (**d**), *Cavia aperea* (**e**), *Lepus capensis* (**f**), *Heterohyrax brucei* (**g**), and *Tragulus kanchil* (**h**). For each one, the cranium and mandible are illustrated in lateral view. Scale bars = 10 mm

an ample laminar origin, with a distinctive anterior sector reaching the anterior end of the antorbital maxillary process, covering the origin of the deepest masseter muscles (a condition similar to that observed in *Ratufa*; Thorington and Darrow 1996).

A zygomatic plate, reaching the rostrum, is present in the sciurids of the extant sample (Fig. 4a, b), as in all Sciuridae and Castorimorpha (i.e., the sciuromorph condition; e.g., Cox et al. 2012). In sciurids, such as *Cynomys*, the development of a zygomatic plate accompanies the presence of an antorbital maxillary process, forming a remarkable morphological convergence to pachyrukhines. As stated by Ercoli et al. (2019), this condition relates to the development of an anterior division of the m. masseter lateralis (= deep masseter), differing from the remaining studied extant models (Fig. 7). The development of the antorbital maxillary process and the rostral portion of the zygomatic plate of *Cynomys* are comparable to those observed in *Tremacyllus*, but smaller than those of the other pachyrukhines that preserve these structures (i.e., *P. bonaerense* and *P. typicum*) (Figs. 3 and 4).

In pachyrukhines, the maxilla extends caudally via a caudal process, which limits the contact between the frontal and the

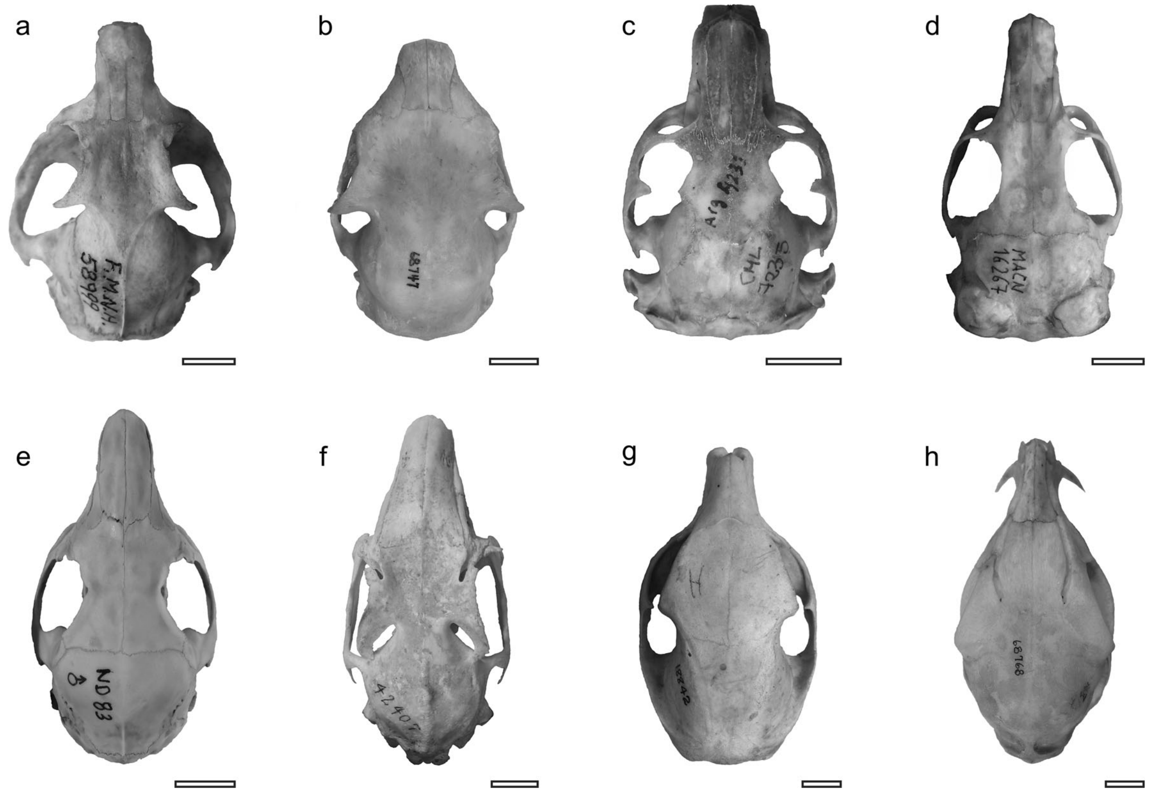


Fig. 5 Representatives of extant taxa used as comparative sample. *Cynomys ludovicianus* (**a**), *Ratufa bicolor* (**b**), *Ctenomys frater* (**c**), *Chinchilla chinchilla* (**d**), *Cavia aperea* (**e**), *Lepus capensis* (**f**), *Heterohyrax brucei* (**g**), and *Tragulus kanchil* (**h**). For each one, the cranium is illustrated in dorsal view. Scale bars = 10 mm

lacrimal bones, to differing degrees (Kraglievich 1926). This process is particularly ample in *P. typicum*, *P. minor*, and *Tremacyllus*, compared to *P. bonaerense*, restricting the contact between the frontal and lacrimal bones in the former species (Fig. 3). Both *Paedotherium* and *Tremacyllus* have rostral bones with fenestrations (= rarefactions) (see also MacPhee 2014, and references therein).

The development of the caudal process of the maxilla and its interference on the contact between the lacrimal and frontal bones is weak in the extant species (Fig. 5). This condition is similar to *P. bonaerense*, highlighting the unique morphology of the other pachyrukhines (*P. typicum*, *P. minor*, and *Tremacyllus*). Compared to pachyrukhines, *Lepus* shows even more strongly developed fenestrations on the rostral bones, and in other cranial regions (Figs. 3 and 4; MacPhee 2014). Similar fenestrations are not present in the other extant representatives (Fig. 4).

Pachyrukhines possess a large, somewhat lateromedially compressed, infraorbital foramen. This foramen has a relatively high position on the lateral rostrum, immediately ventral and medial to the antorbital maxillary process (Figs. 3 and 7). In *P. borrelloi*, the infraorbital foramen and the base of the antorbital maxillary process are both preserved (Fig. 3t) and do not present any remarkable differences from the other species of *Paedotherium*.

Similar to pachyrukhines, the infraorbital foramen is well developed in *Cynomys* and *Heterohyrax*, but is reduced in *Tragulus* (Figs. 3 and 4). In caviomorphs, there is a hypertrophied anterior part of the m. masseter medialis (= m. zygomaticomandibularis), called the infraorbital part, originating from the rostrum and passing through a hypertrophied infraorbital foramen. This characterizes the hystricomorph condition, unique to hystricomorph rodents; myomorph rodents also show a similar condition, but to a reduced degree (Woods 1972; Woods and Howland 1979; Druzinsky et al. 2011). Hystricomorphs differ from non-hystricomorphs in that the origin of m. masseter medialis is restricted to the medial surface of the zygomatic arch. In pachyrukhines, the infraorbital foramen is mediolaterally compressed as in sciuromorph rodents, but located in an elevated position, in contrast to our extant sample, but similar to some marsupials (see Sosa and García López 2018).

MLP 69-IV-6-1, the single specimen of *P. dolichognathum* that preserves incomplete palatal and rostral regions, including cheek teeth, diastema, anterior maxillary process, nasal, frontal, and maxillary bones, displays a very similar configuration to the other *Paedotherium* species, and more particularly to *P. typicum*. It is worth noting that the large posterior extension of the palate in respect to the tooth rows, which is the single trait that apparently differentiates this species from *P. typicum*,

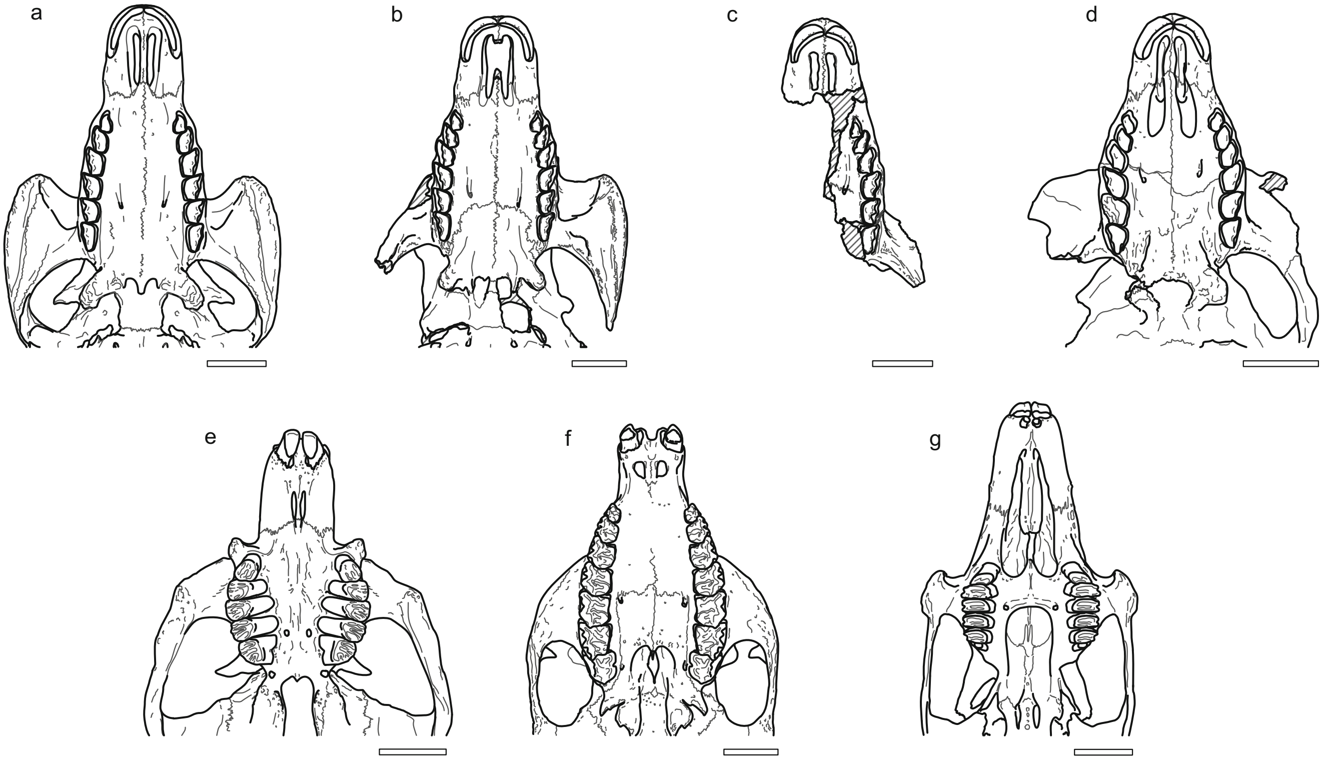


Fig. 6 Ventral view of the anterior region of the cranium. *Paedotherium bonaerense* (**a**), *P. typicum* (**b**), *P. minor* (**c**), *Tremacyllus* (**d**), *Cynomys ludovicianus* (**e**), *Heterohyrax brucei* (**f**), and *Lepus capensis* (**g**). Scale bars = 10 mm

may be an artifact of the crushing, flattening, and overall poor state of its preservation.

Glenoid Fossa and Temporal Fossa

The glenoid fossa of pachyrukhines is mediolaterally wide, without anterior and posterior limits. The jugal bone presents a short and poorly-defined posterior jugal process, immediately lateral to the glenoid fossa. Caudodorsally to this structure, the squamosal bone presents a sharp, anteroposteriorly short margin that delimits ventrally the space for the m. temporal is (Fig. 3). The extant studied sample displays three main morphologies for the glenoid cavity (Fig. 8). *Tragulus* and *Heterohyrax* have a lateromedially elongated glenoid cavity, bounded by high anterior and posterior margins (Fig. 8c). In contrast, in most rodents, such as the studied caviomorphs, the glenoid cavity is anteroposteriorly elongated, forming a narrow, lateromedially limited channel (Fig. 8a). Finally, in *Lepus* and, secondarily, in sciurids (Fig. 8b), the glenoid cavity is relatively ample and poorly delimited, similar to that of pachyrukhines.

