ORIGINAL PAPER

Tracing the Paleobiology of *Paedotherium* and *Tremacyllus* (Pachyrukhinae, Notoungulata), the Latest Sciuromorph South American Native Ungulates – Part II: Orbital, Auditory, and Occipito-Cervical Regions

Marcos D. Ercoli[1,2] · Alicia Álvarez[1,2] · Dionisios Youlatos[3] · S. Rocío Moyano[1,4] · Adriana M. Candela[5]

Abstract

The caudal cranium and occipito-cervical region, although usually overlooked, are informative about the paleobiology of fossil mammals, allowing inquiry into vision and hearing abilities, as well as head and neck postures. Particularly for Pachyrukhinae, some related features remain unexplored. In this contribution, 22 specimens of *Paedotherium* and *Tremacyllus* were analyzed in a mainly qualitative and comparative framework. Pachyrukhines are characterized by having large orbits and hearing cavities, moderate to short necks with generalized morphologies, and S-shape postures. These features allow rejecting some types of specialized digging habits, and support the preference of open or low-humidity environments. *Paedotherium typicum* is distinguished by the presence of laterally oriented eyes, marked vaulted cranium and predominant short extensor and stabilizing neck muscles, and cervico-occipital-hyoid configurations suitable for ventro-flexed resting posture. These features indicate accentuated frontation and panoramic-vision, upward head postures enhancing substrate perception, and the resistance of impacts during leaping-cursorial locomotion. Conversely, *P. bonaerense*, and to lesser degree *Tremacyllus* spp., show less frontation and probably adopted more horizontal head postures. More particularly, stronger ventral and lateral neck and head flexors and extrinsic arm musculature are reconstructed for *P. bonaerense*, compatible with generalist or scratch-digging habits. Its smaller auditory cavities and stronger ear musculature, compared to the contemporary *P. typicum* and especially *Tremacyllus* spp., would indicate larger ears and microhabitat segregation. The integrative analysis proposed here and in the accompanying contribution aims to shed light on convergences with extant models, paleobiology, niche partitioning, and external appearance of the latest rodent-like ungulates.

Keywords Auditory cavities · Cranio-cervical anatomy · Functional morphology · Orbits · Pachyrukhinae · Paleobiology

Introduction

Pachyrukhinae (Hegetotheriidae; Typotheria; Notoungulata, early Oligocene-late Pliocene; Zetti 1972a, b; Reguero 1993; Cerdeño and Bond 1998; Reguero et al. 2007; Reguero and Prevosti 2010) is one of the latest South American native ungulate clades, represented during the late Miocene-late Pliocene by the genera *Paedotherium* and *Tremacyllus*

✉ Marcos D. Ercoli
  marcosdarioercoli@hotmail.com

1 Instituto de Ecorregiones Andinas, Universidad Nacional de Jujuy – CONICET, Av. Bolivia 1239, 4600 San Salvador de Jujuy, Jujuy, Argentina

2 Instituto de Geología y Minería, Universidad Nacional de Jujuy, Av. Bolivia 1661, 4600 San Salvador de Jujuy, Jujuy, Argentina

3 Department of Zoology, Aristotle University of Thessaloniki, School of Biology, GR-54124 Thessaloniki, Greece

4 Centro de Estudios Territoriales Ambientales y Sociales (CETAS), Facultad de Ciencias Agrarias, Universidad Nacional de Jujuy, Alberdi 47, 4600 San Salvador de Jujuy, Jujuy, Argentina

5 CONICET, División de Paleontología de Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, 1900 La Plata, Buenos Aires, Argentina

(Cerdeño and Bond 1998; Giannini and García-López 2014; see also the accompanying contribution Ercoli et al. 2020).

Although the paleobiology of pachyrukhines has been poorly studied (Zetti 1972a; Gomes Rodrigues et al. 2018), there are various contributions that have identified several convergences with lagomorphs and rodents, mainly related to the rodent-like masticatory apparatus and overall small size (Kraglievich 1926; Cifelli 1985; Reguero and Prevosti 2010; Reguero et al. 2010; Croft 2016; Sosa and García López 2018; Gomes Rodrigues et al. 2018; Ercoli et al. 2019; see also the accompanying contribution Ercoli et al. 2020). On the other hand, pachyrukhine similarities to these extant groups can also be traced to other, less studied, anatomical regions, such as parts of the skull and postcranium (Sinclair 1909a, b; Kraglievich 1926; Elissamburu 2004, 2007; Seckel and Janis 2008). Examples of these convergences between pachyrukhines and extant rodents and rodent-like mammals are the enlarged orbits and auditory cavities, rostral bones with rarefactions, presence of intracranial joints and persistent fontanelles in the cranial vault, enlarged scapular metacromion processes, and distal fusion between tibia and fibula, among others (Sinclair 1909a, b; Kraglievich 1926; Elissamburu 2004; Seckel and Janis 2008; Billet et al. 2009; MacPhee 2014). With few exceptionally detailed studies (Elissamburu 2004, 2007 for main appendicular elements; and MacPhee 2014 for the posterior region of the cranium), the latter anatomical regions remain mainly unexplored, resulting in a major barrier for the elucidation of the extensive coexistence and niche partitioning of pachyrukhines.

The above mentioned studies suggest that pachyrukhines lived typically, but not always (Reguero et al. 2015), in open semi-arid and temperate environments (Kraglievich 1926; Cerdeño and Bond 1998; Bond 1999; Croft and Anaya 2006; Candela et al. 2007; Seoane et al. 2017; Domingo et al. 2020). Indeed, regarding locomotion and fossorial abilities, many species have been related to rapid, generalist to cursorial or bounding gaits, and the use of burrows (Cerdeño and Bond 1998; Bond 1999; Elissamburu 2004, 2007; Elissamburu et al. 2011; MacPhee 2014; Muñoz 2017; Lorente et al. 2019), which fit well with the environmental inferences. Moreover, saltatorial or cursorial locomotion has been inferred for *Pachyrukhos* (an early-middle Miocene pachyrukhine), cursoriality for *Paedotherium typicum*, and digging habits for *P. bonaerense* (Kraglievich 1926; Reguero et al. 2007; Elissamburu 2004, 2007; Muñoz 2017; Ercoli et al. 2018 and references therein).

Beyond several contributions dealing with the dietary habits of pachyrukhines, functional implications of other cranial structures, besides the masticatory apparatus, have been generally inadequately studied, with the exception of short, scattered, relevant comments in the literature (e.g., Cerdeño and Bond 1998; Bond 1999; Reguero et al. 2007, 2010, 2015; MacPhee 2014; Gomes Rodrigues et al. 2018). Finally, the

functional anatomy of the occipito-cervical region has never been studied before. Previous authors have used the orientation of the orbits (Heesy 2004; Cox 2008; Hautier et al. 2012; Kraatz et al. 2015) and the morphology of the occipito-cervical configuration in rodents and rodent-like mammals (Howell 1932; Kraatz et al. 2015; Álvarez and Ercoli 2017) to infer aspects of head and neck posture and perception and interaction with the substrate and environment. These inferences indirectly contribute to the understanding of the locomotory habits and substrate preferences of extinct taxa.

The main goal of the present study is the morpho-functional analysis of the orbits, auditory cavities, occipito-cervical region and associated structures of the pachyrukhine genera *Paedotherium* and *Tremacyllus,* assessed through qualitative comparative analyses, providing inferences on different aspect of their paleobiology, such as vision and hearing, as well as head and neck postures related to locomotor modes and substrate preferences. Considering the current knowledge, here we are presenting a reassessment of the functional implications of diverse cranial structures, and the first morpho-functional analysis of the occipito-cervical region of pachyrukhines, in a comparative framework that includes diverse groups of extant model species encompassing different life habits and clades. This study also attempts to contribute to previous paleobiological inferences on the locomotor and fossorial abilities of these taxa, mainly supported by the appendicular analyses of Elissamburu (2004) and the study of the posterior cranial region by MacPhee (2014). In consequence, the common objective of the present study, together with the accompanying one (Ercoli et al. 2020), is to perform a detailed morphological description of several ecomorphologically relevant features of the skull and neck of the pachyrukhines, shedding light on the paleoecology, niche partitioning, and the external appearance that the latest pachyrukhines would have had.

Materials and Methods

Materials included were 22 fossil specimens belonging to the Pachyrukhinae *Paedotherium typicum*, *P. bonaerense*, *P. minor*, and *Tremacyllus* spp. (Appendix 1). We focus on the description and morpho-functional analysis of the orbits, posterior part of the cranium, and cervical region. Available descriptions from the relevant literature were also considered (Kraglievich 1926; Cerdeño and Bond 1998; MacPhee 2014; Ercoli et al. 2018, 2019).

For two taxa, *P. typicum* and *P. bonaerense*, the set of specimens analyzed allowed the description of all the concerned anatomical regions, having one or more specimens of each region preserved. For *P. minor*, there are no specimens preserving the orbits, basicranium, or the cervical vertebrae. In consequence, the descriptions mainly focused on the auditory

region and the occipital plane, the latter described for a single *P.* cf. *P. minor* specimen. *Tremacyllus* spp. preserved almost all the concerned features of the cranium, but only badly preserved remains were analyzed for the cervical region, limiting the comparisons and inferences in this region. The revised specimens of *P. borrelloi* do not preserve these structures, so the species was not included in the present study (Online Resource 1).

A diverse group of small-sized herbivorous extant mammals, of diverse clades and habits, was considered (Appendix 1) as a comparative sample to represent different diets, locomotor styles, and substrate use. This sample included grass-eaters, mixed-feeders, browsers, as well as arboreal, fossorial, generalist, and cursorial species. In addition to the comparative sample considered for the accompanying contribution (Ercoli et al. 2020), *Dolichotis salinicola* was included here in order to add a leaping and cursorial rodent model of similar size to pachyrukhines (~2 kg; Mares et al. 1989; Rocha-Barbosa et al. 2015; Candela et al. 2017 and references therein). Dolichotines have been previously considered as an interesting comparative model regarding size and locomotion in other studies of pachyrukhines (e.g., Bond 1999; Elissamburu 2004; Croft 2016). For details about the life habits of the species of our comparative sample see the Material and Methods section of the accompanying contribution (Ercoli et al. 2020).

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

The results section is organized by anatomical regions (Cranium: orbital region, and cranial vault, and basicranium and occipital plane; Cervical vertebrae: atlas and axis, C3 to C7 vertebrae). For each region, a detailed comparative description for each pachyrukhine species was performed, followed by comparisons with extant models for specific features. Different morphologies observed in extant models with distinct life habits were used for the functional interpretation of the osteological features encountered in the fossil species (e.g., Sargis 2001; Argot 2003). The anatomical terms used for the descriptions follow Cerdeño and Bond (1998), Reguero and Prevosti (2010), Evans and de Lahunta (2013), MacPhee (2014), Álvarez and Ercoli (2017), and Ercoli et al. (2019), and are illustrated in Fig. 1. Following Kraatz et al. (2015), the angle between the occipital and diastema planes

was measured in order to quantify facial tilting, considering its relation to life habits, and particularly locomotor modes.

