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ORIGINAL PAPER

First Approach to the Paleobiology of Extinct *Prospaniomys* (Rodentia, Hystricognathi, Octodontoidea) Through Head Muscle Reconstruction and the Study of Craniomandibular Shape Variation

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Abstract †*Prospaniomys* is a basal octodontoid recorded in the early Miocene in Patagonia (Argentina; Colhuehuapian SALMA). Nearly complete cranial and mandibular remains known for this genus provide a unique opportunity to explore its paleobiology. For this, masticatory muscles were reconstructed and craniomandibular shape variation assessed. While such reconstruction indicates that most masticatory muscles would have presented moderate development, both the masseter lateralis and posterior muscles were poorly developed. In contrast, we found that the temporalis muscle was well developed, while conspicuous postorbital constriction, postorbital processes, and superior temporal lines revealed a substantial orbital portion of this muscle. According to geometric morphometric results, craniomandibular shape was interpreted as generalized. Features such as shortened palate, narrower bizygomatic width, orthodont incisors, enlarged incisive foramina, and a shallow jaw could be linked to epigean habits. The moderate development of auditory bullae in *Prospaniomys* suggests that it is unlikely that it may have lived in extreme arid environments. Additionally, based on its generalized dental morphology, an omnivorous or generalized herbivorous diet that may have included leaves, fruit, and potentially animal matter was inferred. By the early Miocene, Patagonia experienced the initial expansion stage of arid-adapted vegetation, with grasses present in low amounts and abundant forests. Generalized habits and soft and non-abrasive diet suggest that *Prospaniomys* was possibly associated with more closed environments. Morphology alone cannot be used as an environmental proxy, but it could undoubtedly contribute to the interpretations based on data provided by paleobotanical and geological frameworks in studies on the evolution of environments.

Keywords Geometric morphometrics · Masticatory muscles · Functional morphology · Early Miocene · Caviomorphs

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Introduction

Caviomorpha are hystricognathous and hystricomorphous rodents endemic to the Neotropics (Wood 1955; Ojeda 2013). Among them, the Octodontoidea bears the highest specific richness and adaptive diversity (Vucetich et al. 2010a, b; Upham and Patterson 2012; Fabre et al. 2013). Extant Octodontoidea includes the Octodontidae, Ctenomyidae, Echimyidae, Abrocomidae, and Capromyidae (Woods and Kilpatrick 2005; Fabre et al. 2013). Octodontoids from the Oligocene-middle Miocene represent different and independent lineages that are not directly related to modern families (Vucetich and Kramarz 2003; Arnal 2012; Arnal and Pérez 2013; Arnal et al. 2014; Arnal and Vucetich 2015; but see Verzi et al. 2014). One of these basal lineages is represented by *Prospaniomys* (Arnal 2012; Arnal et al. 2014), which is a monospecific octodontoid genus represented by *Prospaniomys priscus* from the Patagonian early Miocene (Colhuehuapian South American Land Mammal Age, SALMA).

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The main goal of paleobiological research is to understand the biological evolution of organisms and primitive communities or biocoenosis through the study of fossil remains (Sepkoski 2009). In this regard, the Cenozoic paleontological record of South American mammals is abundant, especially those of caviomorphs, which provides abundant information on morphological intergeneric variation (Vucetich et al. 2010a, b; Pérez and Vucetich 2011; Álvarez et al. 2011a, b). Despite this, there are few paleobiological works that benefit from the richness of the caviomorph fossil record (De Santis and Moreira 2000; Fernández et al. 2000; Candela and Picasso 2008; Candela et al. 2012; Cox et al. 2015). In this sense, *Prospaniomys* represents the only Colhuehuapian octodontoid with a nearly complete skull providing a unique opportunity to explore diverse aspects of the paleobiology of this rodent.

The analysis of the skull is particularly interesting for paleobiological studies, as it houses the brain and sense organs and forms the orognathofacial complex together with the jaw (Emerson and Bramble 1993). Several factors, such as modes of life, behavior, and diet could encourage morphological adaptations (Hildebrand 1985; Stein 2000). Among the methodologies that paleobiological approaches can use, the reconstruction of musculature provides relevant information that allows generating more reliable models linked to the functioning of the masticatory apparatus. Based on this, several aspects of behavior and diet could be inferred in extinct organisms (see Cox et al. 2015 as an application in an extinct caviomorph rodent). On the other hand, one of the most frequently used techniques to study morphological variation corresponds to geometric morphometrics, which provides highly detailed information on the shape of biological structures (Zelditch et al. 2004). Altogether, these approaches have proven to be effective tools to understand morphological evolution and the paleobiology of organisms (De Iullis et al. 2000; Christiansen 2008; Figueirido and Soibelzon 2010; Prevosti et al. 2012).

The main goal of this work was to undertake the first approach to the paleobiology of the early Miocene octodontoid *Prospaniomys*. In order to do so, we identified the areas of origin and insertion of the principal masticatory muscles and inferred their development. Additionally, we carried out the analysis of craniomandibular shape variation in *Prospaniomys* in an octodontoid context. In order to perform paleobiological inferences about *Prospaniomys*, we compared the morphological features of this genus with those of extant octodontoids for which ecological aspects such as diet and modes of life are well known.

Materials and Methods

Materials

Institutional abbreviations Studied specimens of extinct and extant rodents belong to the following institutions: **CFA**, Fundación Félix de Azara, Buenos Aires, Argentina; **CMI**, Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza, Argentina; **FBM**, Victoria Island Biological Station, Bariloche, Argentina; **MACN PV**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Colección Paleontología Vertebrados, Buenos Aires, Argentina; **MACN Ma**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Colección Nacional de Mastozoología, Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MMPMa**, Museo Municipal de Ciencias Naturales "Lorenzo Scaglia," Mar del Plata, Buenos Aires, Argentina; **MPEF-PV**, Museo Paleontológico Egidio Feruglio, Paleontología Vertebrados, Trelew, Argentina; **UNB**, Mammal Collection of the Zoology Department, Universidade do Brasília, Distrito Federal, Brazil.

The paleobiological study of *Prospaniomys* was based on a nearly complete skull (MACN PV CH1913; Fig. 1a and b) and mandible (MPEF-PV 5039; Fig. 1c). The former comes from outcrops near Cerro Sacanana and the latter from Bryn Gwyn, both outcrops belonging to the Sarmiento Formation (early Miocene localities, Colhuehuapian SALMA) from Chubut Province, Argentina (Fleagle and Bown 1983; Scasso and Bellosi 2004). Although these materials come from different localities, their assignation to *Prospaniomys* was accepted (Arnal 2012), and we therefore combined their morphological information in our analysis.