In *Paedotherium,* the temporal fossa, the origin m. temporalis, is shallow, small, and triangular. It does not reach the midline of the cranium, and in consequence, no sagittal crest is observed. The opposite condition, in the caudal sector of the fossae, is found in *Tremacyllus* (Fig. 3; see also Cerdeño and Bond 1998). Moreover, the temporal fossa of *Tremacyllus* is also larger and more rounded than that of *Paedotherium*.

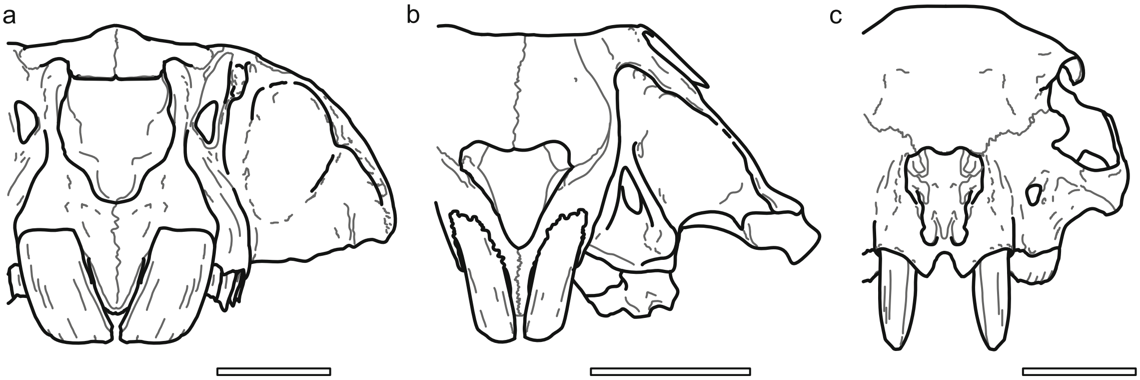


Fig. 7 Anterior view of the cranium. *Paedotherium bonaerense* (**a**), *Cynomys ludovicianus* (**b**), and *Heterohyrax brucei* (**c**). Scale bars = 10 mm

MLP 55-IV-28-82, the specimen of *P*. cf. *P. minor*, with a poorly preserved temporal region, presents a similar, but slightly larger temporal configuration to that of *P. typicum*. *Paedotherium typicum*, *P. bonaerense*, and *Tremacyllus* present a well-defined diagonal crest in the central region of the temporal fossa. This crest is associated with a caudal projection of the squamosal bone and delimits dorsally a dorsal mid-cranial hiatus, evident in some of the best preserved *P. typicum* and *P. bonaerense* specimens (e.g., Fig. 3i; see also MacPhee 2014: fig. 8, and the accompanying contribution; Ercoli et al. in prep.).

In the extant studied taxa, the largest development of the temporal fossa is observed in *Heterohyrax*, while the least developed fossa is found in *Chinchilla* and *Lepus*. In these three genera, the fossa does not contribute to a sagittal crest (Figs. 4 and 5). An intermediate condition is observed in the other studied rodents, either being similar to *Tremacyllus*, or slightly more developed, compared to *Paedotherium* (Figs. 3-5).

Upper Dentition

In pachyrukhines, the upper dental formula is I1, P2–4, M1–3, with a diastema separating the incisors from the cheek teeth. The dentition is euhypsodont, with a simplified occlusal design. The upper molariforms are mesiodistally elongated (resulting in relatively elongated upper cheek teeth rows; Table 1, UMRL/CBL), wider than the lower ones, and have undulated and raised ectolophs (Figs. 3 and 6). These ectolophs form high and large marginal cusps and ridges in the labial surfaces of the upper teeth, along with ample basined lingual surfaces, lingually limited by a slightly elevated margin [Figs. 3 and 6; a configuration referred to as "terraced" by Ercoli et al. 2019, based on Hershkovitz 1967]. This topology is more accentuated in the premolars of *Paedotherium* (especially *P. bonaerense*) than in those of *Tremacyllus*, in relation to the larger development and segregation of the paracone and metacone (see also Cerdeño and Bond 1998; Vera and Ercoli 2018). The premolars of *P. typicum*, *P. minor*, and *P. borrelloi* usually present well-defined sublingual sulci (see Cerdeño and Bond 1998; e.g., Fig. 3g) tending to develop a bilobed morphology. In contrast, the premolars do not present sublingual sulci in *P. bonaerense* and *Tremacyllus* (Figs. 2 and 3a). The degree of mesiodistal imbrication of teeth, the extension and thickness of the enamel, and the mesial convergence of the premolars reach their maximum degree in *Tremacyllus*, followed by some representatives of *P. minor*, and reach their minimum degree in *P. bonaerense* (Figs. 3 and 6). The shape of the occlusal surface of the premolar series is relatively similar to that of the molar series in *P. bonaerense* ("molarization" of premolars; Cerdeño and Bond 1998), but different in the remaining fossil species. In the case of *Tremacyllus*, the occlusal surface of the premolars is mainly flat in lateral view due to the morphology of the cusps and the alignement of the ectolophs, described above (Fig. 3n). The same tendencies can be observed in the lower cheek teeth (see below). The upper molars have an oval to quadrangular occlusal shape, without sublingual sulci (see also Cerdeño and Bond 1998; Ercoli et al. 2018; Figs. 3 and 6).

In pachyrukhines, the upper incisors present a thicker labial enamel layer than lingual one (see Filippo et al. 2020 contra Reguero and Prevosti 2010). Both incisors are labially convex and converge towards the medial plane building up an occlusal surface with a semicircular profile (see similar morphologies in other typotherians, e.g., McCoy and Norris 2012). This profile is less curved in some specimens of *P. typicum* (e.g., MLP 52-IX-28-14, MMP 698-S) and, apparently, in *P. borrelloi* (MLP 57-X-10-88; although not well preserved) compared to that in *P. minor* and *Tremacyllus*. *Paedotherium bonaerense* departs from this morphology, with the distal aspect of the incisors elongated mesiodistally (Figs. 3 and 6).

Among the studied extant species, sciurids, *Tragulus*, and *Heterohyrax* bear brachydont cheek teeth with relatively complex design. The studied caviomorphs and *Lepus* have a hypsodont dentition with simplified design, similar to that of pachyrukhines. The caviomorphs, *Lepus*, and *Cynomys*

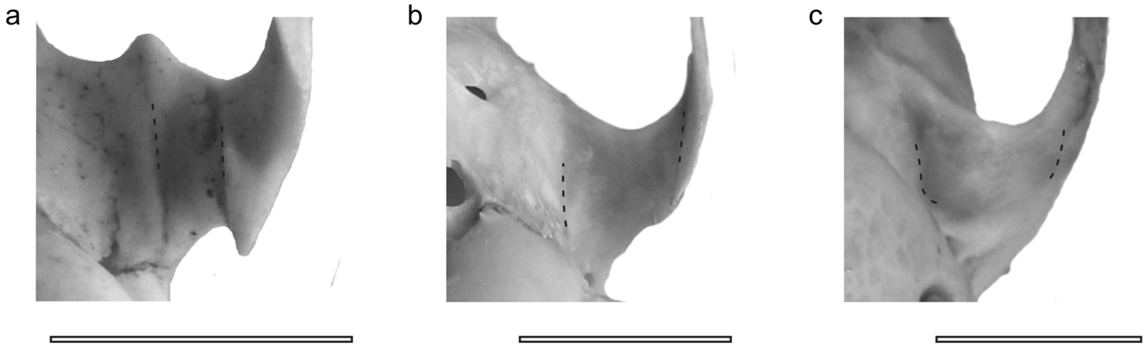


Fig. 8 Ventral views of the posterior root of the zygomatic arch illustrating different configurations of the glenoid cavity for extant taxa. *Cavia aperea* (**a**), *Ratufa bicolor* (**b**), *Tragulus kanchil* (**c**). Dashed lines indicate lateral and medial limits. Anterior is toward the top of each photograph. Scale bar s= 10 mm

display particularly thick enamel layers, which are either labiolingually (e.g., *Cavia*) or obliquely (e.g., *Ctenomys*) directed in occlusal view (Fig. 6). More specifically in *Ctenomys*, an imbricated disposition of the premolars and molars is denoted. In pacyrukhines, the external contour in occlusal view and the large number of premolars and molars are more similar to those observed in *Heterohyrax* and *Tragulus* than in the Glires (Figs. 4g, h; 6). The mesiodistally enlarged cheek tooth series (in relation to cranial length; Table 1), as well as the different width between the upper and lower cheek teeth (exemplified by the M1/m1 relationship; Table 1), reveal that pachyrukhines present intermediate conditions between Glires and the other analyzed mammals. On the other hand, the simplified shape of the mortar and pestle-like morphology of the occlusal surfaces of the cheek teeth is more similar to that of some rodents (e.g., Hershkovitz 1967), including sciurids, than to that of perissodactyls (e.g., Barone 1987), artiodactyls, and hyraxes, or even caviomorph rodents (in which the occlusal surface is flattened). Accordingly, in pachyrukhines, the presence of numerous, simplified, and ever-growing cheek teeth with a mortar and pestle-like morphology form a unique combination among our studied sample (while being present in some other typotherians; e.g., Croft 1999, 2016:158; Croft and Anaya 2006).

The upper incisors of Glires are characterized by a chisel-like morphology, euhypsodonty, and the presence of enamel only in the external layer. Hyraxes, such as *Heterohyrax*, present caniniform incisors, with flattened occlusal surfaces, while these teeth are absent in several artiodactyls, such as *Tragulus* (Figs. 6 and 7). In consequence, all the extant models used in this study differ from the semicircular-contoured, ever-growing incisors of pachyrukhines, as was also described for other typotherians (Cifelli 1993). It is worth noting that in the case of *Cavia*, its occlusal profile is slightly curved. Additionally, a semicircular and flattened occlusal profile is present in extant perissodactyls, composed by smaller and numerous incisives (Popowics and Herring 2006).

Mandible

Horizontal Ramus

In lateral view, the horizontal ramus of pachyrukhines is high, being proportionally shorter and taller in *Tremacyllus* than in *Paedotherium* species [Table 1, MHRH/(LMRL+LDL)]. The mandible presents a smooth, convex ventral margin in almost its entire extension. Its profile, in its anterior sector, is flattened or slightly concave in *P. bonaerense*, *P. borrelloi*, and *P. typicum*, or continuous to be convex in *Tremacyllus* (Fig. 3). In *P. minor* both conditions are observed in the anterior sector (Fig. 3s). All pachyrukhines have a high ascending ramus, with the condyle and coronoid processes well above the tooth rows (Table 1, CH/CIL). Unfortunately, structures posterior to the anterior sector of the base of the coronoid process and the middle sector of the masseteric ridge are not preserved in *P. borrelloi* and *P. minor*.

In the majority of the studied extant species, the horizontal ramus is low (e.g., non-fossorial caviomorphs and particularly *Tragulus*) to high (*Ctenomys*, sciurids, and *Lepus*) [Fig. 4; Table 1, MHRH/(LMRL+LDL)]. In *Heterohyrax,* it is high (Fig. 4g), with a profile similar to that of pachyrukhines (Fig. 3). In all extant sampled taxa, except *Cavia*, the ascending ramus is high, with the condyle well above the level of the lower cheek teeth (with the most extreme degree observed in *Lepus*) as in the fossil taxa (Figs. 3-4; Table 1, CH/CIL).

In pachyrukhines, the mandibular symphysis is fused (as in other notoungulates; see Madden 2015), and its extension is variable. It reaches the anterior level of p4 or posterior of p3 in *P. bonaerense* and *P. borrelloi* or the anterior level of p3 or posterior of p2 in *P. typicum* (except from specimen MMP 698-S, which is considered as a young adult and has the symphysis reaching the middle level of p3), *P. minor* and *Tremacyllus*. In relation to this, the internal foramina of the symphysis (= lingual foramina) are exposed onto its dorsal surface in *P. bonaerense* and *P. borrelloi*, onto the posterior surface in *Tremacyllus*, and on an intermediate position in *P. typicum* and *P. minor* (Fig. 3).