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

Results

Cranium

Orbital Region, Auditory Region, and Cranial Vault

Among pachyrukhines, the orbits are large, posteriorly delimited by a well-defined, blunt, and laterally projected posterorbital process (Fig. 2a, b). This process is slightly larger, more rugous, and caudolaterally projected in *P. bonaerense* than in the other pachyrukhines. The location and orientation of the orbits is somewhat variable among the species of pachyrukhines, in relation to changes in the structures that limit and compound them. In *P. typicum*, the orbits are lateralized, the dorsal margin of the orbital region being convex and higher, and protruding at a higher degree than in *P. bonaerense*. Moreover, in *P. typicum*, the zygomatic arch portion that ventrally delimits the orbits is in a relatively low position (closer to the level of the alveoli of the molars in lateral view). In *P. bonaerense,* the size of the orbits, in relation to the cranium, is slightly smaller than in *P. typicum*, and they show a more elliptical contour, with the dorsal margin more flattened in lateral view (and more convex in the dorsal one). Furthermore, the zygomatic arches of *P. bonaerense* are also relatively dorsally located, farther away from the alveolar line compared to *P. typicum*. These features result in more dorsally oriented orbits for *P. bonaerense*. The morphology of the orbital region of *Tremacyllus* (for which only one specimen preserves complete orbits, MACN Pv 17547) presents shared traits with both *Paedotherium* species. On one hand, the large size and mainly rounded shape of the orbits, with low zygomatic arches, resemble the *P. typicum* condition (Online Resource 1d-f). On the other hand, the dorsal orbital margins are poorly protruding and convex in dorsal view, indicating a somewhat more dorsal orientation of the orbits, as was suggested for *P. bonaerense* (Online Resource 1a-c). On the dorsal aspect of the cranial vault, between the temporal fossae, a midline mark is developed in *P. bonaerense* (Fig. 2a, b), less defined in *P. typicum* and some specimens of *Tremacyllus* (e.g., MACN Pv 2434), but not evident in other specimens of the latter taxa (Online Resource 1e, h). In the orbital region of pachyrukhines, the optic foramina of both sides closely approximate the sagittal plane, immediately dorsal and medial to the alisphenoid canal. The lacrimal foramen opens inside the orbit (Online Resource 2). In the most dorsal aspect of the orbit, just below to the orbital margin, a small foramen seems to represent the foramen for the frontal diploic
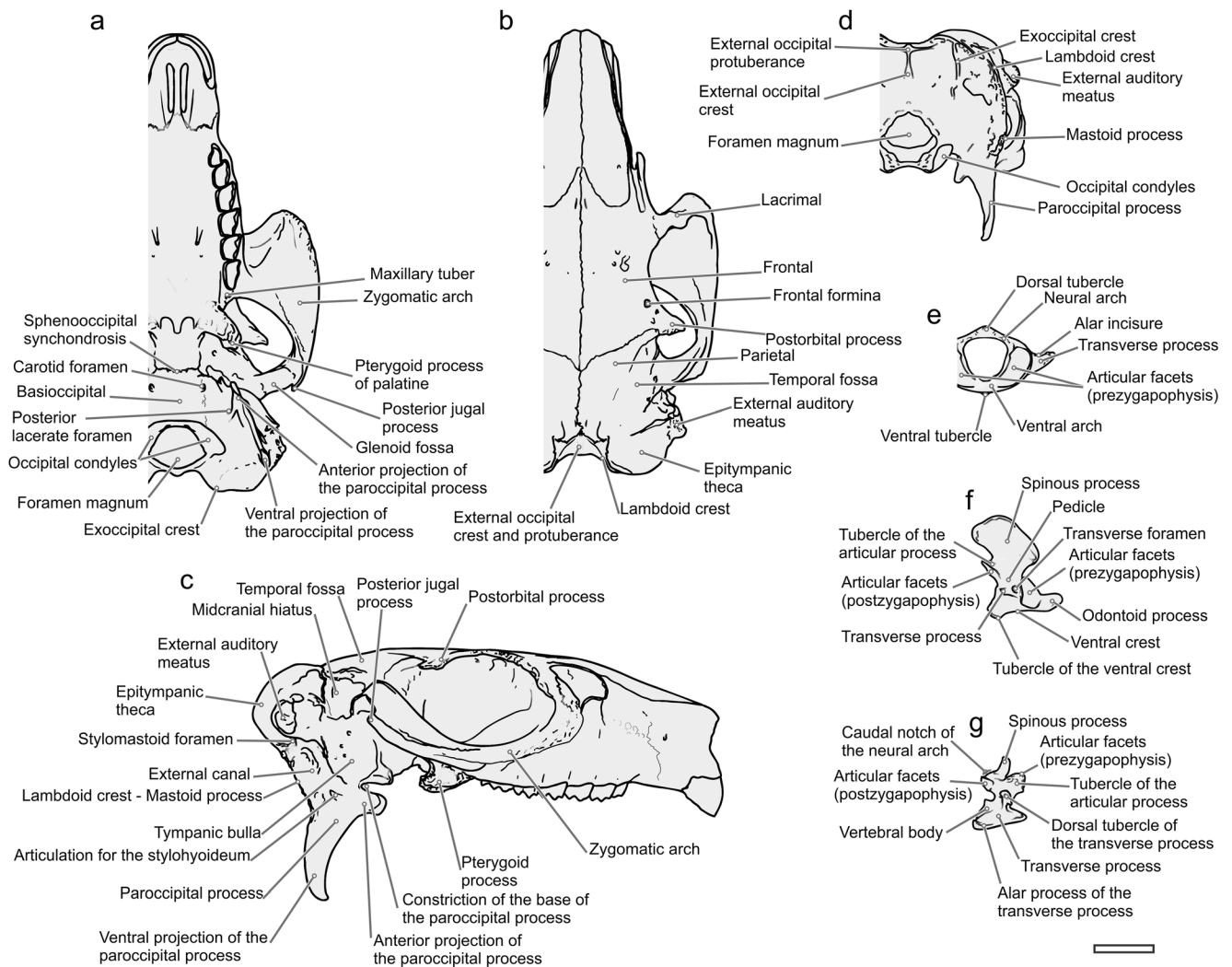
Fig. 1 Anatomical terms used in the descriptions of cranial elements and cervical regions of pachyrukhines and comparative sample. Cranium in ventral (**a**), dorsal (**b**), lateral (**c**), and occipital (**d**) views; atlas in anterior view (**e**); axis (**f**) and sixth cervical vertebra (**g**) in lateral views. Scale bar = 10 mm

vein. A deep and bounded diagonal sulcus with multiple foramina crosses the orbit in an anterodorsal to ventromedial direction. This structure seems to represent the sphenopalatine fissure, apparently containing foramina linking the infraorbital foramen and the sphenopalatine foramen, but specific studies should be carried out to confirm these potential homologies (Online Resource 2). Dorsal to the orbit, there exist frontal foramina (see Online Resource 1).

In our extant comparative sample, the postorbital process is atrophied or reduced in *Chinchilla*, *Cavia*, and *Dolichotis*. In the first two caviomorph genera the process presents a smooth surface, while this process and adjacent surfaces are rugous in *Dolichotis* (Figs. 2e, f, 3d-f). On the other hand, it is extended and contacts the zygomatic arch, forming a postorbital bar, in *Tragulus* (Fig. 3i). A well-developed postorbital process is also present in the other extant representatives, being projecting ventrally in *Heterohyrax*, and laterally or laterocaudally in the remaining taxa.

The postorbital process of pachyrukhines is relatively reduced compared to that of the latter described taxa, but clearly larger than that of caviomorph rodents. The postorbital process of *Lepus* is a well-developed, plate-like process, dorsally located and posteriorly projected (Fig. 2c, d). Part of this configuration is related to the well-developed anterior musculature of the ears (m. frontoscutularis; Bramble 1989). In the postorbital process of *Ratufa* (Fig. 3b), a series of scars form a dorsal crest parallel to the posterior margin of the process, apparently corresponding to the same muscle, while this is not evident for the other extant studied species. In the dorsal midline of the cranium, in front of the temporal fossae, additional scars related to the origin of other auricular muscles are well developed in *Lepus* (Fig. 2c,d), and subtly developed in *Chinchilla* and *Dolichotis* (see also fig. 5 of the accompanying contribution: Ercoli et al. 2020).

Lepus, *Dolichotis*, and *Tragulus* present the most laterally oriented orbits of the sample. In *Ratufa*, *Heterohyrax*, and
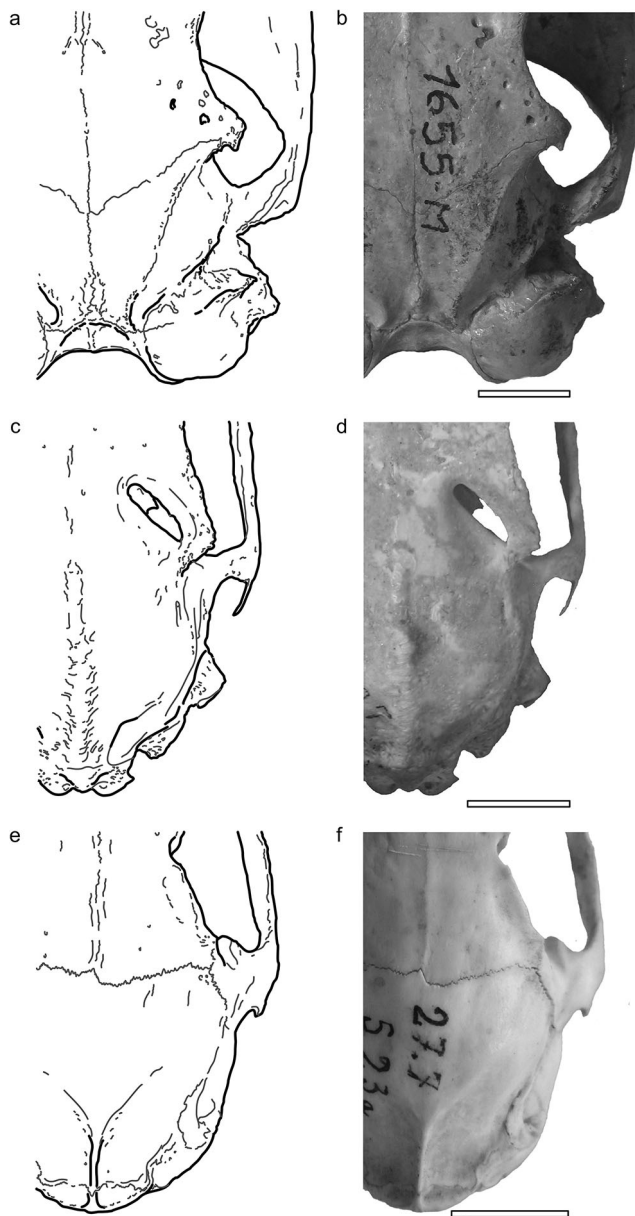
Fig. 2 Dorsal views of the caudal cranium: *Paedotherium bonaerense* MMP 1655-M (**a**, **b**), *Lepus capensis* FMNH 42407 (**c**, **d**), and *Cavia aperea* MACN Ma 27.7 (**e**, **f**). Scale bars = 10 mm

Tragulus, they tilt slightly more anteriorly, and in *Chinchilla*, *Ctenomys*, *Cynomys*, and to a lesser extent in *Cavia*, they tend to tilt dorsally at a higher degree. Despite the subtle differences in pachyrukhines, *P. bonaerense* and *Tremacyllus* are more similar to *Cynomys* and caviomorphs, while *P. typicum* presents a more directly lateral orientation, reminiscent of *Lepus*, *Dolichotis*, and *Tragulus* (Fig. 3; see also fig. 4 of the accompanying contribution: Ercoli et al. 2020).

The external auditory meatus is well developed, opens posteriorly, and presents a dorsal and lateral tilt in all pachyrukhines (Figs. 2a, b, 4). Ventral to the external auditory meatus, there is an external canal (only well-preserved in

P. typicum, *P. bonaerense*, and *Tremacyllus*), limited anteriorly and posteriorly by crests, the former corresponding to the crista meatus of Billet et al. (2009) and MacPhee (2014), and the latter corresponding to the lambdoid crest and mastoid process (see below) (Fig. 4; see also Fig. 1c). This canal extends ventrally, reaching the posterior region of the lateral aspect of the base of the paroccipital process. In the distal part of this canal, there is the tympanic fenestra, of which the exact location is slightly variable, sometimes reaching the base of the paroccipital process. There is no ventral cleft of the external auditory meatus (see MacPhee 2011, 2014) connecting the tympanic fenestra with the external auditory meatus. Conversely, there are multiple foramina along the external canal, including a large, constantly present one in the base of the external auditory meatus, which probably represents the stylomastoid foramen (Fig. 4; see Billet et al. 2009; MacPhee 2011). Based on the preserved remains (i.e., partial remains of *P. minor* MLP 29-IX-2-20 and *P.* cf. *P. minor* MLP 55-IV-28-82), this described morphology could apply to the studied pachyrukhines, but in the case of *Tremacyllus* (Fig. 4d, e), the external canal is less clearly defined than in *Paedotherium* (Fig. 4a-c), in relation to the poorer development of the crests that limit it.

The auditory cavities of pachyrukhines are composed of the tympanic bullae and dorsal epitympanic recesses (Figs. 2a, b, 4; see MacPhee 2014; "bullas post-timpánicas" sensu Kraglievich 1926), which surround dorsally and posteriorly the external auditory meatus. Epitympanic recesses are evident externally by globous epitympanic thecae that cover them, protruding over the dorsal surface of the posterior region of the cranium. Both, the bullae and epitympanic thecae vary in the different fossil species (see also Kraglievich 1926; Zetti 1972a; Cerdeño and Bond 1998). In *P. bonaerense*, the epitympanic thecae are less inflated than in the other pachyrukhines, scarcely surpassing dorsally the lambdoid crest (Figs. 2a, b, 5b). In posterior view, they are located away from the midline of the cranium in *P. bonaerense* (Fig. 5b), and they are closer to each other in *P. typicum* and *Tremacyllus* (Figs. 2b-e, 5a, c). In *P.* cf. *P. minor* (MLP 55-IV-28-82), the epitympanic thecae present an apparently intermediate condition, although the remains of this specimen are poorly preserved. In *P. typicum*, *P.* cf. *P. minor*, and *Tremacyllus*, the epitympanic thecae markedly surpass dorsally the lambdoid crest (Fig. 5a, c; see Kraglievich 1926; Cerdeño and Bond 1998). In ventral view, the tympanic bullae are less developed in *Paedotherium* than in *Tremacyllus*, being largely expanded in the ventral, antero-lateral, and medial direction in the latter (see Online Resource 1a-i). The different development of the bullae results in differences in the occipital plane. In this way, the region of the occipital plane that is closer to the paroccipital process is pretty inflated in *Tremacyllus* (Fig. 5c), moderately inflated in *P. typicum* (Fig. 5a) and *P.* cf. *P. minor*, and mainly flattened in *P. bonaerense* (Fig. 5b; see also MacPhee 2014: fig. 8).
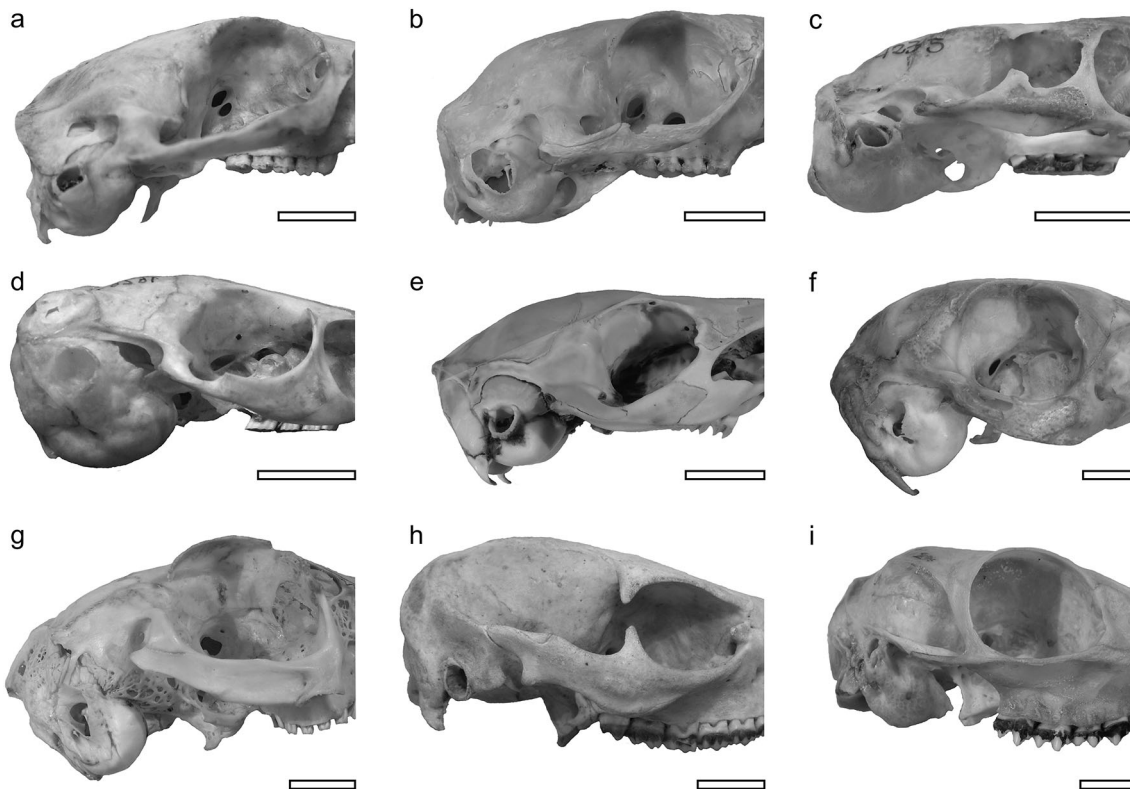
Fig. 3 Lateral views of the caudal cranium and orbital region of the studied extant taxa: *Cynomys ludovicianus* FMNH 58999 (**a**), *Ratufa affinis* FMNH 68747 (**b**), *Ctenomys frater* CML 7235 (**c**), *Chinchilla chinchilla* MACN Ma 16267 (**d**), *Cavia aperea* MMP ND 83 (**e**), *Dolichotis salinicola* FMNH 48019 (**f**), *Lepus capensis* FMNH 79398 (**g**), *Heterohyrax brucei* FMNH 18842 (**h**), and *Tragulus kanchil* FMNH 68768 (**i**). Scale bars = 10 mm