We studied the myological material of one specimen of *Kannabateomys amblyonyx* (Echimyidae; MACN Ma 52.25)

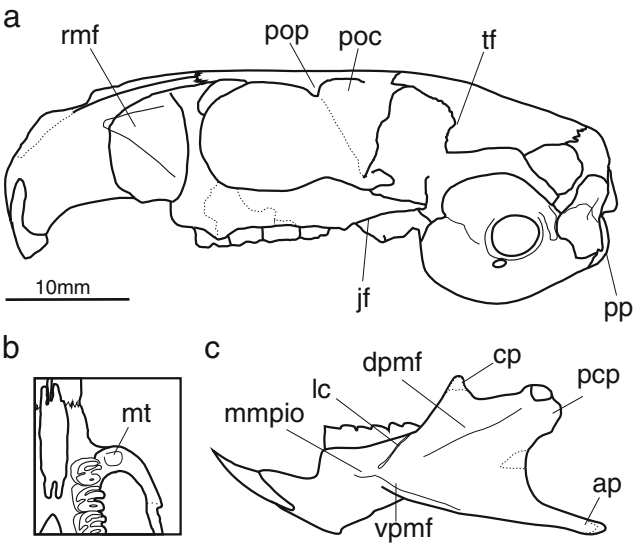

Fig. 1 **a**, **b** Cranial (MACN PV CH1913) and **c** mandibular (MPEF-PV 5039) anatomy of *Prospaniomys*. Abbreviations: *ap* angular process; *cp* coronoid process; *dpmf* dorsal portion of the masseteric fosa, *jf* jugal fossa, *lc* lateral crest, *mmpio* notch for the insertion of the *masseter medialis pars infraorbitalis*, *mt* masseteric tuberosity, *pcp* postcondyloid process, *poc* postorbital constriction, *pop* postorbital process, *pp* paraoccipital process, *rmf* rostral masseteric fossa, *tf* temporal fossa, *vpmf* ventral portion of the masseteric fossa

and one specimen of *Octodontomys gliroides* (Octodontidae; MACN Ma 41.135), because both species have a skull morphology similar to that of *Prospaniomys* (Arnal and Kramarz 2011). Both specimens were originally fixed in a formalin solution (exact solution is not known), and subsequently stored in 70 % ethanol.

We analyzed the craniomandibular shape variation in 14 octodontoid species (Table 1). Systematic arrangement follows Woods and Kilpatrick (2005) except for *Myocastor*, which, according to Fabre et al. (2013), is placed within Echimyidae.

Methods

Muscular Reconstruction

Knowledge on muscle anatomy is not readily available in fossils and is therefore heavily dependent on reconstruction (Bryant and Seymour 1990; Blanco et al. 2012; Lautenschlager 2013). For this purpose, extant taxa offer valuable insights on muscle anatomy and topology. Thus, we used the muscular pattern observed in living caviomorphs to reconstruct the areas of origin and insertions of the main masticatory muscles of *Prospaniomys*. Additionally, we used the data obtained from the dissections (Fig. 2) of the masticatory muscles of *Kannabateomys* and *Octodontomys*, and we followed the muscular scheme of Woods and Howland (1979). We reconstructed the masseter, temporalis, and digastricus muscles of *Prospaniomys*. In caviomorphs, musculus masseter is divided into four branches: masseter lateralis, m. posterior, m. superficialis, and m. medialis. For the superficial masseter we reconstructed two of the three portions [pars principalis and pars reflexa; the latter is characteristic of hystricognathous jaws (Tullberg 1899)] and inferred the presence of the pars anterior. For the medial masseter we reconstructed pars infraorbitalis and pars zygomaticomandibularis. Although masseter lateralis, medialis pars zygomaticomandibularis, and digastricus are partitioned into several subdivisions (Woods 1972; Woods and Howland 1979; Cox and Jeffery 2011), we reconstructed these muscles as a sole muscular mass as their subdivisions are not clearly reflected on the bony sites of attachment. The temporalis muscle is divided into a main portion and an orbital one. The origin area of the pterygoideus muscles (i.e., the pterygoid fossa and adjacent surface on the base of the skull) was damaged in the fossil specimen. Therefore, we were unable to reconstruct these muscles in *Prospaniomys*.

Table 1 Taxa included in the geometric morphometric analyses. N, number of specimens. *Clyomys* was not included in the analysis of the lateral view of cranium

	N	Collection numbers
Abrocomidae		
Abrocoma	6	FBM 01466, CMI 03769, CMI 07011, CMI 07012, CMI 07080, MACN 18828
Ctenomyidae		
Ctenomys	8	MACN 23197, MACN 23205, MACN 23207, MACN 23235, MACN 23236, MACN 23257, MACN 23259, MACN 23263
Echimyidae		
Clyomys	1	UNB 2079
Echimys	3	MACN 31160, MACN 31158, MACN 328
Euryzygomatomys	2	CFA 6001, MACN 18103
Kannabateomys	5	CFA 2413, CFA 4608, MACN 49354, MACN 5147, MACN 5249
Myocastor	7	MACN 16272, MACN 16323, MACN 19367, MACN 19375, MLP 16IV983, MLP 20XII8929, MLP 30XII0272
Proechimys	4	MACN 50339, MACN 50343, MACN 50340, MACN 50343
Thrichomys	6	MMPMa 1243, MMPMa 1246, MMPMa 1247, MMPMa 1248, MMPMa 1296, MMPMa 1297
Octodontidae		
Aconaemys	4	MLP 17II9202, MLP 17II9205, MLP 17II9208, MLP 17II9210
Octodon	5	MLP 12XI0214, MLP12XI0215, MLP 12VII882, MLP 12VII885, MLP 12VII886
Octodontomys	11	MACN 17832, MACN 17834, MACN 17835, MACN 17837, MACN 2792, MACN 2794, MACN 2795, MACN 3052, MLP 25XI981, MMPMa 2532, MMPMa 3557
Octomys	4	CMI 03067, CMI 06852, CMI 6855, IMCN-CM 024
Spalacopus	3	MMPMa 3585, MMPMa 3590, MMPMa 3807
Tympanoctomys	9	CMI 07098, CMI 07249, CMI 07269, CMI 07270, CMI 07271, CMI 07273, CMI 07274, CMI 07275, CMI 07276

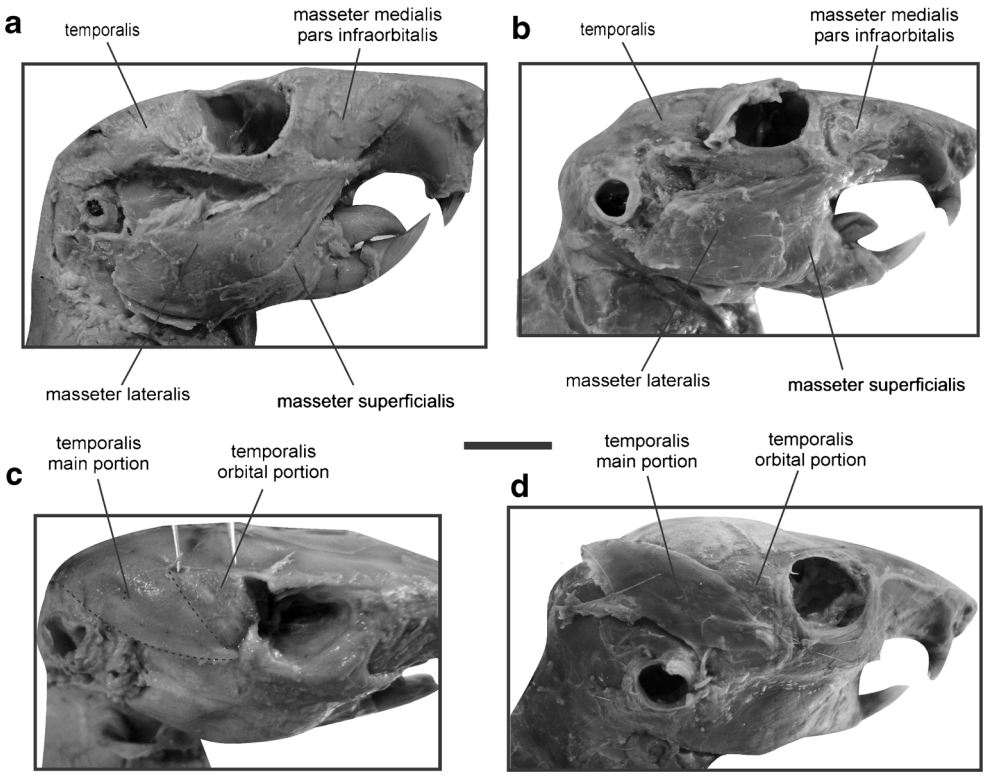

Fig. 2 Muscular arrangements of the living octodontoids dissected: (**a**, **c**) the echimyid *Kannabateomys* and (**b**, **d**) the octodontid *Octodontomys*. **a** and **b** show the overall masticatory muscular arrangement; **c** and **d** show in detail the two portions of the temporalis muscles. Scale bar: 10 mm