Heterohyrax, like pachyrukhines, presents a fused symphysis, differing from the rest of the extant sample (Fig. 9b; Janis 1979). The extension of this structure does not reach the level of the tooth row in many rodents, *Tragulus*, and *Lepus*, but it is more extended in *Heterohyrax* and caviomorphs (Fig. 9a, c). Among the latter, it reaches its maximal caudal extension in *Ctenomys*, extending to the level of the contact between m1 and m2, or m2, in the dorsal view of the mandible (Fig. 9a).

Muscular Insertions and Ascending Ramus

Among pachyrukhines, the masseteric crest is broad and particularly rugged and protrudes in its anterior end. This anterior process is more marked in *Tremacyllus* than in *Paedotherium*. In the case of *Tremacyllus*, the larger development of this process is linked to the delimitation of a concave sector, anterior to it, that forms a wide groove followed, ventrally, by a flat surface. This anterior process has its maximal development at the level of the transition m1-m2 or the middle sector of m2 in *P. bonaerense* and at the level of the middle sector of m2 or the transition m2-m3 in *P. borrelloi*, *P. typicum*, *P. minor*, and *Tremacyllus*. In lateral view, the masseteric crest ends anteriorly with a smooth and extended curvature in *P. bonaerense*, a smooth and short curvature in *P. borrelloi*, and a more marked and short curvature in the remaining fossils (Fig. 3).

The masseteric crest and its anterior process are the insertion sites of mm. masseter superficialis and masseter lateralis. These structures are poorly defined or absent in *Heterohyrax*,

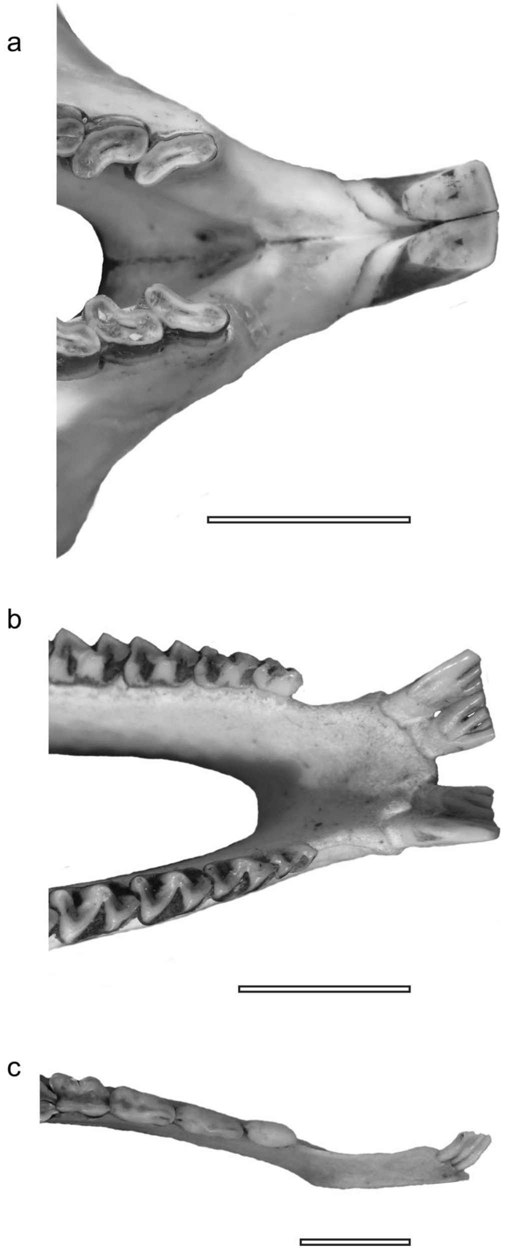


Fig. 9 Dorsal views, slightly rotated toward the lateral plane, of the mandible illustrating different features of the anterior region of the horizontal ramus. *Ctenomys frater* (**a**), *Heterohyrax brucei* (**b**), and *Tragulus kanchil* (**c**); i1 is absent in *T. kanchil.* Scale bars = 10 mm

Tragulus, and some caviomorphs (e.g., *Chinchilla*) (Fig. 4). The masseteric crest is highly marked in *Ctenomys* (Fig. 4c). In *Cavia*, there is a dorsal masseteric crest (= horizontal crest; Pérez 2010) and an associated fossa for the insertion of the deepest masseter muscles (Fig. 4e; m. masseter medialis sensu Woods 1972; personal data). In caviomorphs, there is an anterior scar for the insertion of the infraorbital portion of the m. masseter medialis, which is not homologous to the anterior process of other rodents and mammals (Woods and Howland 1979; Druzinsky et al. 2011; personal data). In sciurids, and especially in *Lepus*, the masseteric crest is well defined (Fig. 4) and presents an anterior process for the insertion of m. masseter lateralis, as in pachyrukhines (Fig. 3; see Ercoli et al. 2019). There is no defined masseteric crest in *Heterohyrax*, but a series of radiating scars (Fig. 4g), which are linked to the insertion of m. masseter superficialis subdivided in bundles by tendinous fasciae, as in other hyracoids (Janis 1983).

As in pachyrukhines, the representatives of Glires possess a groove immediately forward to the masseteric crest and its anterior process, when present (Figs. 3-4). This groove is linked to the passage of the m. masseter superficialis pars reflexa (sensu Woods 1972; see also Scapino 1974), a bundle very well developed in almost all Glires (Woods 1972; Thorington and Darrow 1996; Druzinsky et al. 2011; personal data; but see Cox and Baverstock 2016). Among our study sample, *Cynomys* has the largest groove. In contrast, this bundle and the associated groove are absent in perissodactyls, artiodactyls, such as *Tragulus*, and hyracoids, such as *Heterohyrax* (Fig. 4g, h; Janis 1983; personal data; but see tayassuids in Druzinsky et al. 2011).

In pachyrukhines, the angular process has a rounded contour. The ventral and dorsal masseteric fossae, associated with the insertions of mm. masseter lateralis and medialis, respectively, are well defined. The ventral masseteric fossa is wider and shallower than the dorsal one, which is located at the level of the bases of the condylar and coronoid processes (Fig. 3). However, there are differences in the relative development of the masseteric fossae among taxa. The dorsal fossa is strongly reduced in *P. bonaerense*, and it is larger in *P. typicum*, and wider in *Tremacyllus* (e.g., FMNH 14456, and particularly deep in MLP 95-III-31-15). In the last, it reaches a surface similar to the ventral fossa, in relation to the differences in the available insertion area of the concerned muscles. In *P. borrelloi* and *P. minor*, only the anterior end of both masseteric fossae is preserved, so their exact morphology could not be established. In the anteroventral sector of the dorsal masseteric fossa, there are several foramina of variable position and size. In the posterior sector of this fossa, there is a crest parallel to the posterior margin of the angular process, clearly preserved in *P. bonaerense* and *P. typicum* (e.g., Fig. 3j). In the ventrolateral aspect of the horizontal ramus of all pachyrukhines, there are two mental foramina, one at the level of p4 and the other at the level of the diastema (Fig. 3; see also Seoane et al. 2019). In the medial aspect of the angular process of the *Paedotherium* species that preserve this structures (i.e., *P. bonaerense* and *P. typicum*), there are radial scars that reach the margin, corresponding to the insertion of the m. pterygoideus internus (e.g., Ercoli et al. 2019: fig. 2). This region is not preserved in *Tremacyllus*. Also in medial view, the mandibular foramen is located near the root of m3.

In extant rodents, the angular process is acute and posteriorly projected (Fig. 4a-e), being particularly sharp in caviomorphs (Fig. 4c-e). On the other hand, the contour of the angular process is more rounded in *Lepus*, *Heterohyrax*, and *Tragulus.* In *Lepus* it includes an acute caudodorsal tip, not observed in *Heterohyrax* and *Tragulus* (Fig. 4f-h). *Heterohyrax* presents the highest development of the angular process, with a shape and size similar to that described for pachyrukhines (Figs. 3 and 4g). In its medial aspect, and in relation to the insertions of mm. pterygoid (and particularly m. pterygoideus mediallis), *Cavia* and *Chinchilla* possess a pterygoid shelf of moderate to low development, while these structures and are more markedly developed in *Lepus*, *Ctenomys*, and sciurids. It reaches its highest development in *Cynomys*, where dorsal radial striations and a medially recurved ventral margin are present. Although a pterygoid shelf is not recorded for *Tragulus* and *Heterohyrax*, there are radial striations dorsal to the ventral margin of the angular process, which are especially well developed in *Heterohyrax*. The *Heterohyrax* configuration of the internal aspect of the angular process and pterygoid insertions resembles that of pachyrukhines. However, the fossil taxa display more marked radial scars, which are also reminiscent of those of *Cynomys*.

The ventral and dorsal masseteric fossae, related to the insertions of the mm. masseter lateralis and medialis respectively, are well defined in sciurids, *Ctenomys*, and *Lepus*. In all these taxa, the dorsal fossa is deeper and narrower than the ventral one (Fig. 4). In *Chinchilla*, the configuration of these fossae is similar, but the dorsal masseteric fossa presents an associated incipient dorsal masseteric crest in its posterior region (Fig. 4d). The ventral fossa is barely defined in *Cavia*, but the dorsal one is deepely excavated and delimited by a robust dorsal masseteric crest (Fig. 4e; Woods 1972). In *Tragulus* and *Heterohyrax,* these fossae are hardly visible, but the locations and size of the poorly defined insertion areas of the medial and lateral masseteric muscles (Turnbull 1970; Janis 1983) are similar to those described for sciurids and *Lepus*. In this aspect, sciurids and *Lepus* are similar to pachyrukhines. Additionally, these taxa, and secondarily *Chinchilla* and *Tragulus*, present elongated scars, parallel and lateral to the angular process margin. These scars correspond to the limit of attachments of the m. masseter lateralis and a posterior (non-reflexa) part of the m. masseter superficialis, not present in the other extant representatives (e.g., *Cavia*).

In the studied pachyrukhines, the coronoid process, the attachment site m. temporalis, is only sufficiently preserved or complete in three specimens of *P. typicum* (MMP 1008-M; MLP 12–2703; MACN Pv 17,333; e.g., Fig. 3j) and almost complete in two specimens of *Tremacyllus* (MACN Pv 8161, MACN Pv 8163). The coronoid process is reduced and possesses a large base and acute tip, reaching to a similar level as that of the condyle and distanced from the latter by a short mandibular notch. The base of the process is preserved in other pachyrukhines without major differences (Fig. 3). In medial view, on the base of the coronoid process, there is a fossa linked to the insertion of the deep bundles of m. temporalis, which narrows toward its anterior region (Ercoli et al. 2019: fig. 2). The latter feature is identified in *P. typicum* and *P. bonaerense*, but not in the other pachyrukhines.

The morphology of the coronoid process is highly variable in the extant studied species. *Cavia* presents a reduced coronoid process, which is in an advanced and low position, distanced by a large mandibular notch from the condylar process, which is also located low (Fig. 4e). In *Chinchilla*, the coronoid process is moderately to poorly developed and located in a low position, while the condylar process and the mandibular notch are well developed, and the condyle stands in a high position (Fig. 4d). In *Lepus*, the coronoid process is rounded and recurved medially, associated with a medial sulcus (sulcus ascendens; see Wible 2007, see below), and located at a lower level than the condyle (Fig. 4f). Conversely, in *Tragulus*, *Ctenomys*, and the sciurids, this process is more developed reaching or surpassing the level of the condyle, and the mandibular notch is short or moderately developed (Fig. 4). In *Tragulus*, the coronoid process is particularly high and posteriorly recurved (Fig. 4h; see also Turnbull 1970). *Heterohyrax* presents the largest coronoid process, which surpasses largely the height of the condyle. Both, the coronoid and condylar process are anteriorly tilted and distanced from each other by a short mandibular notch (Fig. 4g). Although the morphology of the pachyrukhine coronoid process does not fit with any extant model, its configuration seems more similar and intermediate to that of *Tragulus* and *Chinchilla*, with a relatively small, but dorsally located, insertion area for m. temporalis.