The external auditory meatus is relatively short and ventrally located in sciurids, *Cavia*, and *Heterohyrax* (Figs. 2e, f, 6a–h). This meatus is relatively long in other species, opening ventrally in *Ctenomys*, and dorsally and markedly laterodorsally directed in *Lepus*, *Chinchilla*, and to a lesser degree in *Tragulus* and *Dolichotis* (Figs. 2c, d, 3, 6), denoting a more similar configuration of the latter to that of the pachyrukhines. The tympanic bullae are reduced (*Heterohyrax*) or moderately developed in most of the comparative extant taxa, while they are hypertrophied in *Ctenomys* and *Chinchilla*, inflating the occipital plane (Figs. 6, 7). In the specific case of *Chinchilla*, the epitympanic thecae protrude on both the occipital and dorsal aspect of the posterior region of the cranium (Fig. 3d). Considering this diversity of morphotypes, pachyrukhines appear more similar to the latter rodents, than the other extant taxa.

The mastoid process is barely defined in pachyrukhines. In general, the mastoid process is defined as the attachment region of the main mastoid muscles (e.g., sternocephalicus pars mastoidea, cleidocephalicus pars mastoidea) and is typically located closer or in continuation with the anteroventral end of the lamboid crest. Considering this, in pachyrukhines it was identified as a poorly defined, rugous scar, immediately caudal to the external canal, and near to the base of the paroccipital process (Figs. 1, 4), probably homologous, at least partially, to the post-tympanic process of Billet et al.

(2009), and the retrotympanic process and its crista lateralis of MacPhee (2014). On the other hand, the anterior crest that limits the external canal (see above), located on the postero-lateral aspect of the bulla, could eventually represent an insertion scar for some advanced mastoid muscles [as in some rodents with large bullae, such as *Dipodomys*, in which some mastoid muscles acquire an advanced insertion (Howell 1932; Ryan 1989)]. In an alternative or complementary way, this anterior crest could also be interpreted as the origin scars of hyoid muscles, considering the proximity of the hyoid articulation (see below).

The mastoid process is well developed in *Cynomys*, *Ctenomys*, *Ratufa*, and *Lepus*, and it is smaller in the rest of the species (Fig. 3). Even in the cases where it is reduced (e.g., caviomorph rodents), it is always a distinctive structure. Pachyrukhines stand out because of the remarkable reduced mastoid process that is hard to distinguish from the lambdoid crest.

There is a midcranial hiatus located between the bullae, squamosal and parietal bones, immediately posterior to the posterior root of the zygomatic arch (MacPhee 2014). This structure is only observed in well-preserved fossil specimens (e.g., *P. typicum* PVL 3386, *P. bonaerense* MACN Pv 10.515; Figs. 2a, 4). Regarding extant models, the midcranial hiatus is comparable to similar structures described for some
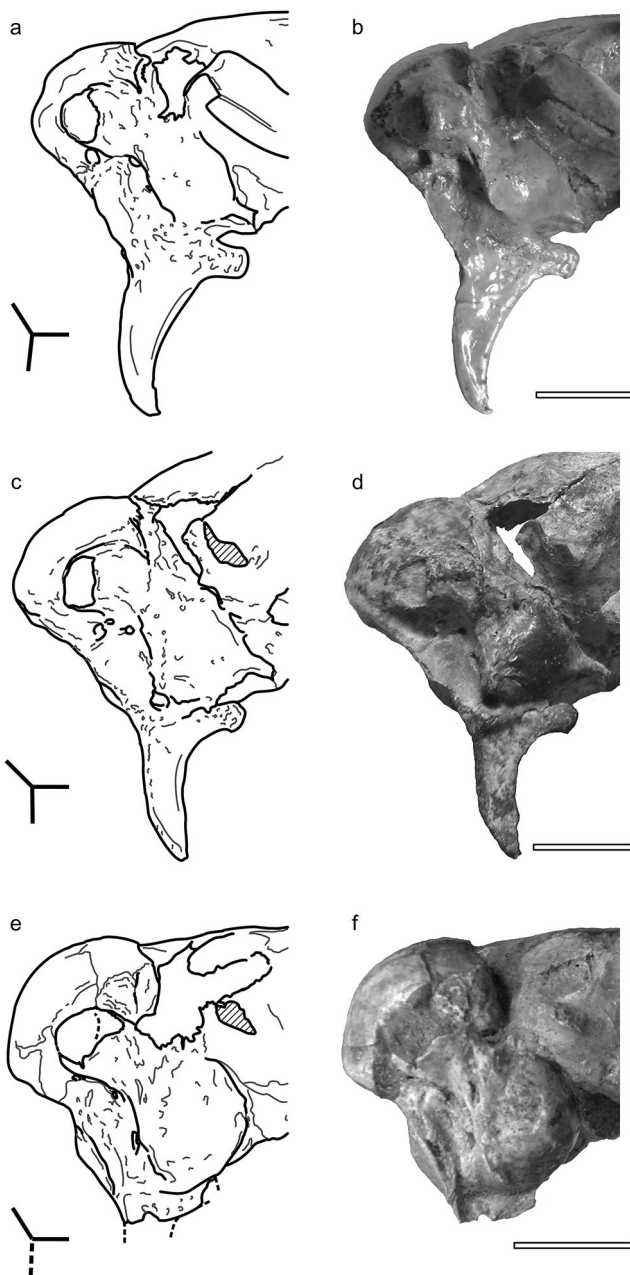
Fig. 4 Lateral views of the caudal cranium: *Paedotherium bonaerense* MMP 1655-M (**a**, **b**), *P. typicum* PVL 3386 (**c**, **d**), and *Tremacyllus* MACN Pv 2434 (**e**, **f**). In the bottom-left corner of each specimen, a tree-line scheme indicates the orientation of the palate, occipital plane, and paroccipital process. Scale bars = 10 mm

lagomorphs [see MacPhee (2014) for further details of this and associated structures].

Basicranium and Occipital Plane

Among pachyrukhines, the posterior lacerate foramen (=jugular foramen; MacPhee 2014) is large and located medial to the base of the paroccipital process. The carotid foramen is located on the suture between the tympanic bulla and the basioccipital bone, distant to the posterior lacerate foramen,

and near the sphenooccipital synchondrosis (see Reguero and Prevosti 2010; MacPhee 2014). In *Paedotherium*, the carotid foramen is relatively large and more separated from the midline of the basicranium. Conversely, in *Tremacyllus*, the carotid foramen is closer to the midline and lateromedially compressed, in relation with the described large development of the bulla (Online Resource 1g).

The lamboid crest is slender and well defined in the dorsal region, but poorly defined ventral to the epitympanic thecae level (Fig. 5). The occipital plane is mainly set at 46° in respect to the horizontal plane (defined by the diastema plane) in *P. typicum* (Fig. 4a, b), while this angle increases to 55° in *P. bonaerense* (Fig. 4c, d) and to 60° in *Tremacyllus* (Fig. 4e, f) (Table 1). The occipital plane of *P. typicum* is, in turn, markedly higher than in *P. bonaerense* and *Tremacyllus* (Fig. 5), and probably *P.* cf. *P. minor* (not measured but inferred from the fragmentary remains). The occipital condyles are mainly restricted to the sides of the foramen magnum, tilting ventrally (Fig. 5).

In the extant comparative sample, the facial tilting ranges between 80° and 100° in sciurids, *Ctenomys*, *Heterohyrax*, and *Tragulus*, while it is nearly 67° in *Cavia* and *Chinchilla*, 53° in *Dolichotis*, and 42° in *Lepus*. Considering these values, pachyrukhines are similar to *Dolichotis*, and intermediate between non-fossorial caviomorphs and *Lepus*, with *P. typicum* showing the most similar values to *Lepus* (Table 1).

The height of the occipital plane varies also in a gradient-like pattern from the relatively flattened forms of *Ctenomys*, *Chinchilla*, and sciurids, and the intermediate shapes in *Heterohyrax*, *Lepus*, *Dolichotis*, and *Cavia*, to the proportionally tall configuration of *Tragulus* (Fig. 7). Interestingly, pachyrukhines also show a similarly wide range of occipital proportions. *Paedotherium bonaerense* is similar to sciurids (Fig. 5b), *Tremacyllus* is intermediate (Fig. 5c), and *P. typicum* approaches the tall configuration of *Tragulus* (Fig. 5a).

In the dorsal aspect of the occipital plane, there is a moderately defined external occipital crest (=medial occipital crest; Nasif and Abdala 2015), more clearly defined in *P. typicum*, medially delimiting a deep fossa on each of its sides (Fig. 2).

The intersection between the lambdoid crest and the external occipital crest projects caudally, conforming an external occipital protuberance, better defined in *Paedotherium* (confirmed for *P. bonaerense* and *P. typicum*; Fig. 5a, b) than in *Tremacyllus* (Fig. 5c; but see MLP 95-III-31-15). The exoccipital crest (O'Leary et al. 2013; =second crest of the occiput; Nasif and Abdala 2015) is well defined and in a relatively medial location in *Paedotherium*, delimiting the lateral margin of the insertions of mm. rectus capitis dorsales, while this crest presents a more oblique direction and lateral position (reaching the level of the occipital condyles) in *Tremacyllus*. On the other hand, the spaces delimited between the crests and scars that indicate the insertion of m. rectus
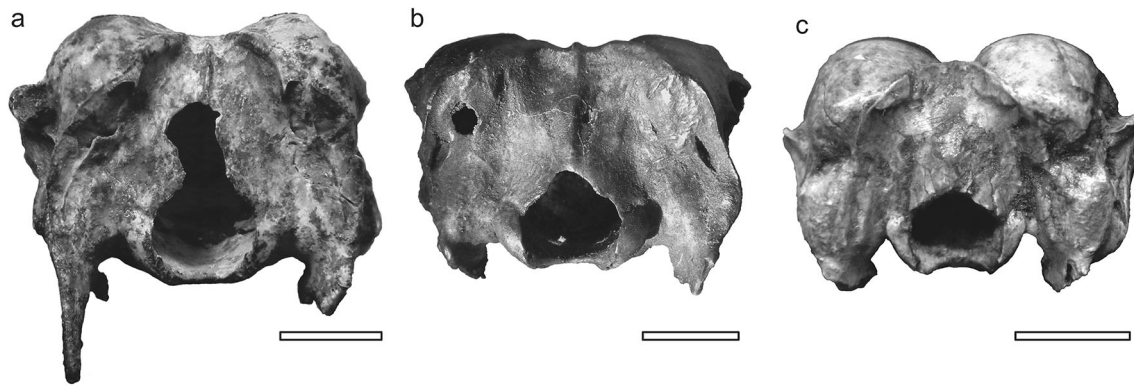
Fig. 5 Occipital views of the cranium of pachyrukhines: *Paedotherium typicum* PVL 3386 (**a**), *P. bonaerense* MACN Pv 7253 (**b**), and *Tremacyllus* MACN Pv 2434 (**c**). Scale bars = 10 mm

capitis lateralis (lateral to the exoccipital crest), are less clearly defined, but seem to be larger in *P. bonaerense* than in *P. typicum*, and intermediate in *Tremacyllus*.