Analysis of Skull and Mandible Shape

We assessed the shape variation of the skull and mandible of *Prospaniomys* and compared it with other octodontoid genera (Table 1). Such analysis was carried out by means of geometric morphometric techniques through the use of two-dimensional landmarks + semi-landmarks that were recorded on digital images using the tpsDig software (Rohlf 2010). Images were standardized for skull, mandible, and camera lens plane position, and the distance to camera lens (Zelditch et al. 2004). We analyzed the skull in lateral and ventral views and the mandible in lateral view, because they depict functionally informative features (e.g., attachment areas of masticatory muscles). We recorded 27 landmarks (17 type I, ten type II; landmark types as defined by Bookstein 1991) + 29 semi-landmarks for the lateral view of skull; 19 landmarks (six type I, 13 type II) + nine semi-landmarks for the ventral view, 11 landmarks (five type I, six type II) for mandible (Fig. 3; Appendix 1). To remove any differences in location, orientation, and scaling (i.e., non-shape variation) of the landmark and semi-landmark coordinates, we performed three separate generalized Procrustes analyses (Rohlf and Slice 1990), one for each shape dataset. The mean shape for each caviomorph genus was computed by averaging the Procrustes shape coordinates. We performed a Principal Component Analysis [Relative Warps (RW) Analysis] on the resulting Procrustes coordinates in order to summarize and describe the major trends in cranial and mandibular shape variation among genera. For the purpose of interpreting morphological features of *Prospaniomys*, we made comparisons with living octodontoids that were distributed among three broad habit categories (Nowak 1991; Eisenberg and Redford 1999; Lessa et al. 2008; Sobrero et al. 2010): epigean (*Abrocoma*, *Echimys*, *Kannabateomys*, *Proechimys*, *Thrichomys*), fossorial (*Clyomys*, *Euryzygomatomys*, *Aconaemys*, *Octodon*, *Octodontomys*), and subterranean (*Ctenomys*, *Spalacopus*). Differences in shape were described in terms of the variation in deformation grids (Bookstein 1991). The morphometric analysis was performed using MorphoJ (Klingenberg 2011).

Results

Reconstruction of Head Muscles

Masseter superficialis

The origin area of this muscle corresponds to the masseteric tuberosity on the ventral surface of the inferior zygomatic root (Woods and Howland 1979). In the case of *Prospaniomys*, it is shallower and shorter laterally than in *Kannabateomys* and *Octodontomys* (Arnal and Kramarz, 2011; Fig. 1b). Hence, a moderate development of the tendon of this muscle can be inferred for the fossil species (Fig. 4a). In caviomorphs, this

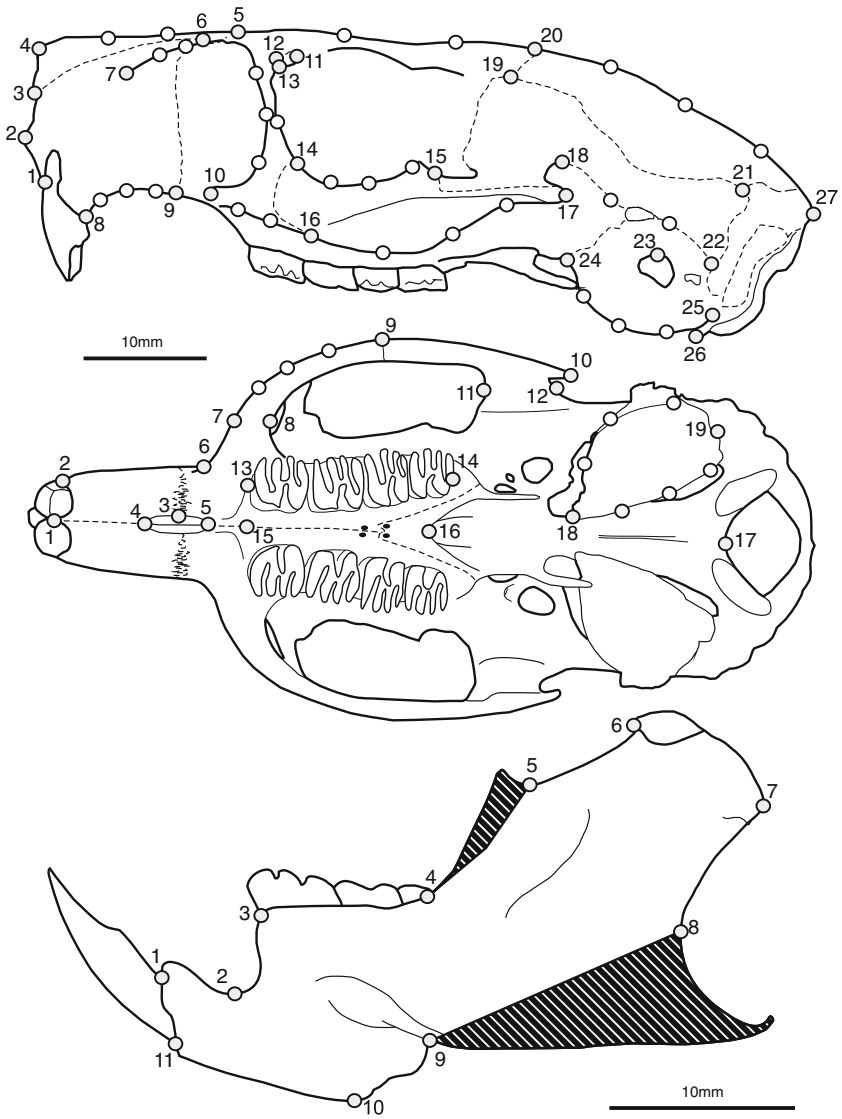

Fig. 3 Schematic representation of the cranium and mandible of the living echimyid *Kannabateomys* showing the placement of landmarks (*gray points*) and semi-landmarks (*white points*) used in the present study. Definition of landmarks is in Appendix 1

muscle is divided into three portions (Woods and Howland 1979). The pars principalis inserts onto the ventral margin of the angular process on the mandible, which extends moderately backwards in *Prospaniomys* (Figs. 1 and 4a). The pars reflexa leaves no marks, so neither its origin or insertion areas nor its development could be accurately determined. However, it usually fills the hystricognathous groove (Woods and Howland 1979) dorsally as far as the postcondyloid process (Woods 1972) (see Woods 1972; Fig. 4d). This part of the mandible is low and little extended in *Prospaniomys*, indicating a likely poor to moderate development of this portion (Fig. 4a). The pars anterior is present in several caviomorphs, and is restricted to octodontoids and chinchilloids [e.g., *Echimys*, *Isothrix*, *Myocastor*, *Ctenomys*, *Octodon*, *Capromys*, *Geocapromys*, *Chinchilla*, and *Lagostomus* (Woods 1972; Woods and Howland 1979; Álvarez 2012)] and is missing in *Erethizon*, *Cavia*, and *Dasyprocta* (Woods 1972). Due to its constant occurrence among octodontoids, its presence could not be discounted for *Prospaniomys* (Arnal 2012; Arnal et al. 2014; Fig. 4a). This portion of the masseter superficialis originates from the main tendon and inserts onto the ventral surface of the alveolar sheath of the mandibular incisors without leaving any marks; consequently, its development could not be estimated for *Prospaniomys*. The features described above suggest an overall moderate development of the masseter superficialis in the fossil.