As mentioned above, the medial aspect of the coronoid process presents a concave surface in *Tragulus* and *Heterohyrax*, and a deep and long sulcus, which extends from the last molar to the condyle in *Lepus*. This structure is in relation to the development of the insertion area of a deep portion of m. temporalis, originating from the posterior wall of the orbit (=temporalis pars orbitalis; Woods and Howland 1979; see also Turnbull 1970) and particularly strongly developed in *Lepus* (ventral head of the lateral deep temporalis sensu Russell 1998; see also Wible 2007) (Fig. 4).

In pachyrukhines, the condyle is rounded and convex and tilts anteriorly, with its anteroposterior extension higher than the lateromedial. The postcondylar process (=postcondyloid process of Woods 1972) is robust and short, with a variable size, at least in the species where it is better preserved (i.e., *P. typicum* and *P. bonaerense*) (Fig. 3).

Among extant species, the morphology of the condyle varies, with the predominance of the mediolateral extension, as in *Tragulus* and *Heterohyrax*, or that of the anteroposterior extension, as in caviomorphs. The condyle is arranged diagonally in sciurids, and it is approximately rounded and anteriorly tilted in *Lepus*. Among pachyrukhines, the shape and tilting could be considered as more similar to that of *Lepus*, although with a greater component of anteroposterior extension, being in this aspect intermediate between *Lepus* and caviomorphs. The postcondylar process shows a moderate to large development among the studied Glires and it is absent in *Heterohyrax* and *Tragulus*. In its lateral aspect, this process is linked to the insertion of a short portion of mm. masseter (posterior masseter of Woods and Howland 1979; see also Cox and Jeffery 2011), and in its medial aspect, to the insertion of m. pterygoideus lateralis. In pachyrukhines, this process is present, but reduced, and associated with a small internal fossa, probably linked to a high positioned m. pterygoideus externus, while the probable scar of attachment of the posterior masseter seems to be better defined ventral to the condyle than to the postcondylar process (similar to *Lepus*, Russell 1998) (Fig. 3).

In the studied extant species, the morphology related to the insertion of m. digastricus can be summarized in two main types. In Glires (sciurids, caviomorphs, *Lepus*), this muscle inserts onto the most anterior region of the ventral aspect of the horizontal ramus, near or including the ventral sector of the symphysis (Crabb 1912; Turnbull 1970; Woods 1972; Thorington and Darrow 1996; personal data on *Cavia*), leaving in this sector a more (e.g., *Cavia*) or less (e.g., *Lepus, Chinchilla*) defined crest-like scar. On the other hand, in *Tragulus* and *Heterohyrax*, as typically in other mammalian clades, the insertion of m. disgastricus is onto the posterior sector of the horizontal ramus, anterior to or in the ventral aspect of the angular process, respectively (Turnbull 1970; Janis 1983; personal data). In these non-rodent mammals no evident scar of attachment and the ventral sector of the symphysis is smooth, in relation to the absence of insertion (Fig. 4). Among pachyrukhines, the form of the insertions of mm. masseter, the possibility that one of the masseteric bundles runs through the groove anterior to the angular process at the medial aspect of the mandible, and the absence of anterior scars that could correspond to the insertion of m. digastricus (Fig. 3) suggest that m. digastricus would have had an anterior insertion, anterior to the groove, but without reaching the symphysis. This condition appears more similar to *Tragulus* than *Heterohyrax*.

The single specimen of *P. kakai* (S. Sal. Scar. Paleo. 2012–045; see Reguero et al. 2015) preserves only the p4, the lower molars, and the associated parts of the horizontal ramus (including the anterior part of the masseteric crest, anterior process and and associated groove for the transit of the m. masseter superficialis pars reflexa), with no major differences from other *Paedotherium* species, such as *P. typicum* and *P. minor*.

Lower Dentition

Pachyrukhines had a lower dental formula of i1–2, p2–4, m1–3. The lower incisors are procumbent with their occlusal surface facing anteriorly. As for the upper dentition, there is an anatomical diastema between the incisors and cheek teeth, and all teeth are euhypsodont (Fig. 3; e.g., Kraglievich 1926; Cerdeño and Bond 1998). The lower diastema is always shorter than the upper one (Table 1, UDL/LDL). The lower teeth are slightly labiolingually narrower than the upper ones (Fig. 3; Table 1, M1W/m1W; see also Ercoli et al. 2018: fig. 8), and the lower left and right series are located closer to each other compared to the upper series (Fig. 3). A recent study carried out a detailed comparison between the morphologies of lower premolars and molars of the fossil taxa studied here (Ercoli et al. 2018). The last molar is always trilobed, while the premolars and the remaining molars are bilobed, with round- to triangular-shaped lobes. Particularly for p3, in *P. minor*, *P. borrelloi*, and some specimens of *P. typicum*, the anterior lobe displays an incision that gives the premolar a trilobed appearance. The degree of molarization and the length of the premolar series diminishes progressively from *P. bonaerense*, *P. borrelloi*, *P. typicum*, *P. minor* to *Tremacyllus* (Ercoli et al. 2018). The occlusal profile is elevated in the lingual aspect, similar to that described for the upper dentition, with a contiguous basined surface, which is labially limited by a slightly elevated labial margin (Fig. 3; see also Ercoli et al. 2018, 2019).

Regarding the lower dentition, the studied extant species vary in their degree of hypsodonty and simplification of occlusal profiles (Figs. 4 and 9). Again, in pachyrukhines, the elongated tooth rows, the numerous teeth, and the external contour of the cheek teeth in occlusal view are reminiscent of brachyodont forms, such as *Heterohyrax* (also similar to the mortar and pestle-like morphology at some degree, but differing in the occlusal design; Figs. 4g and 9b) and *Tragulus* (Fig. 4h and 9c; especially with respect to the morphology of the posterior dental elements). In contrast, hypsodont forms, represented here by the studied Glires, possess reduced dental formulae and, in some cases, simplified occlusal design.

The lower incisors (i1–2) of pachyrukhines are euhypsodont (as I1) and possess both labial and lingual enamel layers (Filippo et al. 2020). The mandible is anteriorly elongated in the species of *Paedotherium* and relatively anteroposteriorly compressed in *Tremacyllus* [Fig. 3; Table 1, MHRH/(LMRL+LDL)]. As described for the upper dentition, the lower incisive arch is wider in *P. bonaerense* and *P. typicum* than in *Tremacyllus* (Table 1, LIAW/MBmR). The incisive arch of *P. bonaerense* is anteroposteriorly elongated and forms a well-defined angular profile. On the other hand, in *P. typicum* and *P. minor* (MMP 251-S), the incisive arch is shorter anteroposteriorly and has a smoother curvature (Fig. 3). In *P. borrelloi*, the incisive arch is not preserved in any specimen. In *Tremacyllus,* the incisive arch is narrower than the middle sector of the diastema and forms a well-defined angular profile between the central incisors (Fig. 3q).

Similarly to what was described for the upper dentition, the studied extant rodents and lagomorphs possess euhypsodont incisors, with a very thick enamel layer, present only on the labial face (e.g., Cox et al. 2012 and references therein). This condition generates the typical Glires morphology, with a pair of chisel-like incisors that form a relatively short but powerful transverse cutting facet (Figs. 4 and 9a). The width of this cutting facet is, in all cases, shorter than the width between the anterior molariforms. In *Heterohyrax*, there is a pair of diverging and euhypsodont incisors at the sides (see Filippo et al. 2020), with a gap in the midline (Fig. 9b). *Tragulus* has three incisors on each side (Fig. 9c), forming an incisive arch, wider than the diastema, and composed of recurved and brachydont teeth (Fig. 4). Beyond these differences, *Heterohyrax* and *Tragulus* share lobes in the first incisor. Interestingly, the incisive morphology of pachyrukhines presents a unique combination of ever-growing incisors, with a thicker external enamel layer, reminiscent of Glires (as well as wombats, see Shockey et al. 2007), but with a recurved and more flattened occlusal surface, more similar to hyraxes, artiodactyls, or perissodactyls (Fig. 3; Barone 1987).

Discussion

Chewing Function

The particular craniomandibular morphology of pachyrukhines and other typotherians has been previously interpreted as indicative of grazing habits (see Introduction), mainly based on their euhypsodont molariform teeth and large development of the masseter muscles, in comparison with ungulate models (e.g., Reguero et al. 2007; Cassini et al. 2011). Shockey et al. (2007; see also Croft 2016; Croft et al. 2020) early observed the particular masticatory features in mesotheriids, underlining the combination of hypsodont dentition and narrow snout morphology, questioning the grazer interpretation for this group and comparing the representatives of this family with wombats. In line with this, Cassini et al. (2011) in their analysis of Santacrucian South American native ungulates including hegetotheriids and interatheriids, and Sosa and García López (2018), studying a diverse sample of typotherians, acknowledged the weakness of analyzing the paleobiology of extinct typotherians considering only extant ungulate models, inasmuch as considering their rodent-like morphological convergences (Sinclair 1909a, b; Patterson 1934; Bond 1999; Shockey et al. 2007; Billet 2011; Reguero and Prevosti 2010; Cassini et al. 2011; Gomes Rodrigues et al. 2018; Sosa and García López 2018; see the wide comparative sample of Croft and Anderson 2008). In the mesowear study by Croft and Weinstein (2008), in which Oligocene representatives of "archaeohyraciids," interatheriids, and trachytheriine mesotheriids were analyzed, it was indicated that despite the general rodent-like cranial similarities of typotherians, their mastication appeared more similar to ungulate than rodent models. However, Croft and Weinstein (2008) did not analyze derived typotherian morphotypes, and only ungulates were considered in their comparative sample, and ultimately recognized limitations in the absence of muscular reconstructions for typotherians. Recent works dealing with muscular reconstructions [but see the pioneer comments on mesotheriids by Patterson 1934] that have considered diverse mammalian masticatory models indicated that the masticatory apparatus of some typotherians combine ungulate and rodent features, but resembles closer rodents and rodent-like mammals (Sosa and García López 2018; Ercoli et al. 2019). Ercoli et al. (2019) even proposed sciuromorphy for pachyrukhines. In line with these previous studies, herein and in the accompanying contribution (Ercoli et al. in prep.), we provide a thorough analysis of the functional morphology and paleobiology of *Paedotherium* and *Tremacyllus*, by considering the entire craniomandibular, dental, and cervical morphology of representatives of these pachyrukhines. The detailed anatomical descriptions presented here reveal that *Paedotherium* and *Tremacyllus* possessed an interesting combination of features and can help understand paleobiological aspects of the group and variants at the generic and specific levels that could eventually enlighten aspects of ecological niche partitioning between them. During the last four decades different authors highlighted this topic as an underexplored field and necessary to be addressed (e.g., Zetti 1972a; Croft 2016).

There is considerable evidence that supports hypsodonty as not necessarily linked to grazing, and as more widely related to the processing of various types of abrasive materials derived from diet or digging activities, such as grit and volcanic ash (Janis 1988, 1995; Janis and Fortelius 1988; Williams and Kay 2001; Verzi and Olivares 2006; Croft and Weinstein 2008; Townsend and Croft 2008; Billet et al. 2009a; Reguero et al. 2010; Damuth and Janis 2011; Strömberg et al. 2013; Madden 2015; Renvoisé and Montuire 2015). In a similar way, when compared with different taxa, the hypsodonty of pachyrukhines in particular (Cassini et al. 2012; Reguero et al. 2015; Ercoli et al. 2019) and other typotherians in general (e.g., Billet et al. 2009a) is not necessarily linked to grazing habits. Consequently, the presence of ever-growing teeth in pachyrukhines could be eventually associated with other factors, or even phylogenetic inertia, taking into account that high-crowned cheek teeth are a plesiomorphic character for Pachyrukhinae (Croft and Anaya 2006; Reguero et al. 2015; Seoane et al. 2017), and probably Typotheria (Billet et al. 2009a; Reguero and Prevosti 2010; Reguero et al. 2010; Billet 2011; Madden 2015). Regarding the proportion of muscles of the masticatory apparatus, pachyrukhines are characterized by a m. temporalis that represents the smallest adductor, while the mm. masseter conform a complex and dominant group (Patterson 1934; Cassini 2011; Cassini et al. 2012; Gomes Rodrigues et al. 2018; Sosa and García López 2018; Ercoli et al. 2019). It is worth noting that the remarkable development of the masseter muscles is not exclusive to grazers, and that a similar or even greater development is present in other herbivores, such as rodents and rodent-like mammals, in association with the anteroposterior effort for gnawing (Turnbull 1970; Fortelius 1985; Axmacher and Hofmann 1988; Cox et al. 2012; Furuuchi et al. 2013; Ercoli et al. 2019).