The paroccipital process (=paroccipital apophysis; Billet et al. 2009) of pachyrukhines presents a particular "inverted L" (or gamma "Γ") laminar morphology, with a minor and
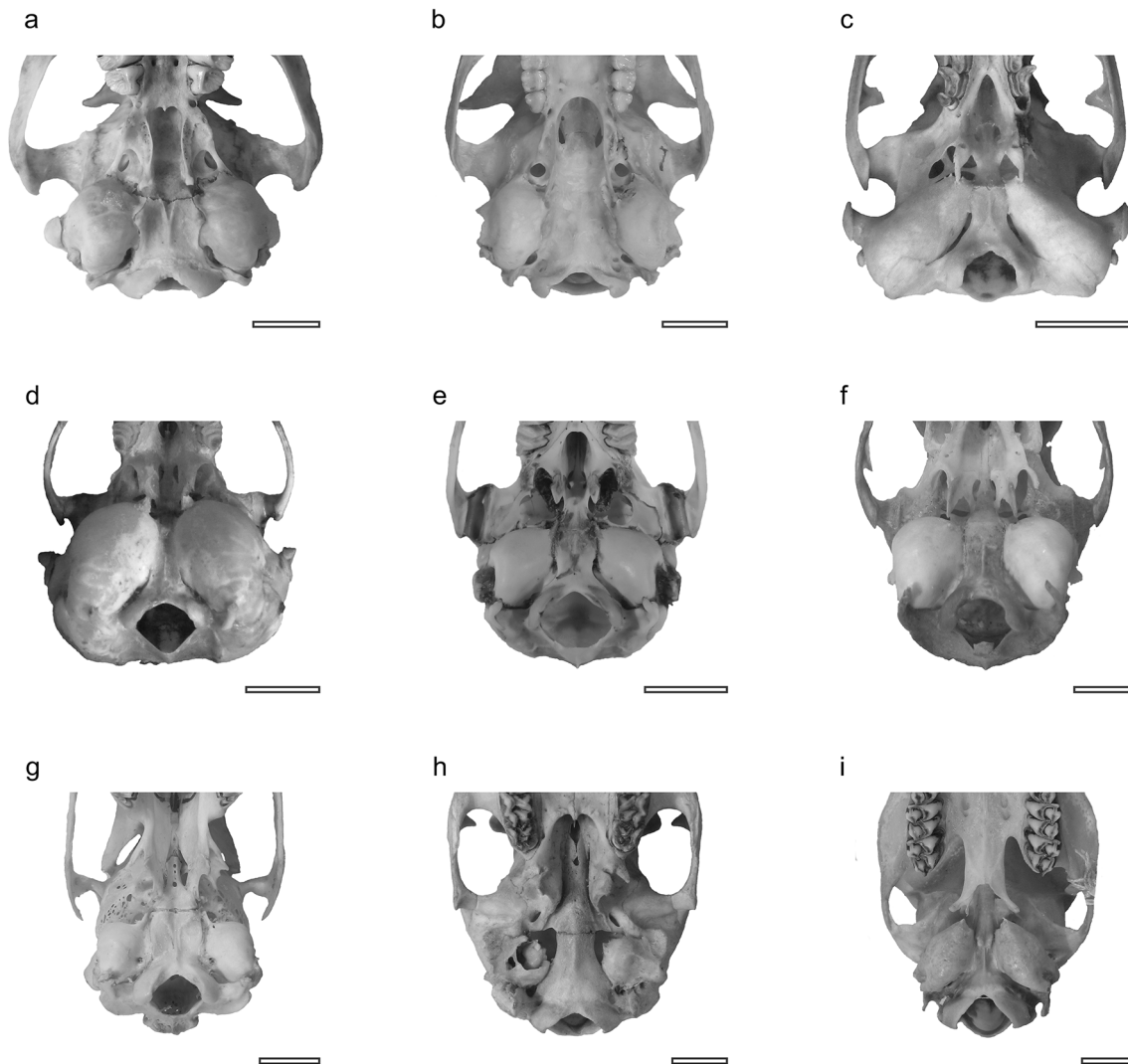
Fig. 6 Ventral views of the basicranium of the studied extant taxa: *Cynomys ludovicianus* FMNH 58999 (**a**), *Ratufa affinis* FMNH 68747 (**b**), *Ctenomys frater* CML 7235 (**c**), *Chinchilla chinchilla* MACN Ma 45.11 (**d**), *Cavia aperea* MMP ND 83 (**e**), *Dolichotis salinicola* FMNH 48019 (**f**), *Lepus capensis* FMNH 42407 (**g**), *Heterohyrax brucei* FMNH 18842 (**h**), and *Tragulus kanchil* FMNH 68768 (**i**). Scale bars = 10 mm
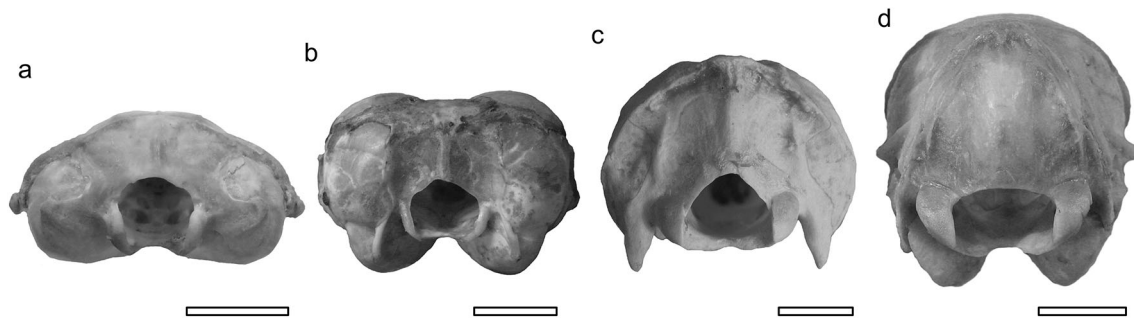
Fig. 7 Occipital views of the cranium of the studied extant taxa: *Ctenomys frater* CML 7235 (**a**), *Chinchilla chinchilla* MACN Ma 45.11 (**b**), *Heterohyrax brucei* FMNH 104600 (**c**), and *Tragulus kanchil* FMNH 68768 (**d**). Scale bars = 10 mm

anterior projection, which presents a robust end, and a major and ventral one, which presents a sharpened and anteriorly recurved end. The lateral aspect of the ventral projection of the paroccipital process presents an ample and shallow fossa (probably in relation to the origin area of the m. occipitohyoideus; Turnbull 1970; Barone 1987; see below and Discussion section), caudally delimited by a caudal ridge or crest. In *P. typicum*, the ventral projection has its major axis extended on the transverse plane of the cranium (i.e., perpendicular to the horizontal plane; Fig. 4a, b), while in *P. bonaerense*, it is tilted slightly posteriorly (Fig. 4c, d). In the studied specimens of *Tremacyllus* the ventral projection is not preserved completely in any specimen, except MLP 95-III-31-15. In this specimen it could be partially observed hovering by its caudal margin and tip from the sediment that surrounded the occipital region. The paroccipital process in this specimen indicates that the ventral projection has a similar direction as *P. typicum*, but with a somewhat shorter length.

As already mentioned, the caudal margin of the paroccipital process forms a crest. This crest continues dorsally with the base of the mastoid process. This crest is very protruding and projects posterolaterally in *P. bonaerense*, is less developed in *P. typicum* and *P.* cf. *P. minor*, and barely visible in *Tremacyllus*. This gradient appears to be in relation to the different degrees of the inflation of the bullae (see above). There is a large depression between the dorsal margin of the anterior projection and the bulla in *P. typicum*, generating a marked constriction of the base of the paroccipital process (Fig. 4a, b). Although only preserving the base of the paroccipital process, *P.* cf. *P. minor* seems to present a similar configuration to that described for *P. typicum*. Conversely, in *P. bonaerense*, the base of the paroccipital process is less constricted, in relation to a shallow anterior depression (Fig. 4c, d). Finally, this constriction is absent in *Tremacyllus*, in relation to a full contact between the dorsal margin of the anterior projection of the paroccipital process and the ventral surface of the very inflated bulla (Fig. 4e, f).

In the *P. typicum* MMP 1008-M, the stylohyoideum is preserved almost completely (Fig. 8). It presents a flattened bar-like shape, somewhat recurved dorsally. The contact of the stylohyoideum and the cranium is represented by a depressed region [which corresponds to the hyoid recess of MacPhee (2014), and the tympanohyal recess of Billet et al. (2009) and Billet (2011)]; its location varies from the

Fig. 8 Lateroventral view of the cervical vertebrae, occipital region, and stylohyoideum of *Paedotherium typicum* MMP 1008-M. Scale bar = 10 mm
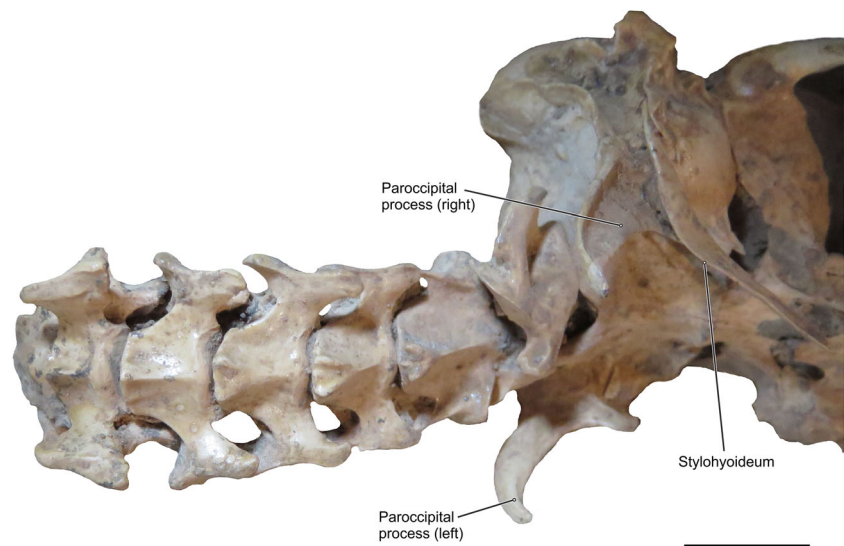
Table 1 Facial tilting values, measured as the angle (°) between the occipital plane and the plane of the diastema of *Paedotherium bonaerense*, *P. typicum*, *Tremacyllus* spp., and extant mammals. Analyzed specimens are indicated in Appendix 1

Species	Facial tilting
Pachyrukhines	
Paedotherium bonaerense	55.40
Paedotherium typicum	46.00
Tremacyllus spp.	60.26
Extant models	
Cavia aperea	66.33
Chinchilla chinchilla	68.07
Ctenomys frater	97.47
Cynomys ludovicianus	88.84
Dolichotis salinicola	52.79
Heterohyrax brucei	89.57
Lepus capensis	41.63
Ratufa affinis	80.88
Tragulus kanchil	80.58

anteroventral to the anterior region of the external canal, near the base of the paroccipital process, and anteroventral to the stylomastoid foramen. In some specimens (right side of *P. typicum* MMP 1008-M, left side of *Tremacyllus impressus* MACN Pv 2434), the articulation between the stylohyoideum and the cranium is covered laterally by the protruding anterior margin of the external canal (Fig. 8; see also Billet et al. 2009). It is probable that the medial aspect of the stylohyoideum and the rugous extreme of the anterior projection of the paroccipital process were in contact, probably via soft tissues, considering their proximity and morphology in the articulated specimens. The stylohyoideum reaches anteriorly to the level of the pterygoid process of the palatine (Sisson and Grossman 1930; see also palatine crests of Billet et al. 2009a, and ectopterygoid crests of Billet 2011). Other elements of the hyoid apparatus are unknown.

Among the extant sample, the exoccipital crest is well defined in *Tragulus*, *Cavia*, and *Cynomys*, poorly defined in *Heterohyrax*, *Dolichotis*, and *Ctenomys*, and absent, or barely defined in *Ratufa* and *Lepus* (Fig. 7). The relatively medial location of this crest in *Tragulus* and *Dolichotis* restricts the available mediolateral space for m. rectus capitis dorsalis, but forms a large dorsoventral space in relation to the high profile of the occipital plane, particularly for the former taxa. Conversely, the proximity between the exoccipital and lambdoid crests restricts greatly the space available for insertion of head rotators (e.g., m. splenius, m. semispinalis). In *Cavia* and, apparently, *Heterohyrax* (although the muscular scars are poorly defined in the latter), and particularly in *Ctenomys* and *Cynomys*, the rectus fossae have a large mediolateral development, but are greatly restricted in the vertical direction in relation to the described occipital plane

profile (Fig. 7). In these taxa, the lateral location of the exoccipital crest is accompanied by a large space between this crest and the lambdoid crest, allowing a large development of the head rotators. Particularly for *Cynomys* and *Ctenomys*, the lateral expansion of the distal region of the lambdoid crest seems to be related to a large insertion of the mastoid musculature (Fig. 7a). In *Lepus*, the rectus fossae are moderately development in the dorsoventral direction but restricted in the mediolateral one, together with large spaces and laterally located insertions of the lateral and oblique occipital musculature. Finally, in *Chinchilla*, the only well-defined scars are those corresponding to m. rectus capitis dorsalis, while the exoccipital and lambdoid crests are laterally located in relation to the inflation of the epitympanic recesses, and not necessarily related to a large muscle insertion area (Fig. 7). *Tragulus*, *Dolichotis*, and *Lepus* present marked external occipital protuberances, bilobed in the case of *Lepus*, located in the most dorsal point of the lamboid crest, linked to the development of a large nuchal ligament and head extensors (Fig. 2c; e.g., Slijper 1946).

The combination of features described for pachyrukhines is not present in the extant studied sample, but the relatively high rectus fossae (a feature particularly accentuated in *P. typicum*) are similar to those observed in *Cavia*. Moreover, the major expansion of the area between the exoccipital and lamboid crests seems to be more similar to that of *Chinchilla* and *Cynomys*, and is partially related to the inflation of the epitympanic recess and, probably, to the large development of the m. rectus capitis lateralis insertion, as in *Cavia* and *Lepus*.

The morphology of the paroccipital process is quite similar in the extant sample, typically shaped as an acute or moderately rounded process, ventrally or anteroventrally (in the case of caviomorphs and *Lepus*) projected. In *Lepus*, *Chinchilla*, and *Ctenomys*, this process is anteroposteriorly flattened, in relation to the accommodation of the well-developed bulla (Fig. 6). The morphology of *Tragulus* is somewhat different from this general pattern, with a paroccipital process mediolaterally flattened (Fig. 6i) and slightly concave on its lateral face (Figs. 3i, 7d). This concave surface, as also inferred for pachyrukhines, corresponds to the origin area of m. occipitohyoideus (Turnbull 1970; Barone 1987). Although much more reduced, this morphology resembles those of pachyrukhines. Nevertheless, none of the extant models showed an inverted "L" shaped paroccipital process, as in pachyrukhines.