Masseter lateralis

In extant species this masseter branch originates from the ventral surface and ventrolateral edge of the maxillary and anterior jugal portions of the zygomatic arch; this origin extends to the inferior jugal process (Fig. 2a–b). In *Prospaniomys*, the

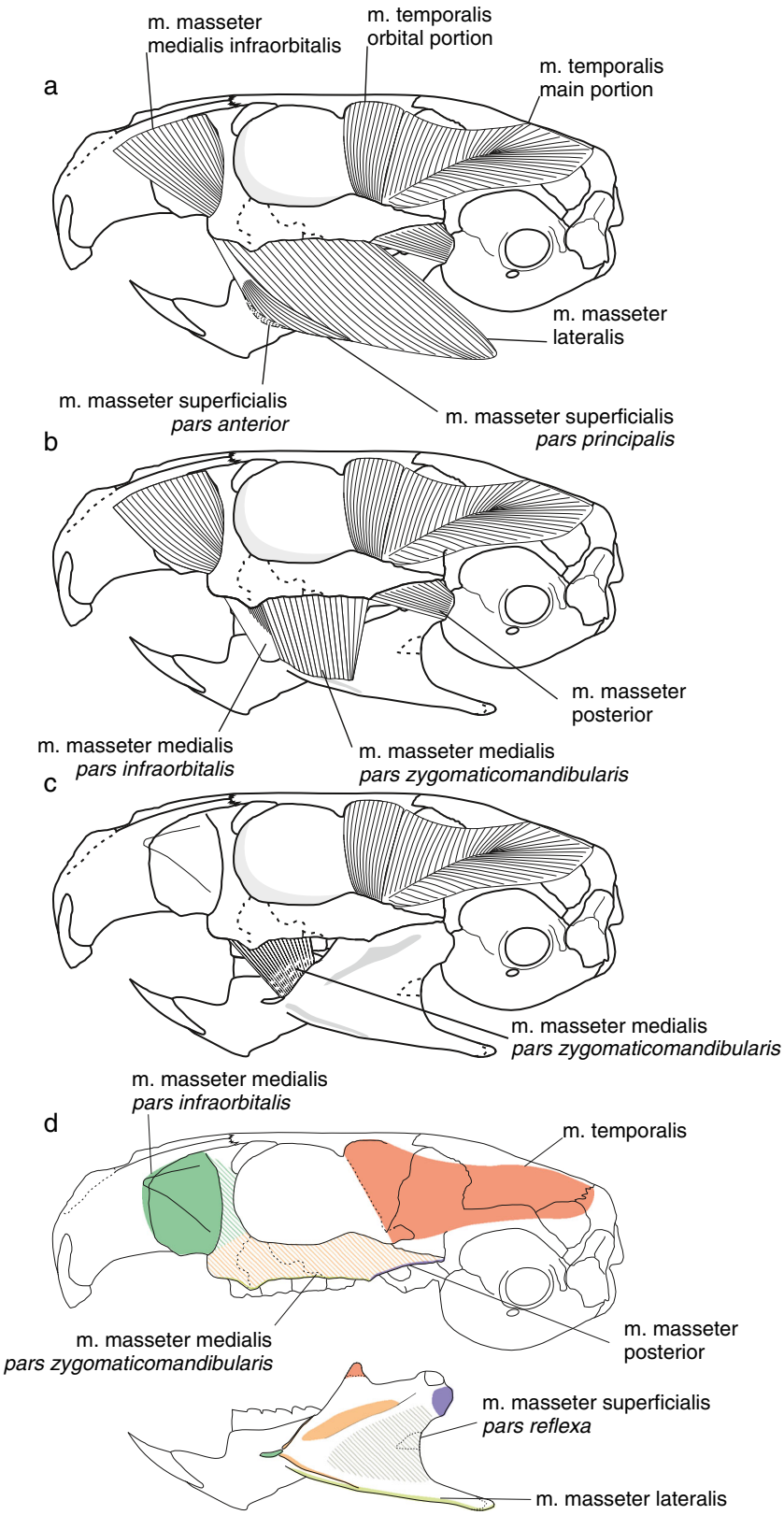

Fig. 4 **a**–**c** Reconstruction of the main masticatory muscles of *Prospaniomys*. **d** Areas of origin (*skull*) and insertion (*mandible*) of the masticatory muscles. Striped areas represent origin and insertion areas onto the medial surface of the bones. Dotted lines indicate broken areas of bones

posterior portion of the horizontal ramus of the zygomatic arch is wider labio-lingually than in the dissected living species due to the absence of a well-developed lateral jugal fossa (Woods and Howland 1979; Fig. 1). The insertion area of this muscle, represented by the dorsal border of the masseteric crest and the ventral margin of the mandible, is not expanded

in *Prospaniomys* (Fig. 1). The anterior portion of the masseteric crest is laterally extended as in the dissected living species, but at the level of the m3 this crest becomes less evident, which indicates that this muscle would not be posteriorly developed as in *Kannabateomys* and *Octodontomys* (Figs. 2b and 4b). Masseter lateralis would have presented a moderate to good development in the fossil genus (Fig. 4a).

Masseter posterior

The origin area of this masseter branch corresponds to the lateral jugal fossa. In *Prospaniomys* it is short and shallow and is only ventrally exposed (Arnal and Kramarz 2011; Fig. 1), unlike in *Octodontomys* and *Kannabateomys* where it is greatly expanded (Fig. 2a and b: this muscle has been removed). Unlike the studied living octodontoids, the fibers would have been almost horizontal and inserted onto a low positioned postcondyloid process (with respect to the level of the occlusal plane of the molars) (Fig. 4b). This process has a moderate expansion in *Prospaniomys* (Fig. 1), slightly larger than in *Octodontomys* and smaller than in *Kannabateomys*. The osteological features suggest poor development of the masseter posterior in the fossil species (Fig. 4b), compared to some living octodontoids (*Kannabateomys*, *Octodontomys*, *Capromys*, *Geocapromys*, and *Plagiodonta*).

Masseter medialis

- pars infraorbitalis: this branch of the masseter medialis originates from the rostral masseteric fossa, which is anteriorly extended in *Prospaniomys* (Fig. 1). In this genus, there is no ridge into the fossa indicating the anterior extension of the muscle, as in *Octodontomys*. The fibers would have been posteroventral and passed through the infraorbital foramen, converging into a robust tendon that inserted into a well-developed notch in the mandible (Figs. 1 and 4b). In *Prospaniomys* this notch lies below m1, and it is parallel to the anteroposterior axis of the mandible, as in *Kannabateomys* and *Octodontomys*, although it is more conspicuous than in the living species. Therefore, a slightly greater development of this muscle than in the dissected living species can be inferred (Fig. 4b).