The presence of a relatively large number of molariform teeth in pachyrukhines can be considered as an indicator, to some degree, of the significance of chewing for food processing, as has been suggested for ungulates (Popowics and Herring 2006; Cassini et al. 2017 and references therein), rodents (e.g., Maestri et al. 2016), and particularly notoungulates (Billet et al. 2009a; Cassini et al. 2017). Particularly for Santacrucian Typotheria, Cassini et al. (2017) suggested that the occlusal surface areas are smaller than expected for their body size, departing from that expected for grazers, which typically show higher values (Mendoza et al. 2002; Cassini et al. 2017).

Although no single morphological trait is an infallible tool to infer the chewing mode and dietary preferences in extinct taxa, the integrated analysis of different structures and features of the masticatory apparatus (e.g., muscular and articular design, tooth wear, etc.) can improve the confidence of inferences related to food acquisition and masticatory modes (Fortelius 1985; Popowics and Herring 2006; Raia et al. 2010; Kubo and Yamada 2014; Green and Croft 2018).

Our analysis shows that many features, including an occlusal pattern of cheek teeth in which there are marginal cusps forming elevated ridges in a mortar and pestle-like morphology, the occlusal surface of the upper tooth series wider than the lower one (Table 1), and the large masticatory muscles that act in a diagonal plane, indicate that transverse movements were an important component during chewing in pachyrukhines (see also Ercoli et al. 2019). As in hyraxes and many ungulates [including extant taxa and other notoungulates; see Cassini et al. 2017], the larger occlusal surface of the upper tooth series in relation to the lower one of pachyrukhines would indicate significant lateral components in chewing movements, because the lower teeth have to slide against the occlusal surface of the upper teeth (Popowics and Herring 2006; Cassini et al. 2017). The upper and lower tooth rows are positioned in such a way (i.e., lower rows are closer to each other than the upper ones; Fig. 3) that only some cheek teeth of one side are in contact with each other during occlusion. These features are related to complex chewing movements and strong efforts concentrated in smaller areas of the tooth series at a time (Greaves 1978, 2012; Popowics and Herring 2006; Crompton et al. 2006), as in the ungulates, hyraxes, and sciurids (especially *Ratufa*) of our comparative sample. Contrary to rodents, such as caviomorphs, the glenoid cavity of pachyrukhines does not present bounded limits (Fig. 8), allowing high degrees of mediolateral movements of the mandibular condyle (Hiiemae and Crompton 1985; Popowics and Herring 2006). As suggested by Ercoli et al. (2019), the pterygoid muscles show a remarkable development in pachyrukhines, which also present a very high ascending ramus of the mandible, similar to that of leporids and ungulates (Turnbull 1970; Barone 1987). This morphology results in a high position of the glenoid fossa, well above the occlusal surface of the tooth rows, which increases the mechanical advantage of the pterygoid muscles and the masseteric complex (Turnbull 1970; Fortelius 1985; Popowics and Herring 2006; Greaves 2012). The pterygoid muscles act mainly in the transverse plane (Maynard Smith and Savage 1959; Turnbull 1970; Janis 1979; De Blieux and Simons 2002), indicating important lateral chewing movements in *Paedotherium* and *Tremacyllus*, as in ungulates and hyraxes, instead of the mainly propalinar (or at least oblique) chewing of many rodents (Turnbull 1970; Janis 1979; Woods and Howland 1979; Lieberman and Crompton 2000; Vassallo and Verzi 2001; De Blieux and Simons 2002; Hautier et al. 2011; Álvarez et al. 2020). These important lateral chewing movements are further substantiated by the presence of a fused symphysis (Fig. 3), an ancestral condition shared with other notoungulates (Madden 2015), but also observed in diverse extant groups, such as hyraxes, perissodactyls, and some artiodactyls (Fig. 9b; Janis 1979; Popowics and Herring 2006) whose mode of mastication is characterized by a strong transverse component of chewing movement, recruiting the muscles of the balancing side during occlusion of the working side (Janis 1979; Greaves 1988, 2012; Lieberman and Crompton 2000; Popowics and Herring 2006). Preliminary observations in pachyrukhines by stereomicroscope of the tooth enamel striae (following the approach of Greaves 1973) confirm the dominance of striations in an oblique, anterolingual-posterolabial, direction, deviating from the sagittal axis of the mandible between 48 and 60°. Similar values or slightly higher were obtained for the upper cheek teeth. These observations further confirm the assertions about chewing movements.

Regarding tooth morphology, extant grazers, as well as consumers of other abrasive foods, present flattened (e.g., equids, caviids, ctenomyids; Fig. 9a) or mainly flattened (e.g., most artiodactyls and secondarily lagomorphs; Fig. 4f) occlusal surfaces, with low cusp relief, which favor high compression and grinding (Hiiemae and Crompton 1985; Fortelius and Solounias 2000; Popowics and Herring 2006). A complex design with a high number of enamel layers is observed in large-sized grazing mammals (Strömberg 2005; Reguero et al. 2010; Cassini et al. 2017). Nevertheless, a relatively simple design, with few but thickened layers, can be observed in small-sized grazers (Reguero et al. 2010; Becerra et al.

2012), as in the grass-eating rodents of our comparative sample (Fig. 9a). In both cases, these layers are mainly oriented perpendicular to the direction of movement during grinding (Greaves 1973, 1982; Wyss et al. 1993; Olivares et al. 2004;Popowics and Herring 2006; Verzi et al. 2010; Becerra et al. 2012).

As previously stated, pachyrukhines present a simple crown pattern, rendering the tooth morphology of pachyrukhines and several typotherians even simpler than of other notoungulates in particular, and ungulates in general (Croft 1999; Cassini et al. 2017). The mortar and pestle-like cheek teeth of pachyrukhines, as well as of other hegetotheriids, imply that the large marginal cusps occlude with the corresponding basined surfaces on the opposed molariforms (Fig. 3; Ercoli et al. 2019). As previously described (e.g., Hiiemae and Crompton 1985), the marginal ridges of the terraced teeth allow for cutting food and reducing it to small-sized particles, and also serve as the walls of the compression chamber during crushing. As was recognized for the hegetotheriid *Hemihegetotherium* by Croft (2016), this morphology segregates hegetotheriids in general, and pachyrukhines in particular, from the expected pattern of the crown molariform morphologies of grazers. Considering the information that comes from chewing modes and morphologies of extant taxa, the cheek teeth configuration of these extinct clades would favor an important component of mortar-and-pestle-like crushing action, instead of an exclusively grinding action (e.g., Fortelius 1985; Hiiemae and Crompton 1985; Popowics and Herring 2006).

Considering this, the absence of numerous or very thick layers of enamel in a parallel arrangement, and the absence of ample or completely flattened occlusal surfaces in the molariform design of pachyrukhines departs from the morphology of high demands of grinding activities of specialized grazers, although it does not preclude potential consumption of grasses.

Nevertheless, it is worth noting some interspecific differences among pachyrukhines that could be related to differential processing of some abrasive items. The mesiodistal imbrication of the premolars and mesially convergent premolar rows of *Tremacyllus* (Figs. 3m, q and 6d), also observed to a lesser degree in *P. minor* (Fig. 6c; see Bondesio et al. 1980; Ercoli et al. 2018; Vera and Ercoli 2018), result in the aligning of multiple enamel margins more or less parallel to a single diagonal with a posterolingual to anterolabial direction, acting as a single functional unit. The main orientation of enamel layers is also a proxy of chewing movements. This is because they are usually perpendicular to enamel striations, the latter being parallel to the chewing direction (Greaves 1973), in congruence with the main posterolabial to anterolingual direction of enamel stration in pachyrukhines (see above). Furthermore, in *Tremacyllus* and *P. minor*, the enamel layers are thick, although not reaching the degree of grass-eating rodents, such as some of the studied caviomorphs (see also Becerra et al. 2012; Vera and Ercoli 2018). Additionally, there is also a strong development of the groove for the pars reflexa of the m. masseter superficialis (see below), and a less marked sciuromorph condition in *Tremacyllus* and *P. minor* than in the other studied pachyrukhines (see also Ercoli et al. 2019). Although departing from the extant grazing and browsing models, these traits indicate a suitable design for relatively increased grinding action compared to other analyzed pachyrukhines, and a more relevant contribution of leaf-grass items in the diet, in *Tremacyllus* and, secondarily, in *P. minor*. Considering that the molars of pachyrukhines are more suitable for crushing than the premolars, the molariform condition of the premolars of *P. bonaerense* (Figs. 3a and 6a; Cerdeño and Bond 1998; Ercoli et al. 2018), including a well-developed and differentiated paracone and metacone, even at the P4 and P3 (diagnostic features of the species; see Cerdeño and Bond 1998; Ercoli et al. 2018), together with the slender enamel layers, and the strongest sciuromorph condition, make this taxon the most specialized pachyrukhine in hard-food items consumption (see also Ercoli et al. 2019). Finally, *P. typicum* and *P. borrelloi* (although scarce information is available for the latter) seem to present an intermediate condition between *P. bonaerense* and *P. minor* (Figs. 3g and 6b; see also Ercoli et al. 2018: fig. 9).

In summary, the singularity of the mosaic of masticatory features of *Paedotherium* and *Tremacyllus* are here interpreted as related to a large mediolateral component in chewing movements, more similar to ungulates and hyraxes than to the propalinal movements of many rodents. Moreover, these features are more compatible with dietary habits that include hard and brittle or turgid fruit food, emphasizing crushing, and secondarily grinding, instead of the extensive grinding of grazers (Hiiemae and Crompton 1985; Fortelius and Solounias 2000; Popowics and Herring 2006).

Incisive Biting, Food Selection, and Digging Habits

An interesting set of rodent-like and gnawing-related traits are present in the craniomandibular complex of pachyrukhines, especially at the incisors, rostrum, and masticatory muscles attachment areas. Rodent-like and wombat-like configurations in some of these structures have been previously reported for different typotherians (e.g., mesotheriids: Patterson 1934; Shockey et al. 2007; Gomes Rodrigues et al. 2018; Sosa and García López 2018; pachyrukhines: Kraglievich 1926; Gomes Rodrigues et al. 2018; Sosa and García López 2018; Ercoli et al. 2019 and references therein). As mentioned previously, the pachyrukhine (and to some extent typotherian) masticatory apparatus is characterized by the complexity and dominance of the masseter group (Patterson 1934; Cassini and Vizcaíno 2012; Cassini et al. 2012; Gomes Rodrigues et al. 2018; Sosa and García López 2018; Ercoli et al. 2019). The muscle proportions suggested by Ercoli et al. (2019) demonstrated that they are only similar to gnawing mammals, i.e., rodents and lagomorphs (Turnbull 1970; Ball and Roth 1995; Druzinsky 2010a). Although not disposed strictly in a transverse plane, the incisors present a large number of similarities with rodents and lagomorphs, as well as wombats (e.g., Shockey et al. 2007; see also Sosa and García López 2018). Relatively large diastemata separate incisors from other teeth, the upper diastema being larger than the lower one (Table 1). As also occurs in other rodent-like typotherians, the upper incisors present a curved profile (e.g., Patterson 1934; Gomes Rodrigues et al. 2018; Sosa and García López 2018), while the lower ones are procumbent, resulting in an anteriorly facing occlusal surface (Figs. 3 and 7a). All these features indicate markedly different movements and functions in the incisors and cheek teeth, and the necessity of anteroposterior movements to the coupling and acting of the incisors. This configuration implies at the same time the phase shift of the cheek teeth series, and the decoupling of the chewing and gnawing functions (Turnbull 1970; Druzinsky 2010a, b; Cox et al. 2012; see also Janis 1979; De Blieux and Simons 2002).