The distal end of the parocciptal process is the site of origin of m. digastricus in all the representatives of the extant sample, and there is no reason to suggest a different condition in pachyrukhines, although the scars are subtle and poorly defined.

The stylohyoideum bones of extant perissodactyls and artiodactyls (e.g., Barone 1987) and pachyrukhines are very

similar, in being a large and mediolaterally flattened structure, holding a large hyoid apparatus. The main difference is the presence of a stylohyoid angle in the case of extant mammals (e.g., equids, many arctiodactyls; Sisson and Grossman 1930; Barone 1987), which is absent in pachyrukhines with a preserved stylohyoideum bone (Fig. 8).

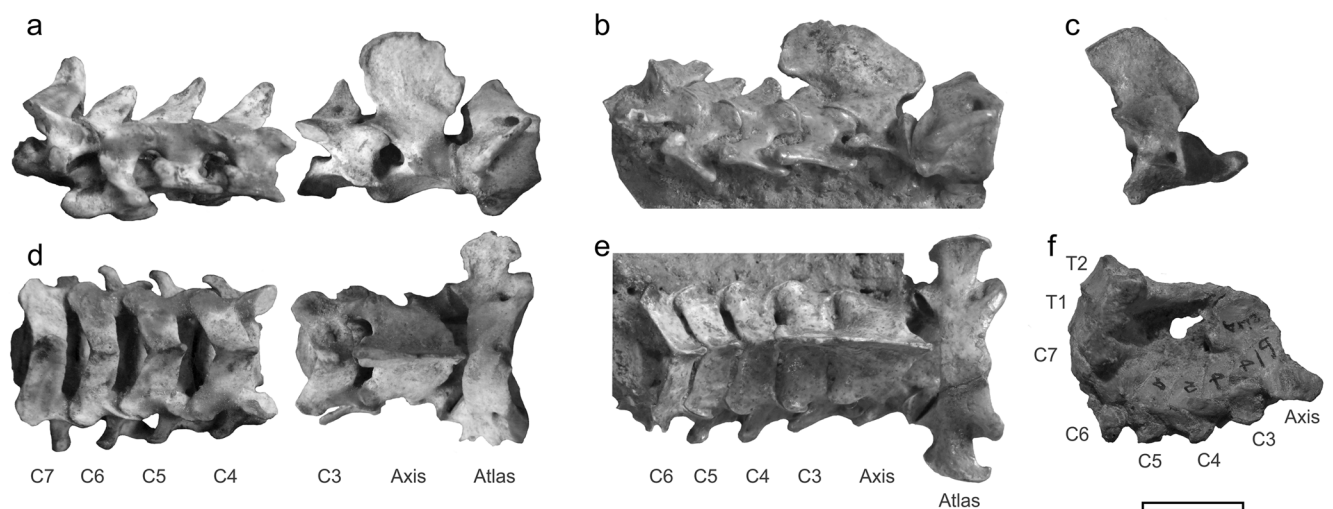## Cervical Vertebrae

Atlas and Axis

Several of the specimens of *P. bonaerense* preserve a partial (MACN Pv 7520) or complete (MLP 99-X-2-1, MMP 158-S, MACN A 1251–52) cervical series. For *P. typicum*, there are isolated elements (axis, C4, C5, and C7) of a young specimen (MMP 668-S) and two complete or mostly complete series (MACN Pv 6436, MMP 1008-M). The available specimens of *Tremacyllus* only preserve incomplete and badly preserved cervical series (e.g., MACN Pv 8157, FMNH 14456), limiting any descriptions and comparisons. As mentioned above, cervical elements for *P. minor* are lacking.

The neural arch of the atlas is anteroposteriorly longer than the ventral one in *Paedotherium* (Fig. 9). The neural arch is flattened in *P. bonaerense* (Fig. 9b) and vaulted and more elevated at the midline in *P. typicum* (Fig. 9a). The dorsal tubercle, origin site of the m. rectus capitis dorsalis minor, is robust and rounded, and typically depressed in the anterodorsal sector (Fig. 9). The ventral tubercle is well developed and caudally located. It is mediolaterally compressed in *P. typicum*, and rounded and robust in *P. bonaerense*. These structures are not known for *Tremacyllus*.

Among extant taxa, the cervical vertebrae are particularly long in *Lepus* (Fig. 10e), *Tragulus*, and to lesser degree in *Dolichotis* (Fig. 10d), highly compressed in *Ctenomys*

(Fig. 10a), and *Chinchilla* (Fig. 10b), and moderately short in the remaining studied extant taxa (e.g., *Cavia*, Fig. 10c). The atlas is relatively flattened in dorsoventral direction in all taxa except in caviomorphs, where the neural arch is very high and vaulted. Regarding this feature, the studied caviomorphs are more similar to *P. typicum*, and the remaining taxa are more similar to *P. bonaerense* (Fig. 9). The ventral tubercle is typically in a caudal location. It is poorly developed in almost all taxa, moderately developed in *Heterohyrax* and *Dolichotis*, and markedly developed in *Cavia* and especially *Lepus*. In the last case, the ventral tubercle is strongly projected caudally, and ends in a bilobed projection. The neural arch is typically more extended in the anteroposterior direction than the ventral one in extant rodents. Both arches are relatively similar in *Heterohyrax*, and are very elongated in *Lepus* and *Tragulus*. The pachyrukhines are more similar to rodents, and particularly *Ctenomys* and *Cynomys*. In pachyrukhines, the pre- and postzygapophyses of the atlas are wide, concave, and dorsoventrally elongated. The prezygapophyses have a protruding dorsal limit (Fig. 9d, e). The prezygapophyses of the atlas are vertically oriented in *Lepus* and *Tragulus*, being particularly wide in the latter. As in pachyrukhines, they are more diagonally oriented in other extant taxa of the sample, with sciurids showing the highest deviation from the transverse plane.

In pachyrukhines, the transverse processes (=alar processes; see Evans and de Lahunta 2013) tilt dorsally. They are short but anteriorly and posteriorly projected in their lateral margin (although in a small degree in the case of the specimen MLP 99-X-2-1 of *P. bonaerense*) (Fig. 9). The caudal margin varies from markedly to slightly concave, and its caudolateral projection reaches the most posterior aspect of the postzygapophysis in the case of *Tremacyllus*. The cranial margin is markedly concave and forms an alar incisure (Fig. 9d, e). The transverse foramen (=alar foramen; see Evans and

Fig. 9 Cervical vertebral series of pachyrukhines in lateral (**a**, **b**, **f**) and dorsal (**d**, **e**) views, and axis in lateral view (**c**). *Paedotherium typicum* MACN Pv 6436 (**a**, **d**), *P. bonaerense* (**b**, **c**, **e**), and *Tremacyllus* FMNH P 14456 (**f**). Different axis morphology described for *P. bonaerense* are shown in MMP 158-S (**b**, **e**) and MACN A 1251 (**c**). Scale bars = 10 mm
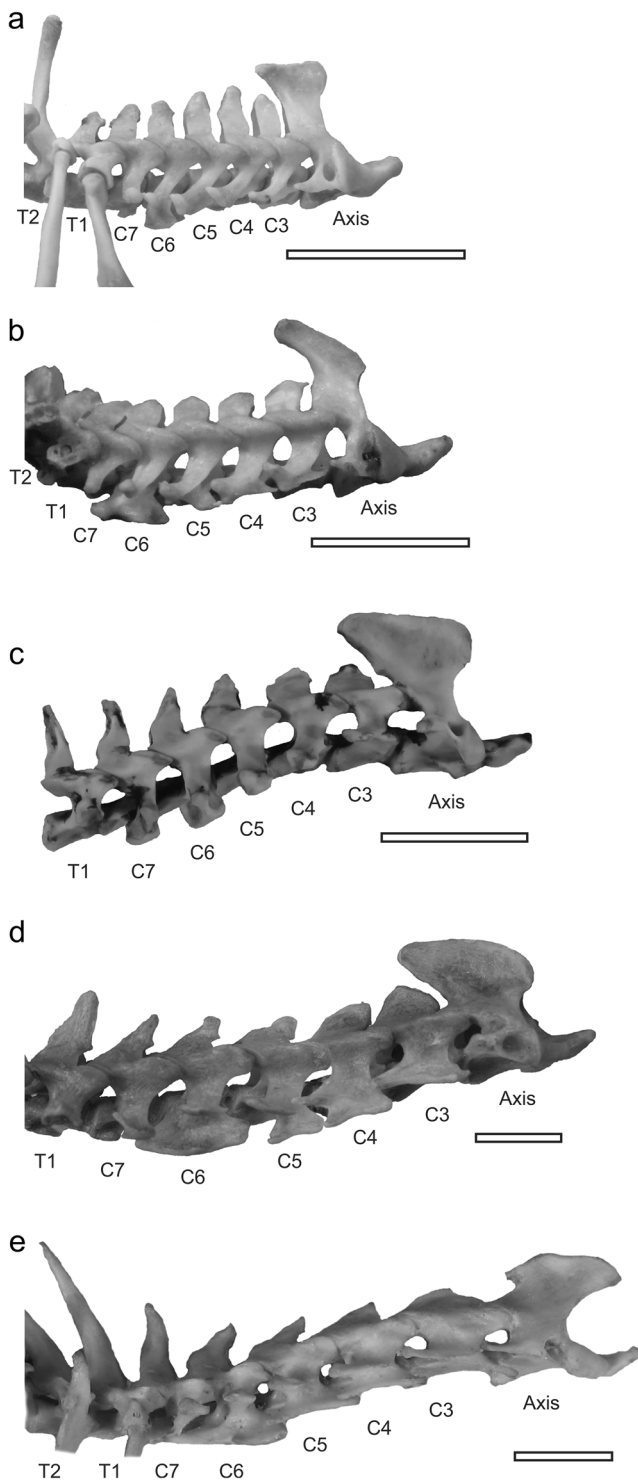
Fig. 10 Cervical vertebral series of the studied extant taxa: *Ctenomys frater* CML 7235 (**a**), *Chinchilla chinchilla* MACN Ma 16267 (**b**), *Cavia aperea* MMP ND 83 (**c**), *Dolichotis salinicola* FMNH 48019 (**d**), and *Lepus capensis* FMNH 42407 (**e**). Scale bars = 10 mm

de Lahunta 2013) opens anteriorly in the anterior aspect of the base of the alar process, and posteriorly in the middle region of the ventral aspect of this process (the latter feature is not preserved in the specimens of *Tremacyllus*) (Fig. 9).

The transverse processes of the comparative extant taxa vary largely in shape and size, including different configurations regarding the dorsal tilting. In *Lepus*, *Tragulus*, *Dolichotis*, *Cavia*, and *Ctenomys*, they are mainly horizontal, with a moderate to large development (especially in *Lepus*), while they are moderately to poorly (especially in *Ratufa*) developed and tilt dorsally in sciurids, *Heterohyrax*, and *Chinchilla*. A moderate development and dorsal tilting of this process was also observed in pachyrukhines.

The axis is a high and robust element in *Paedotherium* (*P. bonaerense* and *P. typicum*; Fig. 9a-c) and *Tremacyllus*, but a detailed morphological description cannot be performed in the latter because of its fragmentary condition (Fig. 9f). The odontoid process is robust and tilts dorsally (Fig. 9c). The prezygapophyses are convex, large, and well separated from each other. The postzygapophyses are mainly flattened, dorsally located, and slightly laterally tilted in both *Paedotherium* and *Tremacyllus*. The ventral aspect of the vertebral body presents a ventral crest with two caudal tubercles that are well defined in *Paedotherium* (Figs. 8, 9a) but poorly defined in *Tremacyllus*. The transverse process of the axis is reduced and perforated in its base by a large transverse foramen (Fig. 9a-c). The spinous process is high and long, with an angled contour. The dorsal margin of this process is mainly straight and its main axis is caudally tilted in *P. bonaerense*, while the dorsal margin is convex and the main axis is vertical in the case of *P. typicum* (MACN Pv 6436; see also Kraglievich 1926) (Fig. 9). The cranial margin of the spinous process is extended in *P. bonaerense* (although in different degrees in the different specimens analyzed; see Fig. 9b, c), with a cranial rounded projection located above the level of the neural arch of the atlas, when the elements are articulated. Conversely, in *P. typicum* the cranial margin is short, and the cranial projection is particularly elevated and sharp, in relation to a vaulted dorsal arch of the atlas (Fig. 9a). The caudal margin of this process is thickened and depressed in the midline. From the axis remains of the *Tremacyllus* FMNH 14456, it can be stated that the general shape of the process is similar to *P. typicum* (Fig. 9f).

Among extant studied taxa, the axis is long in *Lepus* and *Tragulus*, consistent with an elongated cervical series (Fig. 10). In contrast, those taxa with relatively short necks (e.g., *Chinchilla*, *Ctenomys*, and to a lesser degree *Ratufa*), the axes are very compressed (Fig. 10). Finally, the axis is intermediate in the other taxa (Fig. 10). The prezygapophyses are markedly flattened and oriented to the transverse plane in *Heterohyrax* and *Tragulus*, linked to an odontoid process with its main axis anteroposteriorly directed. In the remaining taxa, the prezygapophyses are more convex and laterally tilted (Fig. 10). The studied fossorial taxa (i.e., *Cynomys* and *Ctenomys*) stand out by having very large prezygapophyses, being as tall as the vertebral body and pedicle together (Fig. 10a). The shape of the spinous process of the axis is very variable, in relation to other traits, such as cervical series length,

the morphology of the neural arch of the atlas, and the height of the occipital plane. In *Tragulus*, which is the species with the highest occipital plane, the spinous process is particularly high and anteroposteriorly elongated, followed by *Cavia*, *Dolichotis*, *Heterohyrax*, and *Lepus*, and finally by the sciurids and *Chinchilla*, of which the spinous processes present a small surface in relation to a poor development of the anterior sector and caudal tilting of their main axis (Figs. 7, 10). The spinous process of *Ctenomys* presents a moderate but variable development, being mainly vertically directed (Fig. 10a).