- pars zygomaticomandibularis: this branch of the masseter medialis originates from the internal surface of the horizontal and vertical rami of the zygoma. In *Prospaniomys*, the horizontal ramus is low and the vertical one is robust, although somewhat constrained in its central portion (Fig. 1). This would indicate a development of this muscle similar to that presented by *Octodontomys*, which has similar or slightly smaller origin surfaces (Fig. 2b). Conversely, *Kannabateomys* presents a dorsoventrally higher and labiolingually more extended horizontal zygomatic ramus than in *Octodontomys* and *Prospaniomys* (Fig. 2a). The insertion onto the mandible is variable in the living species, making its reconstruction difficult in *Prospaniomys*. Nevertheless, the mandibular features of the fossil specimen allow us to infer, with some degree of certainty, the insertion areas of this muscle. *Prospaniomys* presents an evident lateral crest (sensu Woods 1972) in the lateral surface of the mandible, at the level of the m1 (Fig. 1), which presents a similar development as that of *Kannabateomys* and it is more conspicuous than in *Octodontomys*. The dorsal portion of the masseteric fossa is well marked (Fig. 1), as in *Octodontomys*. The anterior part of the ventral portion of the masseteric fossa is also conspicuous and has a lateral border (Fig. 1), similar to that seen in *Kannabateomys*. Hence, this muscle would have inserted onto three principal areas in the fossil: the lateral crest, the dorsal portion of the masseteric fossa, and the anterior margin of the ventral masseteric fossa (Fig. 4b, c and d). The above cranial and mandibular features suggest the moderate development of this muscle and an extension similar to *Kannabateomys*, with greater fiber concentration in the anterior portion of the ventral masseteric fossa.

Temporalis

The main portion of this muscle originates in the temporal fossa, which is shallow and considerably more laterally expanded in *Prospaniomys* than in the studied living species. The great extension of both temporal fossae delimited a low sagittal crest (Fig. 1) that is similar to that seen in *Octodontomys* (Fig. 2d). These features indicate a broad extension of the main portion of the temporalis in *Prospaniomys* (Fig. 4a). Additionally, the parietals and the posterior portion of the frontals present low rims, conspicuous postorbital constriction, and a well-developed postorbital process (Fig. 1); all these features indicate the presence of a very well-developed orbital portion of the temporalis, more than in the dissected species (Fig. 4a). The coronoid process and the retromolar fossa represent the insertion areas of the main portion and orbital portion, respectively. Both structures are well developed in *Prospaniomys* (Fig. 1), which corroborates the great development of both temporalis branches.

Digastricus

The paraoccipital process, which represents the origin of the digastricus, is anteroposteriorly compressed and attached to the bulla in *Prospaniomys* (Arnal and Kramarz 2011). The same condition is present in *Octodontomys* and most octodontids. The posterior portion of the mandibular symphisis is the area for the insertion of digastricus but, unfortunately, it was broken in MPEF 5039 (the mandible used here). Therefore, in order to infer the development of this muscle we used specimens MACN A 52–131 (holotype)

and MPEF 7563 in which this portion of the mandible was preserved. On the ventral surface and posterior to the symphysis is a well-marked scar for the insertion of the digastricus that extends upto the posterior border of m1 and a well-developed mental prominence, as in *Kannabateomys*. Such arrangement suggests the presence of a well-developed digastricus.

Morphometric Analysis

The resulting ordination of extant and extinct caviomorphs obtained through the analysis of lateral cranial shape variation is plotted in Fig. 5a. The first three RWs explained 72 % of the total variation. A separation of octodontoid families was observed in the morphospaces of RW1, 2, and more clearly in RW1, 3. At the same time, most fossorial and subterranean taxa grouped together near the central values of the three axes. Octodontids were located near the origin along both axes, except for *Tympanoctomys*, which occupied extreme negative values of RW1; the ctenomyid *Ctenomys* was located on positive values of RW2 and the abrocomid *Abrocoma* distributed with most octodontids; most echimyids were located on positive values of RW1 and negative ones of RW2, except for *Euryzygomatomys*, which was situated near central values and *Myocastor*, which occupied positive values in both axes. *Prospaniomys* was located near central values of RW1 and on slightly negative values of RW2, distributed along echimyids, although its RW1 score matched those displayed by fossorial octodontids and echimyids. The distribution of genera along RW3 was less spread. Octodontids distributed near central values of the axis; *Abrocoma* was located on extreme positive values; and echimyids were distributed along central to slightly negative values of RW3. *Prospaniomys* was located on positive values of RW3, near the fossorial octodontid *Octodon*. Major shape changes toward negative values of RW1 were linked to an enlargement of the auditory bullae, the reduction of the squamosal bone, and a zygomatic arch that tapers backwards. Shape changes associated with negative values of RW2 involved a relative moderate-size of the auditory bullae, narrower and lower rami of the zygomatic arch, ventral inclination of the nuchal plate, and orthodont upper incisors. Cranial shape towards negative values of RW3 was related to a relative moderate-size of the auditory bullae, robust rami of the zygomatic arch, large squamosal bone, and shorter rostrum and masseteric rostral fossa. Shape changes toward positive values could be described as following opposite trends.

The resulting ordination of extant and extinct caviomorphs obtained through the analysis of ventral cranial shape variation is plotted in Fig. 5b. The first three RWs explained 77 % of the total variation. Although the relative position of genera in the morphospace of RW1, 2 was similar to some extent to that obtained for the lateral view of the cranium, which follows the familiar scheme, the dispersion among genera was higher, especially among echimyids. Octodontids appeared along RW1 and towards positive values of RW2; among them, *Tympanoctomys* was distributed on extreme negative values of RW1. *Ctenomys* was distributed on central values of both axes; *Abrocoma* was distributed on negative values of RW2; most echimyids were distributed on positive values of RW1 and some on negative ones of RW2, while *Euryzygomatomys* and *Clyomys* were situated near central values of RW1 and positive ones of RW2; *Myocastor* occupied positive values in both axes. *Prospaniomys* was located near *Abrocoma*. With respect to the morphospace constructed by RW1, 3, octodontids were distributed around central values of RW3; *Abrocoma* occupied positive values of RW3 together with *Ctenomys* and *Myocastor*; echimyids, except *Myocastor*, were distributed along central to slightly negative values of RW3. *Prospaniomys* was positioned at central values of RW3, near the fossorial *Octodon* and *Euryzygomatomys*. Major shape changes associated with negative values of RW1 involved enlarged auditory bullae, narrower bizygomatic width, and shorter inferior root of the zygomatic arch. Cranial shape changes towards negative values of RW2 were related to moderately-sized auditory bullae that are slightly elongated antero-posteriorly, elongated incisive foramina, almost parallel tooth rows, and narrower bizygomatic width at the caudal region of the zygomatic arch. Shape changes associated with negative values of RW3 involved relative moderately-sized auditory bullae, wider incisive foramina, parallel tooth rows, and a shorter rostrum linked to a forwardly extended inferior root of the zygomatic arch. Shape changes toward positive values could be described as following opposite trends.

The resulting ordination of extant and extinct caviomorphs obtained through the analysis of lateral mandibular shape variation is plotted in Fig. 6. The first three RWs explained 70 % of the total variation. Again, fossorial and subterranean taxa grouped together in the morphospace depicted by RW1, 2. Within it, octodontids distributed along RW1 and positive values of RW2; *Abrocoma* was distributed on extreme negative values of RW2; echimyids were situated along positive values of RW1 and on negative values of RW2. *Prospaniomys* was situated at central values of both axes, very close to the epigean echimyid *Thrichomys*. In the morphospace of RW1, 3, octodontids spread along the third axis; *Ctenomys* and *Abrocoma* were situated on negative values of RW3; echimyids were situated on positive values of RW3, with the exception of *Euryzygomatomys*, *Clyomys*, and *Myocastor*, which were located between central and slightly negative values. *Prospaniomys* was distributed on positive values of RW3 where most echimyids and some octodontids were distributed. Major mandibular shape changes toward negative values of RW1 were related to a dorsal expansion of the postcondyloid process and deeper mandibular and semilunar notches. Shape changes toward negative values of RW2