Accordingly, the analysis of the muscular scars and the temporo-mandibular articulation provide indications of how this action could have been carried out. The mandible presents a groove that indicates the presence of a m. masseter superficialis pars reflexa (Fig. 3; see also Ercoli et al. 2019), and the large, parallel, and ventrally projected paroccipital processes (see accompanying contribution Ercoli et al. in prep.) seem to be related to a ventrally located origin of the mm. digastricus. In fact, when the cranium and mandible are articulated, the origin and insertion of mm. digastricus should be placed in an anteroposterior alignment. Both features seem to be related to the recruitment of these muscular bundles to perform anteroposterior movements, in association with the gnawing function (Turnbull 1970; Woods 1972; Druzinsky 2010a, b; Ercoli et al. 2019), and with the chewing movements (Lieberman and Crompton 2000; see above). Regarding mm. digastricus, it is interesting to note that the functional convergence with rodents, to an anteroposterior action and retraction of the mandible, seems to be reached by a different morphological pathway, through the development of a ventrally located paroccipital origin but without advancing the insertion area in the case of pachyrukhines. The condyle and glenoid fossa of the temporo-mandibular joint conform to an anteroposteriorly elongated and smooth surface, allowing these movements, as in rodents and lagomorphs (Fig. 8; Turnbull 1970; Vassallo and Verzi 2001; Becerra et al. 2012), and as also suggested for pachyrukhines by Sinclair (1909a).

Another remarkable rodent-like masticatory feature of Neogene pachyrukhines (also present in other typotherioideans) is the reduced number of incisors, being mainly (lower series) or exclusively (upper series) represented by a middle pair of largely developed, euhypsodont incisors (i.e., i1 and I1 pairs, respectively) (Cerdeño and Bond 1998; Reguero and Prevosti 2010; Gomes Rodrigues et al. 2016; Filippo et al. 2020). It is worth noting that additional lower incisive elements are present in some Oligocene taxa of the subfamily (Seoane et al. 2019), and it is the ancestral condition of typotherians and other notoungulates (e.g., Croft et al. 2003; Billet et al. 2009a; Reguero and Prevosti 2010; Billet 2011). This incisive morphology has been related to the exertion of strong forces in small areas (Hershkovitz 1967; Druzinsky 2010b; Croft et al. 2011; Cox et al. 2012; see also McCoy and Norris 2012) and intense wear (Reguero and Prevosti 2010; Filippo et al. 2020). As occurs in other notoungulates, the enamel layers present differences in their development and arrangement in the labial and lingual side of the incisors (Filippo et al. 2020). In fact, Filippo et al. (2020) considered that the presence of a lingual enamel layer in the incisors of rodent-like (and almost all) notoungulates would hamper comparisons with rodent models. However, in hegetotheriids and particularly in pachyrukhines, the lingual layer is approximately half or even thinner than the labial layer, reflecting a morphological proximity to rodent models. Similar traits could be considered as part of a set of rodent-like features, evidencing not only morphological, but also functional similarities related to gnawing.

The presence of a largely developed posterodorsal process of the premaxillary bone, which contacts extensively with the frontal, has been underscored as a convergence in rodents and lagomorphs, and interpreted as a skull adaptation to gnawing and well-developed incisors (ascending process of the premaxilla; Novacek 1985; Frahnert 1999). Although there is no posterior premaxillary process in pachyrukhines (Sinclair 1909a), it is interesting to note that an analogous process exists. This analogous structure is conformed by the maxillary bone, instead of the premaxillary one (i.e., caudal process of the maxillary; Kraglievich 1926; see Fig. 2b), which possesses a similar extension and position to that described for Glires.

In pachyrukhines, the m. masseter lateralis presents an anterior and advanced bundle originating from the zygomatic plate onto the rostrum (which in turn is inserted on an anterior position of the mandible, in the anterior tuber of the ventral crest). This condition indicates a sciuromorph condition (see Ercoli et al. 2019), and reveals a notable convergence with some derived sciuromorph rodent clades, the only remaining sciuromorph cases in mammals (see Results; Ercoli et al. 2019). This masticatory configuration was previously related to strong incisive work during gnawing by increasing the mechanical advantage of the mm. masseter (Druzinsky 2010a, b; Cox et al. 2012; Gomes Rodrigues et al. 2016), and to hard-food item consumption (Thorington and Darrow 1996; Cox et al. 2012; Casanovas-Vilar and Van Dam 2013; Ercoli et al. 2019). This pachyrukhinae masseteric configuration differs from that inferred for other typotherians, in which the zygomatic plate is large but does not reach the rostrum (e.g., hegetotheriines, most mesotheriids), is relatively reduced (e.g., archaeohyraciids), and, in some cases, accompanied by a descending process for the m. masseter superficialis (e.g., interatheriids) (Sinclair 1909a; Croft et al. 2004; Reguero and Cerdeño 2005; Reguero and Prevosti 2010; Cassini 2011; Billet 2011; Croft 2016; Sosa and García López 2018; Ercoli et al. 2019). Particularly for interatheriids, several other remarkable differences in the snout, masticatory apparatus in general, and tooth morphology in particular, can be denoted, and, as stated by Cassini (2013; see also Sinclair 1909a), different paleobiological inferences to those mentioned above would apply.

Conjointly to a wide zygomatic region, pachyrukhines possess mediolaterally compressed rostra, as in many small herbivore mammals, particularly in sciuromorphous rodents (in which the anterior masseter bundles require a large accommodation space on the rostrum; Wahlert 1985; Frahnert 1999). A narrow snout limits the size and amount of food intake, and is typically related to high selective feeding of specific plants or plant parts, as opposed to bulk feeding. The latter is typical of large grazing ungulates, in which large bites on relatively short grasses are necessary to maintain similar rates of intake of this nutritionally low value food (Janis and Ehrhardt 1988; Bargo et al. 2006; see below). A similar conclusion was achieved for Santacrucian typotherians (Cassini et al. 2012), as well as for mesotheriids (Shockey et al. 2007; Ercoli and Armella, in prep.), whereby relatively high selective feeding strategies seem to have been typical for typotherians.

In summary, many features of the masticatory apparatus of the studied pachyrukhines, including muscles, rostrum, teeth, and articular configuration, support the possibility of selective feeding and strong gnawing, accompanied by a strong component of crushing, and secondarily grinding, during chewing. These morpho-functional features are associated with strong or hard-food item consumption, such as nuts, tubers, stems, and roots. Although the consumption of abrasive particles is supported by some dental features, such as the hypsodonty/euhypsodonty (see also Reguero et al. 2010; Madden 2015; Filippo et al. 2020), and the consumption of some proportion of grasses should not be discarded (especially for *Tremacyllus*; see above), the masticatory apparatus of these pachyrukhines does not seem to be specialized to grass eating, and other reasons can be postulated for this, e.g., grit consumption related to fossorial habits or feeding close to the ground (e.g., Vieytes et al. 2007; Townsend and Croft 2008; Reguero et al. 2010, 2015; Cassini et al. 2011; Strömberg et al. 2013; see below). In contraposition to the grass-eater interpretation that prevailed in recent contributions on pachyrukhines (Reguero et al. 2007; Cassini 2011; Cassini et al. 2011; Seoane et al. 2017; but see Cassini et al. 2012; Cassini 2013; Reguero et al. 2015); Kraglievich (1926), in his pioneer contribution on the anatomy and paleobiology of *Paedotherium*, suggested that the incisive morphology of this taxon indicates an apparent ability of gnawing on bark, stems, and other hard-food items, without discarding the consumption of grasses. Our analyses appear to substantiate these early inferences by Kraglievich.

Is important to denote that, as stated by Zelditch et al. (2020) for sciurids, an anatomical specialization toward strong bitting and hard-food items consumption does not necessarily imply a limitation in the ability to consume softer items. In this way, sciuromorphy and associated features can be understood as related to a morphological specialization that could eventually increase instead of limit the niche breadth (Zelditch et al. 2020), and this fact could be a relevant factor to understand the long evolutionary history together with a relatively conservative masticatory apparatus in pachyrukhines. The acquisition of the specialized masticatory apparatus of pachyrukhines can be tracked as far as the earliest Oligocene representatives of the subfamily, and could be related to the consumption of hard food items, such as hard nuts and fruits, which became abundant in forested environments since the Eocene-Oligocene transition, as was also proposed for sciuromorph rodents (Thorington and Darrow 1996; Collinson and Hooker 2000; Cox et al. 2012; Ercoli et al. 2019). During the subsequent evolutionary history of pachyrukhines, the masticatory apparatus, adapted for strong biting, could have served other biological roles. Climatic changes that occurred since the late Oligocene, and the development of relatively more arid and more open landscapes since the middle-late Miocene (Zachos et al. 2001; Ortiz-Jaureguizar and Cladera 2006; Barreda and Palazzesi 2007; Strömberg 2011; Seoane et al. 2017), and particularly during the late Miocene-Pliocene of the central Pampean region of Argentina (Domingo et al. 2020), resulted in the availability of new ecological niches, such as grasslands, shrublands, and xerophytic woodlands, and the eventual acquisition of subterranean habits to avoid great temperature fluctuations and predation (Nevo 1999; Kinlaw 1999; Ebensperger and Blumstein 2006; Hayes et al. 2007; Upham and Patterson 2015; Álvarez et al. 2020).

Fossorial habits, and particularly scratch-digging, have already been proposed for some Neogene pachyrukhines (*Pachyrukhos moyani*, *Paedotherium bonaerense*, and secondarily *P. typicum*) through the analysis of postcrania (Elissamburu 2004, 2007; Elissamburu et al. 2011; Cassini et al. 2012; see also Croft 2016). Additionally, generalist or digging habits have been proposed as early adaptations for notoungulates, enhanced in various typotherian clades (Shockey et al. 2007; Croft and Anderson 2008; Lorente et al. 2019; see also Elissamburu 2007; Croft 2016). The combination of strong incisor biting and a dentition resistant to abrasive particles could be related to grit consumption, frequently related to digging habits (Vieytes et al. 2007; Cassini et al. 2011; Strömberg et al. 2013; Álvarez et al. 2015; Renvoisé and Montuire 2015). In this way, beyond the absence of specialized tooth-digging morphologies in pachyrukhines, the eventual involvement of the incisors when confronting harder objects during digging cannot be fully discarded, as also occurs in many scratch-digging extant mammals (Fernández 1949; Becerra et al. 2011, 2014; Gomes Rodrigues et al. 2016; Álvarez et al. 2020). Evenmore, digging is required for gaining access to some special hard foot items, such as roots and tubers, and the use of both forelimbs and teeth would be advantageous (Verzi 1994 and citations therein; Townsend and Croft 2008), as was also considered for mesotheriids (Shockey et al. 2007; Croft 2016). The scarcity of soft food items during the toughest seasons in many middle to high latitude environments may force animals to feed on harder resources, such as stems, roots, and tubers, that are vital for survival. This dietary strategy would represent a suitable way to survive during the toughest seasons, alternatively to other ecological strategies, such as migration or hibernation. An extant example is the sciuromorphous fossorial medium-sized *Cynomys*, which inhabit middle to high latitude open environments of North America. Prairie dogs shift from a dicot and grass, leaf spring-summer diet to a diet mainly composed by harder and basal parts of grasses, remaining seeds, prickly-pear cactus, shrubs stems and twigs, and roots during fall-winter, mainly accessed by scratch-digging (Fagerstone et al. 1981; Clippinger 1989). Considering the interspecific variation within this subfamily, a good example of the scenario mentioned above could be the case of *P. bonaerense*, the last known pachyrukhine and one of the most specialized fossorial taxa (Cerdeño and Bond 1998; Elissamburu 2004, 2007; Elissamburu et al. 2011; Ercoli et al. 2018). Previous paleoenvironmental reconstructions indicate that this species, and other pachyruhkines of central Argentina inhabited relatively open and, in some cases, semi-arid environments (Seoane et al. 2017; Domingo et al. 2020), coexisted with caviomorph rodents, such as several fossorial ones, including ctenomyids (Elissamburu et al. 2011; Verzi et al. 2016). The large biting forces interpreted for *P. bonaerense*, suggested by the large incisors and the anterior location of well-developed masticatory muscles, support the eventual contribution of teeth during scratch-digging activities. *Paedotherium bonaerense* coexisted with *P. typicum*, a taxon with a less modified masticatory apparatus and considered as less specialized to fossorial habits by its postcranial anatomy. In fact, *P. typicum* is less frequent in paleoburrows than *P. bonaerense*, substantiating the paleoecological differentiation of these coexisting pachyrukhines (Elissamburu et al. 2011).