From a comparative point of view, the axis of pachyrukhines presents many similarities to that of rodents, and particularly *Cavia* and *Dolichotis*, including a moderate anteroposterior compression, a lateral tilt, convex prezygopophyses, and a dorsally tilted odontoid process. On the other hand, the particularly high and long spinous process of *P. typicum* is more similar to that of *Tragulus*, while the posterior tilting of the spinous process of *P. bonaerense* is similar to *Cavia*, *Dolichotis*, and *Heterohyrax*.

Vertebrae C3 to C7

The vertebrae C3 to C7 of *Paedotherium* are elements with a moderate anteroposterior compression, while a higher degree of compression is observed in *Tremacyllus* (Fig. 9). The articular surfaces are reduced and distanced from each other. The neural arches are elevated, and anteroposteriorly narrow, especially in their midline point, in relation to deep caudal notches (progressively more developed from C3 to C7) (Fig. 9d, e). In *Paedotherium*, the spinous processes of these cervical vertebrae, which serve as the attachment area of multiple, mainly extensor muscles of the neck, tilt cranially at their bases (except for C7), while the dorsal extremes maintain this tilting or acquire a more vertical orientation. The height of the spinous process is typically moderate, with that of C7 dominating over the remaining elements. The C3 spinous process of *P. bonaerense* (Fig. 9b) is shorter than that of *P. typicum* (MACN Pv 6436; Fig. 9a), in relation to the more accentuated caudal projection of the spinous process of the axis in the former species. The morphology of the spinous process changes in the anterior elements of the thoracic region, of which the spinous processes tilt caudally and rapidly but progressively increment in their height toward the posterior elements.

The transverse processes, which serve as the attachment to multiple lateral and ventral flexor muscles of the neck, are variably configured in pachyrukhines. The vertebrae C3-C5 possess broad bases and long alar processes of the transverse processes (see Fig. 1g) in both anterior and posterior directions in *P. bonaerense* (e.g., MMP 158-S), and they are notably more reduced in *P. typicum* (e.g., MACN Pv 6436) (Figs. 8, 9). Concerning the C6 vertebra, the alar process of the transverse process is well developed in both species (but typically and slightly larger in *P. bonaerense*; Fig. 9b). The dorsal tubercles

of C6 and C7 are in a more anterior location in *Paedotherium*, branching off the anterior aspect of the base of the transverse process. The latter process of C6 of *P. typicum* is more ventrally tilted than in *P. bonaerense* (Fig. 9). The remaining cervical muscular attachments, e.g., tubercles of the anterior and posterior articular processes, are reduced. All these processes are insufficiently preserved in *Tremacyllus* to describe them.

The vertebral bodies present their anterior (cranial) faces ventrally tilted and the posterior (caudal) ones dorsally tilted. The ventral tubercles of the cervical vertebrae, related to the insertions of the m. longus colli, are quite variable in pachyrukhines. *Paedotherium bonaerense* possesses bilobed tubercles on C6 and anterior elements, while in *P. typicum* the bilobed tubercles are present up to C4, and a ventral keel, caudally ending at a poorly differentiated single tubercle, is present on C5 (Fig. 8). In any case, bilobed tubercles were observed for C7. All *Paedotherium* specimens present a ventral keel in the midline of the vertebral body of the C6, except from the young specimen of *P. typicum* MMP 698-S, in which there is no differentiated muscular scars on the ventral aspect of this vertebra. In *Tremacyllus*, the ventral tubercles are smaller, bilobed on C3 and C4, single and poorly differentiated in C5, and with absent tubercles and poorly- or non-distinguishable keels in C6 and C7.

Regarding our extant sample, there is a wide range of morphologies for vertebrae C3–7, but three main morphotypes can summarize them. The taxa with elongated necks, i.e., *Tragulus* and, to a lesser degree, *Heterohyrax*, *Dolichotis*, and *Lepus*, present neural arches anteroposteriorly elongated, with relatively poorly developed caudal notches, although progressively more developed towards the caudal elements (Fig. 10d, e). The spinous processes are moderate (*Lepus* and *Dolichotis*) to high (*Heterohyrax* and *Tragulus*), increasing their height gradually toward the first thoracic elements, the latter being slightly to markedly tilted in caudal direction. The ventral tubercles and the transverse processes are large. The dorsal tubercles of the transverse processes are robust and typically caudally directed (especially in *Tragulus*, *Dolichotis*, and *Lepus*) and are very well differentiated, even in the cranial elements. Finally, the articular facets are more vertical in *Lepus* and *Tragulus* than in the remaining extant representatives (Fig. 10).

In species with moderate to short necks, such as *Cavia*, *Chinchilla*, and *Ratufa*, the neural arches are slender and the caudal notches well developed in all these cervical elements, and even for the axis. The spinous processes are moderate (*Cavia*) or short (*Ratufa* and *Chinchilla*), representing a transition between the height of the spinous process of the cervical elements and thoracic ones, which is relatively abrupt in *Cavia*, but gradual in *Ratufa*. The transverse processes, and especially the alar ones, are gracile, with the dorsal tubercles slender but laterally extended (Fig. 10b, c).

Finally, the third group, containing the fossorial rodents *Ctenomys* and *Cynomys*, shows compressed cervical vertebrae

with reduced caudal notches, and very marked imbrication between elements (Fig. 10a). In *Cynomys*, the morphology of the contact between the axis and C3 prevents any movement. The development of the transverse processes of the middle and posterior elements is larger (*Ctenomys*) or similar (*Cynomys*) to the studied non-fossorial rodents. Nevertheless, there are important differences in the orientation of these processes. Both fossorial species present less laterally projected transverse processes of the axis and middle cervical vertebrae (C3 of *Cynomys*, C3-C5 of *Ctenomys*), which contrasts with the laterally projected alar processes of the atlas and mediolateral expansion of the occipital plane (see above). Interestingly, caudad to the cervical series with atrophied spinous processes, the spinous process of the second thoracic element is markedly developed and vertically orientated in *Cynomys* and, especially, in *Ctenomys* (Fig. 10a). In the latter, this process is robust at its tip, differing from the other extant analyzed taxa and pachyrukhines (e.g., *P. typicum* MACN Pv 6436; *P. bonaerense* MLP 99-X-2-1).

Considering the different morphologies of the extant comparative sample, the moderately compressed configuration, with large notches between vertebrae, and with moderate development of the main muscular processes of C3-C7 in pachyrukhines is more reminiscent of that of rodents, such as *Cavia*, and to a lesser degree to hyraxes, such as *Heterohyrax*.

Although the morphology of the transverse processes in pachyrukhines is intermediate between caviomorphs and hyracoids, there is noteworthy variation between the different *Paedotherium* species. In *P. typicum*, the alar processes of the transverse processes are somewhat reduced and the dorsal tubercles are laterally orientated (Figs. 8, 9a, c). On the other hand, in *P. bonaerense* the transverse processes are anteroposterioly extended, and the dorsal tubercles less protruding (Fig. 9b, e). These differences indicate increased similarities between *P. typicum* and non-fossorial rodents (e.g., *Cavia*), and between *P. bonaerense* and fossorial rodents (e.g., *Ctenomys*, *Cynomys*) and to a lesser degree *Heterohyrax* (Figs. 9, 10). The well-developed ventral tubercles of pachyrukhines, progressively accentuated from *Tremacyllus* to *P. typicum* and finally *P. bonaerense*, resemble that of species with moderate to long necks, such as *Cavia*, *Dolichotis*, *Lepus*, and *Tragulus*. Finally, *Tragulus* and the pachyrukhines share an advanced location of the dorsal tubercle of C6, a condition not observed in the other studied extant taxa.

Discussion

Eyes and Vision

Pachyrukhines had large, well-developed orbits (see Scott 1913). The morphology of the orbits and related structures (e.g., postorbital bar, position and shape of zygomatic arch)

is very variable among clades and may be related to different masticatory models (e.g., less lateralized orbits when the mm. temporales show large development; see Noble et al. 2000; Cox 2008; Hautier et al. 2012), the development of other structures (e.g., bullae; Howell 1932), habitats exploited, and different daily activity patterns (e.g., Hautier et al. 2012; Moyano et al. 2018; Olivares et al. 2020). Among the studied pachyrukhines, *P. typicum* possesses orbits with the more marked lateral orientation, enabling a wider angle of vision (enhanced panoramic visual field; Howell 1932; Heesy 2004). *Paedotherium bonaerense* and, to a lesser degree, *Tremacyllus*, have orbits oriented more dorsally.

The ventral orientation of the occipital plane and vaulted cranium of pachyrukhines, especially marked in *P. typicum* (Fig. 4a; Table 1), would have increased the facial tilt in a resting position and contributed to the frontation of the orbits (Howell 1932; DuBrul 1950; Kraatz et al. 2015). In fact, the facial tilting of pachyrukhines is similar to dolichotines and more accentuated (i.e., lesser angular values) than all the remaining extant models, except lagomorphs (Table 1; see also Kraatz et al. 2015: fig. 6). These results indicate that pachyrukhines would have an intermediate configuration, between leaping-cursorial and more generalized taxa (e.g., *Tremacyllus* and *P. bonaerense*), or even present facial tilting values within the range of the analyzed leaping-cursorial models (e.g., *P. typicum*) (Table 1). When compared with other pachyrukhines, *P. typicum* is characterized by the relatively more vertical projection of the spinous process of the axis (Fig. 9a), probably improving the mechanical advantage of mm. rectus and obliquus capitis in ventro-flexed positions, and in turn, limiting the degree of dorsiflexion of the atlanto-occipital joint (Sargis 2001; Flores and Díaz 2009). Additionally, the more ventrally directed paroccipital process of *P. typicum,* and apparently of *Tremacyllus* (instead of caudoventrally directed as in *P. bonaerense*), would contribute to avoid interference between the paroccipital process and associated structures and the anteroventral region of the neck in the mentioned posture. As described by Kraatz et al. (2015) for lagomorphs, all these features are part of a functional complex that would have allowed the largest frontation of orbits in *P. typicum*. The frontation of orbits enhances substrate perception and is related to fast-moving epigean species (e.g., DuBrul 1950; Kraatz et al. 2015; Olivares et al. 2020). The ventral orientation of the occipital plane and the set of above described associated features could also contribute to the positioning of the head in a higher and more posterior location above the body and neck, and a more vertical orientation of the anterior cervical region (Howell 1932; DuBrul 1950; see below). This configuration, convergently evolved in leaping-cursorial rodents and lagomorphs, is related to the stabilization of the head position and the resistance of reaction forces generated during the takeoffs and landings of strong jumps (DuBrul 1950). A different postural interpretation has been

suggested for other herbivores, such as rhinoceroses, in which larger tilting of the occipital plane is related to grazing on ground level instead of browsing on higher vegetation (Schellhorn 2018 and references therein). Nevertheless, this functional interpretation suitable for understanding the occipital configuration of these large herbivores (which additionally possess columnar limbs and horizontal necks, and consequently access to ground vegetation is a challenge) does not seems to fit well for the smaller morphotypes, such as the ones studied here, in which the leaping-cursorial adaptations seem more relevant.

Strikingly, the pachyrukhines, from *Tremacyllus* and *P. bonaerense* to *P. typicum*, seem to have developed the progressive changes of the same set of characters, from generalist (e.g., *Ochotona* and *Cavia*) to leaping-cursorial specialist glires (e.g., *Lepus* and *Dolichotis*; DuBrul 1950; MacPhee 2014). These characters are the vaulting of the dorsal aspect of the cranium, the dorsally positioned and laterally orientated orbits, the ventrally directed occipital plane and condyles, the convex and caudoventrally directed cranial base, and the forward positioning of structures below the basicranium (see above the changes mentioned for the paroccipital process).

These morphological changes suggest that pachyrukhines possessed frontation of the orbits and sight above their bodies, enhancing substrate perception, as suitable for saltatorial and cursorial species (Howell 1932; Kraatz et al. 2015). *Paedotherium typicum* would be closer to a leporid or dolichotine model (Bramble 1989; Kraatz et al. 2015), but less extremely modified. MacPhee (2014) summarized some of these and other convergent traits with lagomorphs, such as the persisting cranial fontanelles and rarefaction of bones of the rostrum, the reduced and bar-like squamous portion of the squamosal, and the inferred intracranial joints, which result in lighter crania and shock-absorbing mechanisms in mammals that perform "ballistic" bounds (Bramble 1989; MacPhee 2014). Considering all these traits, *P. typicum* could be behaviorally linked to more accentuated epigean and leaping-cursorial habits, compared to the somewhat more generalized gaits of *P. bonaerense* and, probably, *Tremacyllus*. These paleobiological characterizations fit with (or at least do not contradict) previous inferences, based on postcranial analyses (Scott 1913:478; Kraglievich 1926; Elissamburu 2004, 2007; MDE personal observations; see also comments of Seckel and Janis 2008; Ortiz et al. 2017).