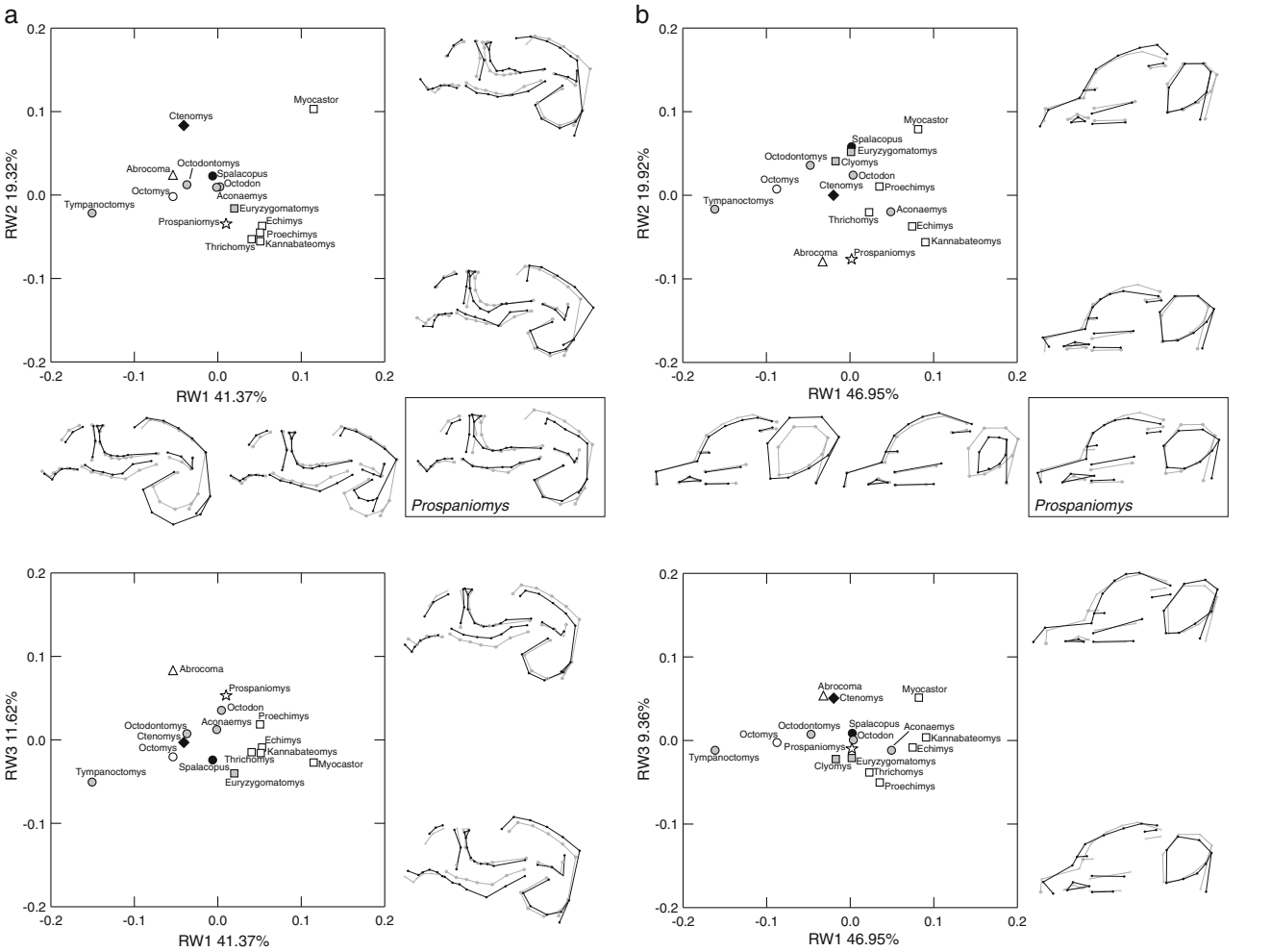

Fig. 5 Ordination of octodontoid genera in the morphospaces defined by the first three relative warps obtained in shape variation analyses of (**a**) lateral view and (**b**) ventral view of cranium. Symbols represent caviomorph families: *triangles*, abrocomids; *circles*, octodontids; *squares*, echimyids; *diamonds*; ctenomyids; *star*, *Prospaniomys*. Colors represent habits: *white*, epigean; *gray*, fossorial; *black*, subterranean. Cranial shape changes along relative warps (RW 1, 2, 3), from negative (−) to positive (+) values, are shown as deformation grids

involved shallower mandibles with longer diastemata, a shallower semilunar notch, and a backwardly elongated postcondyloid process. Shape changes associated with negative values of RW3 involved deeper mandibles and diastemata.

To sum, *Prospaniomys* showed a variable relative position throughout the analyses. It was located close to octodontids, especially to the fossorial *Octodon*, in cranial analyses, although it shared some features of the cranial ventral view with the epigean *Abrocoma*. Its mandibular shape was basically similar to that of the epigean echimyid *Thrichomys*. The fossil species showed a relatively moderate-sized auditory bullae, a slightly shallow horizontal ramus of the zygomatic arch, and a shorter masseteric rostral fossa. In addition, it showed enlarged incisive foramina, orthodont incisors, slightly convergent tooth rows, and a reduced bizygomatic width at the caudal region of the zygomatic arch. Regarding the mandible, it was slightly shallow, as well as were the semilunar and mandibular notches.

Discussion

This study represents the first attempt to reconstruct the masticatory musculature of an early Miocene octodontoid. The accomplished reconstruction indicates that most masticatory muscles of *Prospaniomys* would have presented a moderate development, except for the temporalis and masseter posterior. The reconstructed configuration matches the overall myological arrangement present in caviomorphs (Woods 1972; Woods and Howland 1979; Cox and Jeffery 2011), including the octodontoids *Octodontomys* and *Kannabateomys* studied here for the first time. Most muscles were reconstructed with confidence because their origin and insertion areas correspond to well-defined and constant cranial and mandibular structures (e.g., the temporal fossa and coronoid process for the temporalis). However, other muscular features were reconstructed with a degree of uncertainty given that the attachment areas are