Regarding feeding habits, *P. typicum* (and probably *P. borrelloi*), *Tremacyllus*, and *P. minor*, and *P. bonaerense* can be viewed as a gradient from lesser to higher degree of curvature of the occlusal profile of incisors (especially clear in the upper series; Fig. 3, see also Ercoli et al. 2018: fig. 9), and consequently, a progressively deeper than wider incisor occlusal surface. Beyond the distinct incisor morphologies from extant models, these differences could be interpreted in a similar way to that proposed for rodents (e.g., Agrawal 1967; Croft et al. 2011; Becerra et al. 2012). They should represent different stages in a gradient of functions from cropping action on leaves of monocots or dicots, to digging or stronger gnawing action on fruits or seeds, respectively. Nevertheless, some extant exceptions (e.g., slender incisors and grass-eating habits in *Cavia*; Croft et al. 2011) call for more cautious interpretations in the Pachyrukhinae.

As was mentioned above, a well-supported relationship between rostrum shape and forage selection abilities is known for ungulates (e.g., Janis and Ehrhardt 1988; Solounias and Moelleken 1993; Tennant and MacLeod 2014) and other mammals (e.g., Bargo et al. 2006), in which a broad snout is related to reduced forage selection abilities and bulk feeding. Nevertheless, the benefits of bulk feeding strategies in large mammals, i.e., the presence of ample surfaces of relatively short and nutritionally poor dietary items are not clearly present for small herbivores (Demment and van Soest 1985), in which a single grass leaf could represent a relatively large quantity of food. In consequence, small mammals would not need to confront a wide area with a wide snout to eat grasses. Additionaly, it is worth noting that the relatively high metabolic rate of small-sized herbivores compels a more selective, diverse, and enriched diet, than one based exclusively on grasses (e.g., Clauss et al. 2013). Following that, even the more specialized grass-eating small mammals include other items in their diets (e.g., *Cavia, Lepus*; Bernal 2016; Johnston et al. 2019), an additional reason not to expect wide snouts. On the other hand, considering that absolute bite force is directly related to size, hard-food item comsuption could be a major challenge for small-sized species. Thus, hardness and form of each unit of food item could be more relevant for small mammals. Considering that, the relatively small size of the incisors, in addition to the acute rostrum of *Tremacyllus* and *P. minor*, seem more suitable for high selection abilities during food intake and small or weaker biting, probably related to the consumption of smaller or relatively softer food items than the other pachyrukhines. In these two taxa, the lack of the advancement of the anterior part of the m. masseter lateralis recorded in *P. bonaerense* also supports this statement. Additionally, the rostral morphology of these Neogene pachyrukhines could be related to less usefulness for eventual collaborations during digging activities.

Soft Tissues of the Oronasal Region

Beyond the spatial limitations in the rostrum that impose sciuromorphy, in which the development of the zygomatic plate limits the lateral expansion of the infraorbital foramen (Vianey-Liaud 1985; Korth 1994; Thorington et al. 2012), the latter is very large in pachyrukhines (Fig. 7), similar to the condition found in some rodents, such as *Cynomys*. A relatively large infraorbital foramen also occurs in other typotherioids with expanded zygomatic plates, such as mesotheriids (except by *Mesotherium*; see measures of Townsend and Croft 2010: Table 3, considering the specimen reassignments of Armella and Ercoli 2018) and hegetotheriines (e.g., Croft and Anaya 2006; M.D.E pers. obs.). Following Muchlinski (2010), the size of this foramen is directly associated with the development of the infraorbital nerve, which passes through it. In relation with this, the great development of this foramen in these taxa is probably related to a high development of vibrissae and other mechanoreceptors of the maxillary region (Muchlinski 2010), useful for spatial tasks and object recognition (Brecht et al. 1997; Muchlinski 2010). Different configurations of mesotheriid snout morphology and their paleobiological inferences are under study (Ercoli and Armella in prep.).

Apart from caviomorph rodents, in which the infraorbital foramen is hypertrophied and serves as passage of the m. masseter medialis pars infraorbitalis (as, to a lesser degree, in myomorphs), the dorsal position of the infraorbital foramen of pachyrukhines (similarly to, or even more dorsally located than in other typotherians; Croft et al. 2003: fig. 1) differs from the ventral location of the remaining compared extant taxa. The same condition was noted by Sosa and García López (2018) for extant vombatid marsupials. The dorsal location of the infraorbital foramen in pachyrukhines and vombatids allows the accommodation of the large roots of the euhypsodont cheek teeth, and a similar relationship would influence the location of the infraorbital foramen in other South American native ungulates. In contrast, other extant hypsodont or euhypsodont lineages (e.g., castorid, heteromyid, and geomyid sciuromorphous rodents; Howell 1932; Korth 1994; Madden 2015) circumvented this situation by an advanced position of the foramen, in front of the level of the first cheek tooth and/or a ventral location of the alveoli.

Rodents are characterized by the presence of infoldings of the lips just behind the incisors, the inflexa pellita. These infoldings allow a major separation of the gnawing function, protecting the gingiva (Landry 1970:362; Ade 1999; Frahnert 1999:232; Banke et al. 2001; see also Howell 1932). In almost all mammals the incisive foramina (or at least, their anterior margins) are located immediately behind the incisors (Fig. 10a), in relation to the openings of the nasopalatine ducts and the incisive papilla (or palatine papilla; e.g., Broman 1919) connected with them, functionally related to the reception of chemical signals and odor when the vomeronasal organ is present (Quay 1954; Hart et al. 1988; Frahnert 1999; Evans and de Lahunta 2013). Nevertheless, in rodents, in relation to the large development of an inflexa pellita, the nasopalatine ducts and the anterior margin of the incisive foramina are positioned more posteriorly (being either elongated or not), at the middle or at the posterior region of the diastema, connected with the papilla just behind the infoldings of the lips (Fig. 10b; Table 1; Quay 1954; Landry 1970; Novacek 1985; Ade 1999; Frahnert 1999). In the case of lagomorphs, the inflexa pellita is also well developed but to a lesser degree than rodents, so the connection between the incisor region and the oral cavity persists, and the nasopalatine ducts open behind the incisors, as in other mammals (Ike 1990; Frahnert 1999). In lagomorphs, the incisive foramina are slightly enlarged in a posterior direction (Wible 2007; see also Table 1), displacing the posterior extreme of the incisive foramina just a little away from the area of action of the anterior teeth. The implications of the posterior extension of the incisive foramina is not clear (but see Quay 1954; Agrawal 1967:308), but could be eventually related to the necessity of a connection with the oral cavity of soft tissues along the posterior margin of the incisive foramina. This is the case of the major palatine arteries (Bugge 1968; Besoluk et al. 2006; Evans and De Lahunta 2013; see minor palatine artery in Gregg and Avery 1971) and associated nerves that cross and supply the palate, emerging from the palatine foramina and entering the incisive ones through its posterior region, and then reaching the nasal region and rostral septal branch (Fig. 10a; Bugge 1968; Evans and de Lahunta 2013:454–455). Accordingly, the posterior extensions of the incisive foramina in lagomorphs could be related to preventing the major palatine arteries from entering the gnawing area, as they leave the hard palatal region at a sector protected by the inflexa pellita. In consequence, there is a partial separation of the transit area of these main hard palatal arteries from the area of gnawing, and differing from rodents by maintaining an anterior exit of the nasopalatine ducts. In rodents the separation of the transit of the major palatine arteries and gnawing area is complete because the former is located behind a full closure of the inflexa pellita, in relation to the ability of tooth-digging or processing harder objects compared to lagomorphs (Fig. 10a, b; Frahnert 1999:241).

The morphology of the incisive foramina of pachyrukhines resembles the condition present in lagomorphs and rodents (Fig. 10; Table 1). The remarkable posterior extension of the caudal end of the incisive foramina, reaching the posterior half of the diastema as typical in rodents, differs from the condition typically observed in extant taxa and almost all other typotherians (e.g., Patterson 1934; Croft and Anaya 2006; Billet et al. 2009a; but see below). This could suggest the presence of similar structural constraints between soft tissues to those encountered in Glires, suggesting a rostral

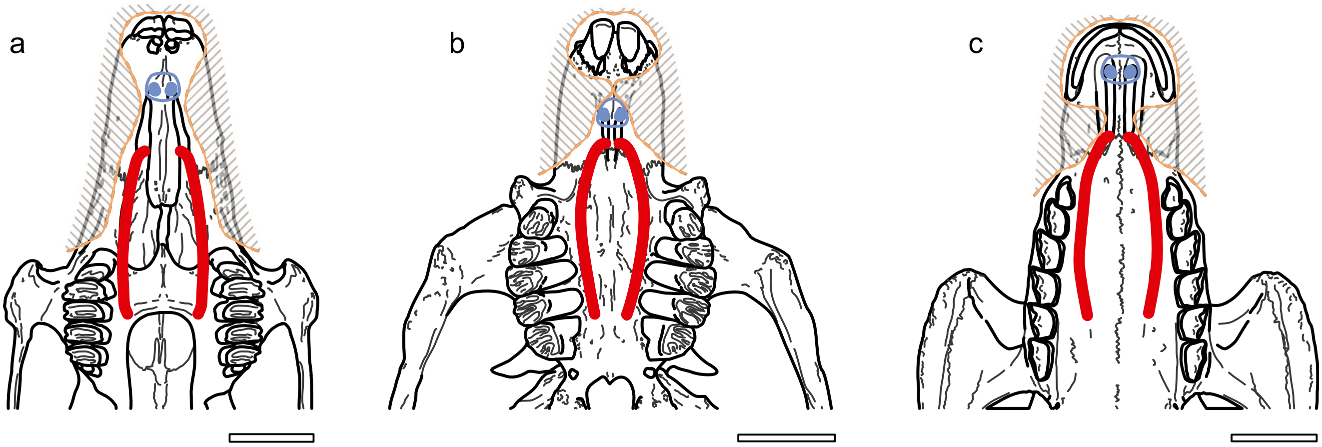


Fig. 10 Soft tissues of the palatal and snout regions that illustrate different configurations of the infoldings of the lips, incisive papillae, and palatine arteries in rodent and rodent-like taxa. *Lepus capensis* (**a**), *Cynomys ludovicianus* (**b**), and *Paedotherium bonaerense*. In extant taxa, the outlines are based on the studies of Broman (1919), Bugge (1968), Ike (1990), and Ade (1999) (see also Evans and De Lahunta 2013). See discussion for inferences for the fossil taxon. Infoldings of the lips (inflexa pellita) are indicated by dashed brown and orange lines and stripped fills; incisive papilla and associated opening of the nasolacrimal ducts are in thin solid blue lines (in the anterior region of the incisive foramina), and palatine arteries in thick solid red lines (connecting the palatine foramina with the posterior regions of the incisive ones). Scale bars = 10 mm

morphology compatible with the presence of infolding of the lips developed to some degree. Interestingly, in mesotheriines, the posterior extreme of the incisive foramina, reaching a posterior position, in tandem with extensive diastemata could lead to similar interpretations (Ercoli and Armella in prep.). On the other hand, in pachyrukhines, the incisive foramina, reaching the region of the incisors, are similar to the condition observed in most mammals including lagomorphs, but different from rodents. This may indicate the presence of an incisive papilla positioned just behind the incisors, instead of just behind the infolding of the lips, as in rodents (Fig. 10; Broman 1919). Finally, the presence of large post-incisive depressions in *Tremacyllus* (Figs. 3l; 6d) may suggest differences in the soft tissues of the anterior palatal region compared to *Paedotherium*, although their morpho-functional interpretation remains obscure.