Paroccipital Process and Hyoid Apparatus

The paroccipital process of pachyrukhines presents a particular gamma-shaped morphology, which was not observed in the compared extant taxa. Nevertheless, in relation to its large development and transverse flattening, some similarities can be traced with other typotherians (e.g., Billet et al. 2009) and extant artiodactyls, such as *Tragulus* (Figs. 4a, b, 8), and

particularly perissodactyls, such as *Equus* (Barone 1987). Following anatomical comparisons with perissodactyls and artiodactyls and considering the preserved hyoid portion of *P. typicum* (specimen MMP 1008-M; Fig. 8), the anterior process developed in the paroccipital process, could contribute, via connective tissues, to the support of the major horn of the hyoid apparatus. Alternatively, it would serve as an origin area of m. stylohyoideus (in association or not with other muscles originating from this process) that would have originated from the paroccipital process instead of the stylohyoideum bone. A cranially located origin of this muscle also occurs in some rodents, lagomorphs, hyraxes, and the hippopotamus (e.g., Sprague 1942; Jouffroy and Lessertisseur 1971). If this reconstruction is correct, it would indicate a well-developed and forwardly located m. stylohyoideus, contributing to the rising and forwarding of the hyoid apparatus. Additionally, the extended depressed scar along the lateral aspect of the ventral projection of the paroccipital process, and the moderately expanded proximal region of the stylohyoideum were surely the origin and insertion area of the m. occipitohyoideus ("jugulohyoideus" of Sprague 1942 and Turnbull 1970; "mastoideostyloideus" of Jouffroy and Lessertisseur 1971; Barone 1987; Pérez et al. 2010), of which the main function is to move the hyoid posteriorly. The articulation between the bulla and the stylohyoideum is deep and, when sufficiently preserved, seems to guide and limit the maximum range of movements in the anteriorposterior direction (e.g., *P. typicum* MMP 1008-M; *Tremacyllus* MACN Pv 2434). Following the morphofunctional reasoning of Pérez et al. (2010) and the functions of the muscles involved in the inferred paroccipital osteomuscular configuration, the pachyrukhine hyoid was greatly developed and mobile at some degree in its proximal region, in connection with a relatively mobile tongue. Finally, these interpretations should be considered with caution based on the limited available information, the absence of other preserved hyoid elements, requiring more studies and fossil material for a better understanding of this region in pachyrukhines. Considering the subtle differences in the orientation of the paraoccipital process, it is probable that the hyoid apparatus was more forwardly located in *P. typicum* than in *P. bonaerense*, in relation to head and neck postural differences (see below).

Cervical Musculature and Posture

Functional interpretations of the neck morphology are very complex. This is because the cervical vertebrae bear the origin and insertion areas for several metameric muscular systems with diverse functions, which, in turn, can be related to different biological roles (e.g., locomotion, alimentation; Slijper 1946; Argot 2003; Danowitz and Solounias 2015; Ercoli et al. 2017). In addition, available morpho-functional studies

of the neck are not abundant. Beyond these caveats, given that the cervical region is the origin of muscles involved in head and arm movements, its morphology is also very informative for understanding to what extent the masticatory apparatus and forearms are involved, acting separately or in tandem, in functions where both regions could be recruited, such as predation (prey apprehension) and burrowing (tooth- or scratch-digging).

In addition to the already discussed orientation of the occipital plane, other features of the occipito-cervical region of pachyrukhines are similar to those observed in the non-fossorial rodents of our comparative sample (e.g., *Dolichotis*, *Cavia*, *Chinchilla*).

The anteroposterior extension of the neural arch of the atlas is moderate to low, similar to rodents and different from the studied leporid and artiodactyl models, which would indicate a wide freedom of movements and minimal interference between structures during dorsiflexion of the neck (Sargis 2001; Argot 2003; Ercoli 2015). Regarding the other cervical vertebrae, they are moderately compressed and display intervertebral articulations with generalized morphology, the spaces between the neural arches are moderate to well developed (present even in the middle elements), there is no fusion or imbrication between the cervical elements, and the spinous processes are moderately developed. Based on these traits, pachyrukhines would have moderate to short necks, with high capacity of dorsiflexion of the middle and posterior cervical vertebrae. This would have allowed the adoption of a resting posture characterized by a neck retracted in an S-shape, which together with the occipital anatomy (see above) could indicate upward head postures, typically occurring in small quadrupedal mammals (Graf et al. 1995; Arnold et al. 2017; Nalley and Grider-Potter 2017). This morphology is somewhat different from what is observed in *Tragulus*, *Lepus*, *Dolichotis*, and *Heterohyrax* (see Danowitz and Solounias 2015; Arnold et al. 2017), in which the cervical regions (and specifically the middle elements) are elongated; the processes where the ligaments and dorsal muscles attach (e.g., spinous processes) are more developed, and the neck base and the atlas-axis complex assume most of the mobility in the dorsoventral direction (Slijper 1946:56; Graf et al. 1995; Danowitz and Solounias 2015; Arnold et al. 2017). The morphology displayed by pachyrukhines is clearly different from that observed in some specialized ecomorphs, such as bipedal bounders, chisel-tooth diggers, and aquatic species, in which the anterior sector of the neck includes imbricated and/or fused elements that are also anteroposteriorly compressed. Specifically, for fossorial forms, the ecomorphological requirements of those habits result in horizontal resting postures of the neck and often with greater restrictions on mobility between cervical elements (Hatt 1932; Slijper 1946; Gambaryan et al. 2005; VanBuren and Evans 2017), especially in the case of the species that breakdown or throw out the soil with their head (Gambaryan

et al. 2005). For the latter ecomorphs, the minimal development of the cervical spinous processes, added to the marked development and vertical orientation of the spinous processes in the first thoracic elements [accompanied in some cases by the advancement of the lambdoid ridge, see Agrawal (1967); Gambaryan et al. (2005)], would be related to a large space of accommodation and mechanical advantage for mm. splenius and semispinalis cervicalis [some of the main extensors of the head and neck which are markedly developed and active for head lifting during excavation; Gambaryan et al. (2005)] and main neck ligaments (Carrizo and Díaz 2013; Ercoli 2015). This set of features is typically observed in specialist fossorial taxa, such as tooth-diggers, in which the soil is broken or thrown out by head movements (e.g., *Spalax*), but are also encountered in scratch-diggers, which use the head for throwing soil (e.g., *Myospalax*; Gambaryan et al. 2005). In our comparative sample, these features are also observed, although much less markedly, in *Ctenomys* (Fig. 10a; and to a lesser degree in *Cynomys*), which could imply that the dorsiflexion of the neck is relevant to the repertory of movements of this mainly scratch-digging taxon. A different condition is observed in non-fossorial herbivore mammals, in which the spinous processes tilt caudally, and neck resting postures are more elevated (Slijper 1946; Gambaryan et al. 2005). The overall condition of pachyrukhines is more similar to that latter group and argues against tooth-digging abilities or, at least, indicates the absence of active head-lift movements for digging.

Beyond generalities about the cervical morphology and posture common to all pachyrukhines, there is a set of features that point out marked differences among species, both in the muscular proportions and the configuration of attachment scars in the occipital plane, and in the relative development of the processes of the vertebrae. Variations in these traits indicate differences in the spatial accommodation of the different occipito-cervical muscles and are informative about the different motor abilities of the neck in each species.

In *P. typicum*, the occipital plane, the neural arch of the atlas, and the cervical spinous processes are taller, or more vertically directed, than in *P. bonaerense* (Figs. 5, 9). As a first appreciation, this would indicate a larger development and greater mechanical advantage of the main dorsal and medial bundles of the occipital (e.g., rectus capitis dorsalis) and cervical (e.g., spinal and transverse-spinal systems) musculature involved in stabilization or extension of the neck and head (e.g., De Blieux and Simons 2002; Evans and de Lahunta 2013; Álvarez and Ercoli 2017). Nevertheless, considering the mentioned postural changes between these taxa, these morphological differences could, at least partially, reflect a compensation of the mechanical advantage of these muscles in the more ventroflexed typical postures of *P. typicum*. In this species, the alar processes of the transverse processes are somewhat reduced and the dorsal tubers have a more lateral

orientation compared to *P. bonaerense*. Although different interpretations are possible due to the high number of muscular groups attaching to those structures (e.g., Argot 2003:283; Ercoli 2015:345–346), the morphology of *P. typicum* could be interpreted as related to a lateral cervical muscular configuration with a relatively large development of the short bundles belonging to the intertransversarii system (that occupy the space between adjacent transverse processes) and relatively less development of the long bundles that reach the cervical region to insert into the alar processes (e.g., scalenus, longus colli; Jouffroy and Lessertisseur 1971; Argot 2003; Gambaryan et al. 2005; Flores and Díaz 2009; Álvarez and Ercoli 2017; Ercoli et al. 2017).

A distinct configuration is observed in *P. bonaerense*. The occipital plane is more mediolaterally extended (especially the space between the lambdoid and exoccipital crests, Fig. 5b), the spinous process of the axis is tilted caudally, and the alar and the ventral processes and tubercles of the cervical vertebrae are well developed. These features suggest the large development and increased mechanical advantage of the lateral and oblique occipital muscles (involved in movements away from the parasagittal plane; e.g., mm. rectus capitis lateralis and obliquus capitis; Radinsky 1981; Argot 2003:281; Flores and Díaz 2009; Ercoli 2017) and the presence of well-developed long-bundled muscles that would have been located in the lateral and ventral aspects of the neck (e.g., m. longus colli and main lateral neck muscles; Gambaryan et al. 2005; Flores and Díaz 2009; Álvarez and Ercoli 2017; Ercoli et al. 2017). Furthermore, in *P. bonaerense,* the less differentiated and smaller lateral projection of the dorsal tubercles (Fig. 9) indicate a smaller development of the short bundles of the mm. intertransversarii and a larger space for accommodation of the main lateral muscles that run parallel to the cervical vertebrae and attach to the atlas, and to the occipital and mastoid regions of the cranium (Ercoli 2015). These include the lateral and ventral flexors of head and neck, arm protractors, and scapular rotators (e.g., m. omotransversarius, m. sternocephalicus, m. cleidocephalicus, anterior bundles of the mm. scalenus). The condition of *P. bonaerense* is reminiscent of that described for *Cynomys* and *Ctenomys* compared to their non-digging relatives. Regarding *Tremacyllus*, the information about the morphology of the cervical and occipital regions is very sparse, but in some traits it shows intermediate conditions between *P. typicum* and *P. bonaerense*, although it would be differentiated from both, by having a shorter and more delicate neck, with smaller vertebral processes.

From this morphological variability among pachyrukhines, we infer that *P. typicum* would have presented a weaker neck but with abilities for stabilization, control, and extension reinforcing the muscles that support the head and neck, which could be useful to maintain the head in position during rapid bounding-cursorial locomotion. On the other hand, *P. bonaerense* would have had a more robust neck with important lateral and ventral movements, and a more robust anchor for the extrinsic musculature of the anterior limb. As can also be inferred from the frontation degree of the orbits and of the locomotory abilities mentioned above (and see Elissamburu 2004, 2007), the variations in the osteomuscular proportions of the occipito-cervical sector of *P. typicum* and *P. bonaerense* fit quite well with the differences observed between the most cursorial and epigeous rodents and those with more generalized habits (e.g., *Heterohyrax*) or some digging specializations, respectively (see Agrawal 1967; Álvarez and Ercoli 2017). The larger spaces for the accommodation of some of the main extrinsic muscles of the forearm that run through the lateral aspect of the neck could be considered as a support to the previous suggestion of a scratch-digging morphotype for *P. bonaerense* (Elissamburu 2004, 2007). Furthermore, its morphology is clearly different from that observed in specialized tooth-digging taxa, as well as those of scratch-diggers that use the head during burrowing, which display short necks with restricted intrinsic movements and powerful neck extensors (e.g., Agrawal 1967; Gambaryan et al. 2005; VanBuren and Evans 2017). In summary, the more flattened head and the relatively strong neck of *P. bonaerense*, although too long and mobile for active head-lift movement during breakdown or throwing of the soil, would fit with the morphotype of a scratch-digger that may transit along narrow spaces (Agrawal 1967; Gambaryan et al. 2005; Ercoli et al. 2017). Beyond that, this inference does not exclude the possibility of an eventual assistance of the incisors and the occipito-cervical region during other burrowing actions (e.g., biting or pulling subterranean obstacles), or even other activities, in which specific neck movements might be involved (e.g., feeding; Argot 2003).

Bullae, Ears, and Hearing

Small mammals in relatively arid environments are typically characterized by the presence of large auditory cavities, including inflated bullae and epitympanic recesses, to improve low-frequency hearing (Lay 1972; Mason 2016 and references therein). This feature is shared by representatives of many mammalian clades, including carnivorans, dasypodids, rodents, and macroscelideans (Lay 1972; Huang et al. 2002; Squarcia et al. 2007; Mason 2016; Alhajeri and Steppan 2018), and was also observed in *Chinchilla*, among our comparative sample (see Rosowski et al. 2006; Álvarez et al. 2013). Several possible explanations have been proposed for this relationship, including the better air-transmission of low-frequency sounds through large distances in desert environments and detection of ground vibrations for predator avoidance (Lay 1972; Mason 2016 and references therein). The studied pachyrukhines with preserved auditory regions (*Tremacyllus* spp., *P. bonaerense*, *P. typicum*, and *P.* cf.

P. minor) possess large bullae and also large epitympanic recesses (Figs. 2, 4) suggesting adaptations to relatively low-humidity environments, as previously suggested by Cerdeño and Bond (1998). The study of the external neuromorphology of *P. bonaerense* (= *P.* "*insigne*") by Dozo (1997) also agrees with a relatively important level of specializations of the auditory region of this taxon.

Beyond that, there are different configurations of the auditory cavities within pachyrukhines, with *P. bonaerense* having the smallest bullae and epitympanic thecae (that cover the epitympanic recesses; see MacPhee 2014; Mason 2016), and *Tremacyllus* spp. characterized by larger bullae (in both relative and absolute values) than any *Paedotherium* species (Cerdeño and Bond 1998; Ercoli et al. 2018).