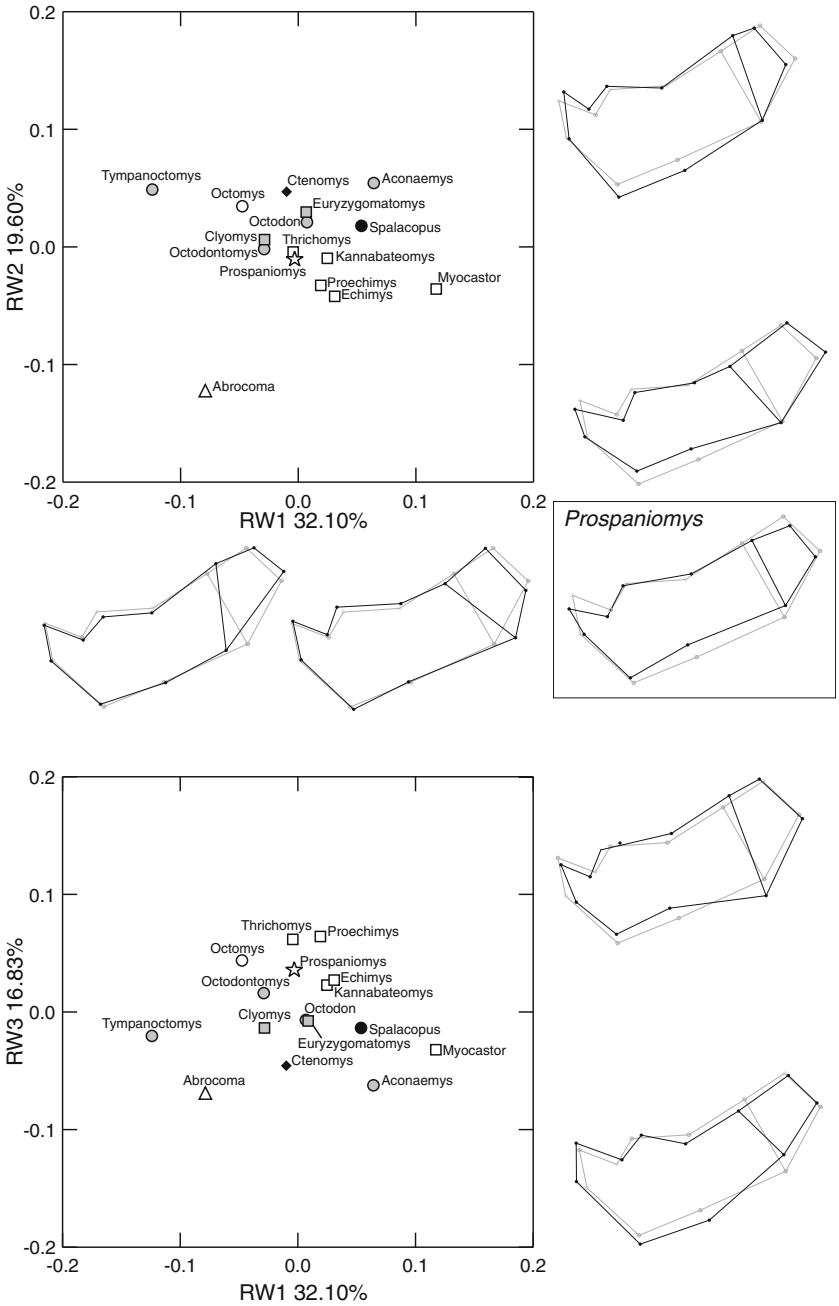

Fig. 6 Ordination of octodontoid genera in the morphospaces defined by the first three relative warps obtained in shape variation analysis of mandible. Symbols represent caviomorph families: *triangles*, abrocomids; *circles*, octodontids; *squares*, echimyids; *diamonds*; ctenomyids; *star*, *Prospaniomys*. Colors represent habits: *white*, epigean; *gray*, fossorial; *black*, subterranean. Mandibular shape changes along relative warps (RW1, 2, 3), from negative (−) to positive (+) values, are shown as deformation grids

not well defined: the insertion of the masseter superficialis leaves little scarring on the mandible and its reconstruction was estimated based on scanty osteological features.

One of the most variable muscles among caviomorphs, especially regarding the insertion area, is the masseter medialis pars zygomaticomandibularis. Overall, two morphologies can be distinguished among octodontoids: on the one hand, *Kannabateomys* and other echimyids (see Woods 1972:fig. 3; Woods and Howland 1979:fig. 10) present a concentration of fleshy fibers inserted onto the anterior end of the mandibular masseteric crest and the ventral masseteric fossa; on the other hand, *Octodontomys*, as well as other octodontids (and chinchillids, Wood and White 1950:fig. 3; Becerra et al. 2011:fig. 4; Álvarez 2012) show the insertion of this muscle onto the dorsal masseteric fossa. A third condition, interpreted as a modification of the latter, is represented among extant members of Caviidae (Cavioidea), in which the dorsal masseteric fossa and the notch for the insertion of the masseter medialis pars infraorbitalis are surrounded by a conspicuous crest (horizontal crest sensu Pérez 2010; see Woods 1972). A condition similar to that observed for echimyids is inferred for *Prospaniomys*; this configuration could suggest stronger vertical forces exerted by these muscles to elevate the jaw against food resistance when gnawing at the incisors (see discussion

for the anterior part of the deep masseter in Hiiemae 1971; Cox et al. 2012, 2013). A similar function could be regarded for the masseter medialis pars infraorbitalis, although a forward origin for this muscle in *Prospaniomys* suggests that it could be involved in the generation of uniform forces along the tooth row during chewing, which would be necessary when processing vegetal material (Herrel et al. 2012).

Associated with the overall moderate development of musculature inferred in *Prospaniomys*, the masseter lateralis and superficialis showed less development than in the dissected living octodontoids. Additionally, the presence of a short and shallow lateral jugal fossa indicates the poor development of the masseter posterior, unlike most octodontoids (*Octodontomys*, *Kannabateomys*, *Myocastor*, *Proechimys*, *Euryzygomatomys*, *Capromys*, *Geocapromys*, *Plagiodonta*, and *Abrocoma*). At the same time, the jugal fossa of the fossil is slightly more developed than in non-octodontoids caviomorphs (e.g., *Cavia*, *Dasyprocta*, *Lagostomus*, and *Coendou*; Woods 1972). Consequently, *Prospaniomys* would have presented an intermediate degree of development of masseter posterior between that of the octodontoids and non-octodontoids caviomorphs, which would suggest a relatively moderate force exerted by this muscle (see Becerra et al. 2014). Regarding the digastric muscle, it is classified as a mandibular depressor (Hiiemae 1971; Gorniak 1985; Lev-Tov and Tal 1987); a relatively large size of this muscle could be related to a wide and powerful opening of the mandible (as it is related in Carnivora; see Scapino 1976), which could be linked to the type of diet proposed for *Prospaniomys* (see next paragraph).

In contrast with the overall moderate development of masseteric musculature, the temporalis would have been well developed. The conspicuous postorbital constriction, postorbital processes, and superior temporal lines observed in *Prospaniomys* reveal a likely substantial orbital portion of the temporal muscle, which is somewhat similar to the condition observed in *Myocastor* (Woods and Howland 1979). It has been suggested that a well-developed orbital portion is used to stabilize and elevate the mandible (Hiiemae 1967; Cox and Jeffery 2011). Markedly, the postorbital constriction in *Prospaniomys* is more developed than in any other fossil or living caviomorph. A large postorbital process, which is related to the presence of a robust postorbital ligament, and a pronounced postorbital constriction, prevents orbital content distortion (due to the action of masseter and temporal muscles) and the consequent disruption of oculomotor precision (Heesey 2005; Herring et al. 2011). This condition could be related to a predominance of crushing movements during mastication rather than grinding (see Klingener 1964; Woods 1972; Cox and Jeffery 2011). As previously mentioned, *Prospaniomys* would have presented an overall moderate development of masticatory muscles, with predominance of both masseter medialis and temporalis. This condition would suggest that *Prospaniomys* may have been efficient for gnawing at the incisors and processing food through the combination of grinding and, most probably, crushing movements. Additionally, the tooth morphology of *Prospaniomys* [brachyodont and tetralophodont upper and lower cheek teeth; sub-quadrangular and bunolophodont, with evidenced cusps in young-adult specimens, narrow crests, and wide and relatively deep valleys (Arnal and Kramarz 2011)] is typically associated with relatively soft or omnivorous diets (Marschallinger et al. 2011; Lister 2013).