Dietary Habits and Paleoecological Characterization of the Species of Paedotherium and Tremacyllus

All pachyrukhines share a relatively important development of the mechanoreceptors of the snout (inferred through the development of the transit region of the infraorbital nerve) revealing the importance of the spatial detection of objects prior to gripping or during gnawing. The masticatory apparatus of the studied pachyrukhines also suggests a decoupling in the moments and type of movements executed during the activities of incisors and cheek teeth, respectively. Furthermore, there is anatomical evidence, such as the configuration of teeth and diastemata and the location of the palatal foramina (and in consequence, of the soft tissue transit zones related to them), that suggest a spatial and protective barrier conformed by infoldings of the lips, between the incisive region, for initial food processing, and the oral cavity. This morphology reinforces the inferences about increased gnawing capacities and ecological convergence with rodents and rodent-like extant taxa. The muscular reconstruction along with tooth morphology indicate the ability of hard-food item comsuption, and the relative importance of crushing over grinding, expressed in different degrees in the different late Neogene studied pachyrukhines. Although the euhypsodont dentition would enable life habits linked to the ingestion of biotic and abiotic abrasive items (e.g., grass consumption or interaction with dusty substrates or environments by gnawing, eventual tooth-digging, or consumption of subterranean food items, among others; see above), from our morpho-functional analysis (see also Ercoli et al. 2019) it follows that grass consumption was not the main ecological factor that conditioned the evolution of the masticatory apparatus of the pachyrukhines. Moreover, hegetotheriids (McCoy and Norris 2012; Ercoli et al. 2019), and to some degree some other typotherioids (e.g., Shockey et al. 2007; see above), seem to be linked to dietary habits related to the differential acquisition and processing of diverse dietary hard-food items, but more studies are needed. Beyond that, some of the analyzed Neogene pachyrukhines present anatomical traits linked to improvement at some degree of grinding abilities, but without getting closer to strict grazing morphologies.

Tremacyllus* and *P. minor Both taxa are known as the smallest studied pachyrukhines, coexisting along the late Miocene (and with *P. borrelloi* for the some specific localities of central Argentina; see below), with *Tremacyllus* outlasting by reaching the Pliocene (Cerdeño and Bond 1998;

Elissamburu 2004; Ercoli et al. 2018). In *Tremacyllus*, a set of features, such as the alignment and thickening of the enamel layers, relative flattening of the premolars, and the lesser degree of sciuromorphy, suggests a masticatory apparatus allowing a relatively greater grinding action than in the other studied pachyrukhines, and potentially a more relevant participation of grasses or dicot leaves in its diet. The narrow rostral shape of *Tremacyllus* indicates the highest forage selection abilities, and together with a not particularly advanced position of masseter attachments and the weaker biting efforts, they suggest the consumption of relatively small, specific plant parts and relatively soft food items, compared to the other pachyrukhines. In many of these ecomorphological features, *P. minor* is most similar to *Tremacyllus*, so niche partitioning is difficult to understand. Nevertheless, *P. minor*, in addition to features linked to hearing (see accompanying contribution Ercoli et al. in prep.), presents a less modified premolar configuration and relatively larger snout, which could contribute to some microhabitat partitioning.

Paedotherium bonaerense This species is the largest of the studied pachyrukhines, but highly overlapping in size with *P. typicum* (Ercoli et al. 2018). *Paedotherium bonaerense* coexisted with *P. typicum* and *Tremacyllus* throughout most of the Pliocene (Cerdeño and Bond 1998; Elissamburu 2004; Deschamps 2005). Although none of the studied pachyrukhines presents the set of traits expected for tooth-digging specializations, scratch-digging abilities have been proposed for *P. bonaerense* (Elissamburu 2004, 2007; Elissamburu et al. 2011). As in living scratch-digging mammals, the eventual assistance of incisors when confronting hard substrates would be expected. Moreover, in comparison with other pachyrukhines, *P. bonaerense* appears to have increased abilities of processing hard and brittle or turgid food, presenting the highest degree of sciuromorphy, the largest development of masticatory muscles, and the molariform morphology most suitable for crushing. These abilities, together with the enhanced fossorial capacities, in contrast to the cursorial adaptations of *P. typicum* (Elissamburu 2004), and the large size, in comparison to the much smaller *Tremacyllus*, could very likely represent the main segregating ecological factors with these species.

Paedotherium typicum* and *P. borrelloi *Paedotherium typicum* and probably *P. borrelloi* (species known by fragmentary remains) present intermediate morphologies of the masticatory apparatus region and associated snout structures and dietary habits, between *Tremacyllus* and *P. bonaerense*, for almost all features. Nevertheless, *P. typicum* departs from the other pachyrukhines by having a less curved incisive arch and from *P. bonaerense* by having a shorter rostrum. Although differences are subtle, and there are exceptions to the ecomorphological patterns related to this feature (e.g., Croft et al. 2011), the morphology of *P. typicum* could be related to better cropping action or relatively poorer selective capacities during feeding. Although the remains of *P. borrelloi* are too fragmentary for a more complete view of its paleoecology, it seems to present intermediate ecomorphological features between *P. typicum* and *P. bonaerense*, but departs from both by having the smallest size. Beyond that, the fossil record indicates that *P. borrelloi* was restricted to central Argentina and was older than the latter taxa, but coexisted with the similar smaller-sized *Tremacyllus* and *P. minor* (Zetti 1972a; Ercoli et al. 2018). In this case, *P. borrelloi* would have differentiated by a more specialized crushing dentition, but the fragmentary remains preclude further comparisons.

Final Comments

Considering the limitations involved in the reconstruction of soft tissues of lineages with a long evolutionary history and without living representatives, such as notoungulates, relevant information about sensorial capabilities related to the development of snout mechanoreceptors, and food item preferences, selection, acquisition, and processing in the incisive and buccal regions could be partially reconstructed for the pachyrukhines *Paedotherium* and *Tremacyllus*. Moreover, through the analysis of the anatomical variability among pachyrukhines, some paleobiological differences were proposed, providing clues about the potential partitioning of ecological niches between these fossil species.

Interestingly, some dental traits traditionally considered in taxonomic studies can be best understood when further linked to functional and dietary specializations. Indeed, these ecological drivers have been proposed as tightly related to the morphological evolution of other typotherians (e.g., Croft et al. 2003). For example, Madden (2015) denoted that imbrication results in an increasing of the number of shearing blades. The imbricated and lingually curved premolar series, for which *Tremacyllus* represents the extreme case within pachyrukhines, increase the number of enamel layers oriented perpendicular to the mastication movements, a feature that improves the grinding component during chewing of grasses and leaves. Conversely, the "molarization" of premolars, for which *P. bonaerense* represents the extreme case, multiply the number of teeth with molar-like morphologies, which are interpreted as improving the crushing component when processing hard or turgid fruits. Considering that these and other dental features independently developed in different clades during notoungulate evolutionary history (e.g., see Croft and Weinstein 2008; Billet et al. 2009a; Reguero and Prevosti 2010), the detection and interpretation of morpho-functional complexes proposed here also could be relevant in order to evaluate the functional significance and independence of characters in future phylogenetic studies.

Apparently different to interatheriids, the masticatory apparatus of typotherioids in general, and of derived lineages such as the late Neogene pachyrukhines in particular, seems to have been modified to allow the consumption of hard-food items. Beyond anatomical variability, typotherioid representatives have not turned much away from this common denominator (e.g., Kraglievich 1926; McCoy and Norris 2012; Ercoli et al. 2019). In this way, they would be adapted for processing diverse hard items potentially available in the different environments in which they lived, allowing them to expand or differentiate their ecological niches compared to other herbivores (Zelditch et al. 2020). For pachyrukhines, the sciuromorph masseteric configuration and associated modifications of the masticatory muscles, together with strong incisors and crushing molariforms, are the main features that support this inference. It is worth noting that, in the case of other typotherians, such as hegetotheriines (e.g., *Hegetotherium*) and mesotheriines, the masticatory apparatus shares some of these features and was also related to intense incisive biting forces. Regarding *Hegetotherium*, its masticatory configuration was interpreted as specifically related to woodpecking habits (McCoy and Norris 2012). This different interpretation would be related to some traits that distinguish hegetotheriines from pachyrukhines, such as a short snout, prognathous upper incisors, and exaggerated klinorhynchy (McCoy and Norris 2012). However, more studies of hegetotheriines in particular and Hegetotheriidae in general, are needed. Moreover, a differential paleobiological characterization for hegetotheriines agrees with the absence or the relatively poor development of some rodent- and gnawing-like traits, which are present in pachyrukhines (e.g., reduction of the dental formula and large anatomical diastemata, sciuromorphy). The present and other recent studies are contributing to the identification of morphological differences with paleobiological implications between different typotherian groups, deepening beyond the general characterization of the clade as rodent-like mammals, and proposing different dietary habits, including the differential acquisition and processing of diverse dietary hard-food items.

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Author Contributions MDE conceived the study; MDE and AA acquired all the images used and made the anatomical descriptions; MDE and AA wrote the manuscript. MDE and SRM built the figures. DY and AMC revised it critically. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Appendix 1 List of studied fossil and extant specimens. Preserved main regions are indicated in the case of fossil specimens: C = cranium, M = mandible

Fossil specimens

Paedotherium bonaerense

MACN A 1251–52 (C, M), MACN A 7214 (C), MACN Pv 7520 (M), MACN Pv 18,098–100 (C); MLP 99-X-2-1 (C, M); IDGYM s/n (C, M); MMP 158-S (C), 1655-M (C); Cerdeño and Bond (1998) (C, M)

P. typicum

MACN Pv 5751 (M), MACN Pv 6436 (C, M), MACN Pv 10,513 (M), MLP 12–1782 (C, M), MLP 52-IX-28-14 (C), MMP 698-S (C, M), MMP 1008-M (C, M), PVL 3386 (C), Kraglievich (1926) (C, M), Cerdeño and Bond (1998) (C, M)

P. borrelloi

MLP 57-X-10-21 (C, M), 57-X-10-62 (M), 57-X-10-88 (C), 57-X-10-142 (M)

P. minor

MLP 26-IV-10-37 (M), MLP 29-IX-1-116 (C), MLP 29-IX-2-20 (C, M), MLP 29-IX-2-102 (M), MLP 29-IX-2-103 (M), MLP 29-IX-2-157 (C), MLP 55-IV-28-30 (C, M), MMP 464-M (M)

P. cf. *P. minor*

MLP 55-IV-28-82 (C)

Tremacyllus spp.

FMNH P 14456 (C, M), FMNH P 14465 (C); MACN Pv 2434 (C, M), MACN Pv 2913 (C), MACN PV 8157 (C, M), MACN Pv 7207 (M), MLP 95-III-31-15 (C, M)

Extant specimens

Cavia aperea

MACN Ma 27.7, MMP ND 83

Chinchilla chinchilla

MACN Ma 45.11, MACN Ma 16267

Ctenomys frater

CML 7235, MACN Ma 27.122

Cynomys ludovicianus

FMNH 14964, FMNH 58999

Heterohyrax brucei

FMNH 18842, FMNH 104600

Lepus capensis

FMNH 42407; MACN Ma 26084

Ratufa affinis

FMNH 68746, FMNH 68747

Tragulus kanchil

FMNH 68768, FMNH 68778

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