Given that *P. typicum*, *P. bonaerense*, and *Tremacyllus* are recorded together in Pliocene deposits of the coast of Argentina (Cerdeño and Bond 1998; Elissamburu et al. 2011; Seoane et al. 2017), and that the *Paedotherium* species are even associated with the same burrows (Elissamburu et al. 2011), the observed differences could be related to microhabitat or other ecological differentiations. An extant example is *Elephantulus*, which possesses auditory cavities significantly smaller than those of other coexisting macroscelideans and rodents, associated with its rock-dwelling habits, in contrast to the open areas exploited by the other taxa (Mason 2016). Following this idea, the morphology of *Tremacyllus* and *P. typicum* could fit better with the utilization of more open areas than *P. bonaerense*, but other ecomorphological interpretations cannot be discarded. For example, Howell (1932: 390-392; see also Mason 2016) documented that among mammals inhabiting arid environments, long eared (i.e., larger pinnae) species possess relatively reduced auditory cavities. *Paedotherium bonaerense* is the pachyrukhine with the smallest auditory cavities, which also bears the largest origin scar for the m. frontoscutularis (discerned by the rugose posterior margin of the postorbital process; Fig. 2a, b), one of the largest muscles that supports and moves the ears. Bramble (1989) suggested that a large development of this muscle and its origin area in leporids is linked to the necessity to support the large erected ears. Interestingly, some additional well-developed scars in the midline of the cranium at the level of the parietal bones observed in both *Lepus* and some pachyrukhines are particularly marked and protruding in *P. bonaerense*. These marks seem to correspond to the origin of other main ear muscles (e.g., mm. parietoauricularis and parietoscutularis; Barone 1987; König and Liebich 2016; Kneepkens and Macdonald 2010; Evans and de Lahunta 2013). Furthermore, MacPhee (2014) suggested an additional scar, the "theca spine" developed in the anterodorsal region of the bullae of pachyrukhines, as indicative of a probable large development of the m. parietoauricularis (Fig. 4a, b), indicating the presence of large heavy ears (MacPhee 2014:39). Although the morphological differences between

pachyrukhines are smaller than those between extant models, the size differences of the bullae and the muscular scars suggest the possible presence of large ears in *P. bonaerense*, probably smaller ones in *Tremacyllus*, and most likely an intermediate condition for *P. typicum*.

Paleobiology and paleoecological roles of *Paedotherium* and *Tremacyllus*

The analysis of the middle and posterior cranial regions, and the cervical vertebrae, allowed the reconstruction of several ecomorphological traits for the studied pachyrukhines, related to vision, hearing, head posture, movements, and, indirectly, some aspects linked to locomotory habits. The morpho-functional analysis of these poorly studied (or previously not considered) anatomical regions complements the bigger picture of the paleobiology of these remarkable rodent-like notoungulates.

As common traits, pachyrukhines possess large orbits, highly specialized auditory structures (in relation to the presence of remarkably inflated bullae and epitympanic recesses, and associated brain structures), and modified cranial structures related to lightening and shock-absorbing mechanisms: features linked to leaping-cursorial habits (Scott 1913; Dozo 1997; Cerdeño and Bond 1998; MacPhee 2014), and the preference of inhabiting relatively low-humidity environments (Cerdeño and Bond 1998; but see Reguero et al. 2015). In relation to this, the facial tilting values (a measure closely related to the frontation of orbits and substrate perception during rapid locomotion; Kraatz et al. 2015) of pachyrukhines overlapped with the values of the leaping-cursorial *Dolichotis*, and were intermediate between the more specialized leaping-cursorial lagomorphs and the rest of the studied extant models, indicating a relatively high specialization to leaping-cursorial habits. This conclusion fits with those of the previous studies of Kraglievich (1926) and Elissamburu (2004, 2007) on the appendicular skeleton. These studies suggested several cursorial adaptations for pachyrukhines (enhanced in *P. typicum*) and particularly for hind limbs and autopodia (e.g., well-developed third trochanter, fusion of tibia and fibula, digitigrady or unguligrady, and reduction of the lateral digits). Additionally, some cranial modifications related to shock absorption during bounds and leaping-cursorial adaptations (e.g., lighter crania and shock-absorbing mechanisms) were also described by MacPhee (2014), in agreement with the presented inferences and comparisons in the present study.

The occipito-cervical anatomy of pachyrukhines indicates movable and moderate to short necks, which do not fit with some specialized fossorial ecomorphs (Gambaryan et al. 2005; see above). Beyond this overall characterization, the studied Neogene pachyrukhines present remarkable differences between these and other features.

Tremacyllus* and *Paedotherium minor These two species, and particularly *P. minor*, are known from relatively fragmentary remains, so the paleobiological inferences are more limited. The partially preserved cervical region of *Tremacyllus* indicates that the species would have a relatively shortened and more delicate neck than *Paedotherium*. *Tremacyllus* was characterized by the presence of a greater inflation of the auditory cavities in comparison to *Paedotherium* in general and *P. bonaerense* in particular. This morphology can be related to better sound perception in drier environments. Nevertheless, considering the conjoint record of representatives of both genera during late Miocene and Pliocene (Cerdeño and Bond 1998; Deschamps 2005; Montalvo et al. 2016), there should have been potential microhabitat differentiation (see Mason 2016), in which *Tremacyllus*, and to a lesser degree *P. typicum* and *P. minor*, would be better specialized to patches of open areas than *P. bonaerense*. Regarding *P. minor*, the major differences in the studied regions, with respect to *Tremacyllus,* are related to the less inflated auditory cavities, but almost all the other structures studied here (e.g., orbits, paraoccipital processes, cervical vertebrae) are unknown for the taxon as far as we know.

Paedotherium bonaerense This species is characterized by a relatively flattened configuration of the occipital plane, relatively reduced spinous processes of posterior cervical vertebrae, and the large development of the transverse and ventral processes in the cervical region. These features indicate a large attachment area for the main ventroflexors and lateroflexors of the neck, and some arm protractors and scapular rotators. This configuration indicates a relatively generalized but also a stronger build of the occipito-cervical region of *P. bonaerense* compared to *P. typicum* and probably *Tremacyllus*. These inferences fit well and complement the interpretation of more generalist or scratch-digging habits for this species compared to *P. typicum*, based on the presence of a large attachment for the main arm extensors and digital flexors and heavily built proportions of the forearm (Elissamburu 2004, 2007). Additionally, beyond the absence of a specialized tooth-digging morphology, the eventual involvement of the incisors when confronting harder obstacles during brachial digging cannot be discarded, as is the case in extant scratch-digging taxa (Fernández 1949; Becerra et al. 2011). A stronger neck could be of substantial assistance in similar situations. A set of features present in *P. bonaerense*, including the larger development of the origin scars of the main ear muscles, and some traits of the auditory region (Howell 1932; Mason 2016; see above), seems to indicate that this species could have the largest ears among the studied pachyrukhines, adding new lines of evidence for this inference raised previously by MacPhee (2014).

***Paedotherium typicum* (Fig. 11)** As was stated above, *P. typicum* would have possessed an auditory configuration and associated structures related to enhanced low-frequency sound perception, preferring incursions into more open patches than its contemporary congener *P. bonaerense*. The configurations of the orbits and facial tilting, as well as the direction of the paraoccipital processes and the inferred osteomuscular cervical configuration indicate that *P. typicum* is the studied pachyrukhine taxon with more upright and stabilized head postures above the body, better panoramic vision, and, in turn, the highest degree of frontation. These latter features are related to the ability of enhancing the perception of the forthcoming substrate during fast-moving epigean running (Howell 1932; Kraatz et al. 2015). All these features, and previous locomotor inferences (Elissamburu 2004, 2007; MacPhee 2014), suggest the presence of cursorial appendicular proportions, the ability of performing fast, rather than powerful movements, and shock-absorbing cranial mechanisms; *P. typicum* would have been the more specialized leaping-cursorial Neogene pachyrukhine. Considering the almost intermediate masticatory apparatus configuration of *P. typicum* with respect to other pachyrukhines such as *Tremacyllus* and *P. bonaerense* (with these taxa possessing more marked abilities to process abrasive and hard objects, respectively; see accompanying contribution Ercoli et al. 2020), the locomotor specialization was probably the main ecological factor that

Fig. 11 Life reconstruction of *Paedotherium typicum*, as a sciuromorphous rodent-like notoungulate, in an upward head resting posture, feeding on hard-food items; illustrating some of the main inferences treated here and in the accompanying contribution (Ercoli et al. 2020)

would have differentiated *P. typicum* from its contemporary relatives.

Final Conclusions

The detailed morpho-functional analyses of the craniomandibular and cervical regions and paleoecological inferences of the latest sciuromorph notoungulates presented in this and the accompanying contribution (Ercoli et al. 2020) allow us to elucidate novel aspects of their rodent-like convergences, as well as to further elucidate their unique combination of features and their interspecific variations.

Beyond the analysis of the typical structures considered in paleobiological reconstructions (e.g., teeth and masticatory muscle attachments), a particular effort has been put to analyze the configuration of some other structures with complementary functional or paleobiological information. Some of the reconstructed features, such as visual field, muscular and postural reconstruction of head, neck, and preserved parts of the hyoid apparatus, and soft tissue reconstructions, including the probable presence of infoldings of the lips and the ear morphology, represent a novelty for pachyrukhines in particular, but also for fossil mammals in general.

The ecomorphological inferences derived from this and the accompanying contribution (Ercoli et al. 2020), as well as the available information, indicate that during the late Miocene only small pachyrukhines (*Tremacyllus* spp., *P. minor*, *P.* cf. *P. minor*, *P. kakai*; Cerdeño and Bond 1998; Reguero et al. 2015; Montalvo et al. 2016; Ercoli et al. 2018), with dietary habits related to high selection of relatively softer and small food items and with mainly epigean habits and a preference for relatively open areas, coexisted in diverse regions of Argentina (from northwestern to central Argentina). More particularly, *Tremacyllus* seems to represent the most modified Neogene lineage that was specialized in several of these aspects. On the other hand, the presence of *P. kakai* in relatively forested and humid environments (Reguero et al. 2015) could suggest variations from this general pattern or a more important environmental plasticity than previously proposed for late Miocene pachyrukhines. However, more fossils are required for a clearer view. During the terminal Miocene (Huayquerian South American Land Mammal Age), larger and progressively more morphologically diverse representatives appeared in the fossil record of specific regions, such as the first record of *P. typicum* in central-western Argentina (Huayquerías Formation; Vera and Ercoli 2018), and *P. borrelloi* in central Argentina (Cerro Azul Formation; Zetti 1972a), including cursorial forms, and masticatory features that indicate hard-items as a more important component of the diet than the smaller pachyrukhines mentioned. During almost all of Pliocene, the small-sized *Tremacyllus* and the larger *P. typicum* coexisted, in addition to a new ecomorph represented by *P. bonaerense* (Cerdeño and Bond 1998;

Deschamps 2005). The last presented a large number of distinctive features, including large-size, digging and less-cursorial adaptations, and the most specialized masticatory apparatus to hard-food item processing. This specialized species represents the most abundant representative of *Paedotherium* in central Argentina during the end of the Pliocene, and the latest surviving lineage of the family (Cerdeño and Bond 1998).

Zetti (1972a) early recognized a differential abundance of the latest pachyrukhine representatives in different localities and ages of the Neogene, but also considered the limitations of our paleoecological knowledge to attempt to explain it. The overwhelming predominance or exclusive presence of *Tremacyllus* or the smallest *Paedotherium* species in northwestern, central-western, and central late Miocene localities of Argentina could be related to the presence of relatively open and drier environments (e.g., Cerro Azul, Arroyo Chasicó formations; Montalvo et al. 2016; Sostillo et al. 2018; Domingo et al. 2020), and the availability of relatively soft and small food items exploited by these taxa. It is important to underline that Domingo et al. (2020) recently proposed diverse habitats (Arroyo Chasicó Formation) or relative dry environments (Salinas Grandes de Hidalgo Formation) for central Argentina, further indicating that notoungulates occupied the more open and drier patches. Differently, the abundance and diversification of pachyrukhines as reflected by the largest and disparate *Paedotherium* species (along with the smaller *Tremacyllus*) during the Pliocene in central-eastern Argentina, could suggest the occupation of new different niches, and a larger diversity of exploited dietary items. This appears to be in accordance with the reconstructed temperate, diversified, and relatively rich environments during this period (e.g., Farola de Monte Hermoso, Chapalmalal formations; Fernández et al. 2000, Cione et al. 2015) in comparison with the previous ones (Domingo et al. 2020). These paleobiological interpretations of pachyrukhines, in addition with the analysis of other paleoenvironmental proxies, could contribute to the understanding of paleoecological and paleoenvironmental changes along the Neogene of southern South America.

Appendix 1. List of analyzed fossil and extant specimens. Preserved main regions are indicated in the case of fossil specimens: C = cranium, V = cervical vertebrae. All extant specimens and indicated fossil ones (ft) were used to calculate facial tilting

Fossil specimens

Paedotherium bonaerense
MACN A 1251-52 (C, V, ft), MACN A 7214 (C, ft), MACN Pv 7520 (V), MACN Pv 18098-100 (C, ft); MLP 99-X-2-1 (C, V, ft); IDGYM s/n (C); MMP 158-S (C, V), 1655-M (C, ft); Cerdeño and Bond (1998) (C)

P. typicum
MACN Pv 6436 (C, V); MLP 12-1782 (C), MLP 52-IX-28-14 (C, ft); MMP 698-S (C, V), MMP 1008-M (C, V, ft), PVL 3386 (C), Kraglievich (1926) (C, V), Cerdeño and Bond (1998) (C)

P. minor
MLP 29-IX-2-20 (C)

P. cf. *P. minor*
MLP 55-IV-28-82 (C)

Tremacyllus spp.
FMNH P 14456 (C, V, ft), FMNH P 14465 (C, ft); MACN Pv 2434 (C, V, ft), MACN Pv 2913 (C, ft), MACN Pv 8157 (C, V, ft), MLP 95-III-31-15 (C)

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
Dolichotis salinicola
FMNH 48019, MACN Ma 17366
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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