Regarding the craniomandibular shape analysis, the main distribution pattern of octodontoids followed the systematic arrangement of families used in the analysis, although a clear array of fossorial and subterranean taxa around central areas of the morphospaces was evident. The most divergent shapes were displayed by *Tympanoctomys*, *Myocastor*, and *Abrocoma*, by the presence of a hypertrophied auditory bulla, a robust zygomatic arch, and a long rostrum, respectively, and differences in mandibular shape. *Prospaniomys* differentiated from the remaining studied taxa in the ventral view of cranium (together with *Abrocoma*) by the length of the incisive foramina and the narrowness of the zygomatic arch. The position of *Prospaniomys* in morphospaces was variable because it was located among epigean octodontoid taxa (*Thrichomys* or *Abrocoma*), or near fossorial ones (*Octodon*). Features such as shortened palate, narrower bizygomatic width, orthodont incisors, enlarged incisive foramina, and a shallow mandible could be linked to epigean or fossorial habits, but may indicate the absence of tooth-digging habits, like those displayed by the subterranean *Ctenomys* and *Spalacopus*. Tooth-digging requires greater development of the masticatory muscles, especially of the masseter group (see Becerra et al. 2014), as well as procumbent incisors suitable to deal with the substrate when excavating their burrows (Stein 2000; Becerra et al. 2012). On the other hand, the relative size of the auditory bullae was demonstrated to have a clear association with environmental variation (in terms of vegetal cover and humidity) among caviomorphs (Hautier et al. 2012; Álvarez et al. 2013). In particular, caviomorphs with enlarged auditory bullae are adapted to semi-arid/arid environments (Ebensperger et al. 2006, 2008; Traba et al. 2010). Bullar hypertrophy is especially marked in desert-adapted octodontids such as *Tympanoctomys* and *Pipanacoctomys*, which are convergent with other desert-specialist rodents such as the North American heteromyid *Dipodomys* (Ojeda et al., 1999; Mares et al. 2000). The adaptive meaning of this pattern is not clear, but the most accepted hypothesis proposes that a large bullar size would increase sensitivity to low-frequency sounds as a strategy to detect predators in open environments (Lay 1993). Thus, a moderate development of auditory bullae in *Prospaniomys* would suggest that this rodent would not have lived in an extreme environment like the above-mentioned octodontids.

Another important ecological feature that derives from using morphological analyses is the diet. Most living rodents are herbivorous or omnivorous while some species are carnivores, piscivores, and insectivores (Samuels 2009). Caviomorphs can be regarded as mainly herbivorous (Croft et al. 2011), while some echimyids species are omnivorous or at least incorporate some animal material (Nowak 1991); insectivory has been proposed for some extant echimyids and fossil octodontoids (Vucetich and Verzi 1996; Lessa and Costa 2009). Broadly, herbivores can be split into generalized and specialist categories (Samuels 2009). Generalized herbivores have a diet composed primarily of soft leafy vegetation or seeds whereas specialist herbivores are those that consume fibrous plants such as grasses that contain silica particles (i.e., phytoliths) and can include dust and grit (Samuels 2009). Herbivores present a generally more massive skull linked to a greater development of masticatory and neck muscles, and show a variable degree of incisor procumbency. These features are exalted in specialist rodents as grass consumption demands greater occlusal pressure that can be accomplished by the enlargement of these muscles (Satoh 1997; Samuels 2009). In addition, the ingestion of intrinsic and exogenous abrasives by graminivorous species is related to an increase in tooth wear and the degree of hypsodonty (Williams and Kay 2001). Among caviomorphs, taxa that are known to feed on grass have hypsodont molars (see Williams and Kay 2001), whereas the diet of living taxa that present low-crowned teeth, as is the case of living echimyids, includes leaves and fruits and may incorporate insects (Nowak 1991; Croft et al. 2011). Hence, the overall moderate development of the masticatory musculature displayed by *Prospaniomys* could suggest an omnivorous or generalized herbivorous diet. Additionally, an anteriorly extended masseter medialis pars infraorbitalis can be related to nuts and seeds gnawing, or to folivory (Cox et al. 2012, 2013; Herrel et al. 2012). Moreover, the molar morphology, the moderate tooth row length, and the presence of orthodont, short, and uncompressed incisors (Arnal and Kramarz 2011) are features that can be linked to this kind of diet (Croft et al. 2011).

Paleoclimatic conditions inferred for the early Miocene of central Patagonia characterize this period as the initial stage of expansion of arid-adapted vegetation, although with grasses still present in low amounts and abundant forests (Barreda and Palazzesi 2010; Barreda et al. 2010). The craniomandibular and muscular configurations, together with a soft and non-abrasive diet and epigean/fossorial habits (and excluding a specialist herbivorous diet and tooth-digging activities if this taxon was a burrower at all) inferred for *Prospaniomys*, suggests that this genus was a taxon possibly associated with environments with a certain degree of vegetal cover and non-arid conditions. Nevertheless, *Prospaniomys* co-habited with other potentially adapted caviomorphs, according to their dental morphologies, to more open environments with xerophitic elements [i.e., cephalomyids (Ameghino 1897; Kramarz 2001a), chinchilloids (Kramarz 2001b; Vucetich et al. 2010a), and eocardiids (Ameghino 1887; Pérez and Vucetich 2012)].

The reconstruction of the ecological and behavioral features within a paleobiological framework represents a required tool to interpret the ecological role of extinct organisms within the community they were part of, and it gives valuable information to improve our understanding of the evolution of species. Furthermore, although morphology alone cannot be used as an environmental proxy, it could undoubtedly benefit from the interpretations based on data provided by paleobotanical and geological frameworks in studies on the evolution of environments.

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Appendix 1

Definition of landmarks used in this study (numbers as in Fig. 3). *Lateral view of cranium*: 1, anterior lower end of premaxillary bone (on sagittal plane); 2, anterior upper end of premaxillary bone (on sagittal plane); 3, anterior end of suture between nasal and premaxillary bones; 4, anterior end of nasal bone; 5, junction of sutures among premaxillary and frontal bones, and dorsal margin of cranium; 6, junction of sutures among premaxillary, maxillary, and frontal bones; 7, anterior end of masseteric fossa of rostrum; 8, antero-ventral border of incisor alveolus; 9, junction between maxillar-premaxillar suture and ventral margin of rostrum; 10, most anterior point of zygomatic arch; 11, junction between lacrimal and frontal bones on antero-dorsal margin of orbit; 12, junction of sutures among maxillary, lacrimal, and frontal bones; 13, junction between jugal and lacrimal bones on anterior margin of orbit; 14, dorsal junction between maxillary and jugal bones; 15, dorsal junction between jugal and squamosal bones; 16, ventral junction between maxillary and jugal bones; 17, posterior tip of zygomatic arch; 18, postero-dorsal end of cranial glenoid fossa; 19, junction of squamosal, frontal, and parietal bones; 20, junction between frontal-squamosal suture and dorsal margin of skull; 21, junction of squamosal, parietal, and occipital bones; 22, junction of squamosal, occipital, and tympanic bones; 23, most dorsal point of

external auditory meatus; 24, anterior end of auditory bulla; 25, posterior end of auditory bulla; 26, tip of paraoccipital process; 27, most posterior point of skull. *Ventral view of cranium*: 1, lateral edge of upper incisor; 2, medial edge of upper incisor; 3, junction between maxillary-premaxillary suture and lateral margin of incisive foramen; 4 and 5, extremities of incisive foramen; 6, intersection between margins of rostrum and zygomatic arch; 7 and 8, maximum length of ventral root of zygomatic arch; 9, lateral junction between maxillary and jugal bones; 10, posterior tip of zygomatic arch; 11 and 12, anterior and posterior ends of glenoid fossa, at their mid-point; 13 and 14, anterior and posterior ends of tooth row; 15, junction between maxillary and palatine bones in sagittal plane; 16, posterior (midsagittal) tip of palate; 17, most ventral point of foramen magnum; 18 and 19, anterior and posterior ends of auditory bulla. *Lateral view of mandible*: 1, anterodorsal border of incisor alveolus; 2, extreme of diastema invagination; 3, anterior end of mandibular tooth row; 4, anterior end of base of coronoid process; 5, maximum curvature of incisura mandibulae; 6, anterior edge of condylar process; 7, posterior-most edge of postcondyloid process; 8, maximum curvature of curve between postcondyloid process and angular process; 9, dorsal-most point on ventral border of mandibular corpus; 10, posterior extremity of mandibular symphysis; 11, anteroventral border of incisor alveolus.

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