



Functional morphology of the forelimb of Early Miocene caviomorph rodents from Patagonia

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Caviomorph rodents (New World Hystricognathi) are represented in the Santa Cruz Formation of Patagonia (Early Miocene, Santacrucian) by four superfamilies. From this unit, excellent cranial and associated postcranial remains of *Neoreomys*, *Eocardia*, *Schistomys* (Cavioidea), *Perimys* (Chinchilloidea) and *Steiromys* (Erethizontoidea) are known. To interpret their use of substrate, a comparative description of limb bones (scapula, humerus, radius and ulna) of the five genera was performed within a taxonomic and ecologically diverse sample of extant rodents. Using palaeobiological inferences based on the habits and functional morphology of members of the extant sample, hypotheses were generated for the use of substrate by the Santacrucian taxa. *Neoreomys* would have had a marked flexo-extension capacity of the humerus and a moderate flexion of the manus. This genus and *Eocardia* would have had a complete and stabilized forearm extension, with wide stride and moderate extension of the forearm for the latter. *Schistomys* presents features similar to *Eocardia*. *Perimys* would have had strong external rotation of the humerus, moderate flexion of the manus and moderate, complete and stabilized extension of the forearm. *Steiromys* would have had good pronation/supination capacity, strong internal rotation of the humerus and flexion of the forearm and manus. *Neoreomys* would have been ambulatory and an occasional runner. *Eocardia* and *Schistomys* would have been good runners. *Perimys* would have been a digger and *Steiromys* a climber. This morphological disparity reflects a high ecological diversity, compatible with differential use of space during the Santacrucian. □ *Biomechanics, palaeobiology, palaeoecology, Santa Cruz Formation, substrate use.*

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Hystricognathi, one of the main clades of Rodentia, are represented in South America by the endemic group Caviomorpha (Wood & Patterson, *in* Wood 1955). Among the Caviomorpha, four main clades are identified as superfamilies, both in traditional systematic proposals and in the more recent cladistic analyses: Erethizontoidea (porcupines), Octodontoida (spiny rats, coruros, coypus and hutias), Chinchilloidea (chinchillas, plains viscacha and pacaranas) and Cavioidea (agoutis, cavies, maras and capybaras) (Huchon & Douzery 2001; Blanga-Kanfi *et al.* 2009; Fabre *et al.* 2012). During a large part of the Cenozoic (from the Middle Eocene in Peru and the Early Oligocene in Chile; Flynn *et al.* 2003; Antoine *et al.* 2012), a taxonomically diverse group of caviomorphs evolved in isolation in South America. In the early Miocene Santa Cruz Formation (SCF) of Patagonia, an important and diverse sample (20 genera *sensu* Scott 1905) of caviomorphs is recorded (Ameghino 1887; Scott 1905; Candela 2000; Pérez 2010). The four extant superfamilies

were already represented in the SCF, which allows comparison of the Santacrucian and extant rodents within the same taxonomic levels (Candela *et al.* 2012).

The SCF is the most geographically large and fossiliferous Tertiary continental unit of Argentina, appearing discontinuously in localities scattered throughout the southern Patagonia (Marshall 1976; Vizcaíno *et al.* 2012). The outcrops of the SCF of the Atlantic coast between the Coyle and Gallegos rivers contain exceptionally rich faunal remains with an excellent state of preservation (Vizcaíno *et al.* 2010, 2012). Tauber (1997) described a series of fossil levels with vertebrate remains and proposed a biostratigraphical system. However, recent reviews indicate that many of them represent different facies rather than a temporal sequence (Fleagle *et al.* 2012; Perkins *et al.* 2012). Thus, the fossil levels 1–7 proposed by Tauber (1994) for this part of the coast have been considered to contain a single palaeofauna (Kay *et al.* 2012). The fossils studied in this work are

present in at least one of four localities (Anfiteatro, Estancia La Costa, Puesto Estancia La Costa, Cañadón Silva) that represent a brief temporal span (Kay *et al.* 2012; Perkins *et al.* 2012).

Here, we study five genera of three superfamilies of Santacrucian caviomorphs for which clearly associated and well-preserved cranial and postcranial remains are known: *Neoreomys*, *Eocardia* and *Schistomys* (Cavioidea), *Perimys* (Chinchilloidea) and *Steiromys* (Erethizontoidea). As discussed in Vizcaíno *et al.* (2012, 2016), the characteristics of Santacrucian remains make them especially well-suited for investigations on palaeobiological aspects. In the above-mentioned literature, a protocol for palaeobiological studies is proposed, based on at least three key biological attributes: body size, substrate use and preference (including posture and locomotion), and trophic habits.

In this contribution, we present a review and expansion of previous hypotheses (*Neoreomys*, *Eocardia* and *Steiromys*; Candela & Picasso 2008; Candela *et al.* 2012) focused on functional morphology of the forelimb in a comparative approach, as well as new analyses for unexplored taxa (*Schistomys* and *Perimys*). This work is part of a larger analysis of the whole appendicular skeleton, which includes inferences based on both forelimb and hindlimb morphology. The goals were to analyse anatomical features to reconstruct the set of functions that the limbs of different taxa were able to perform and then infer faculties allowed by those functional properties. Finally, we hypothesize on biological roles on a contextualized palaeoautoecological framework.

Materials and methods

Institutional Acronyms: AMNH, American Museum of Natural History, New York, USA; CNP, Centro Nacional Patagónico, Puerto Madryn, Argentina; MACN, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina; FMNH, Field Museum of Natural History, Chicago, USA; MCN, Museu de Ciências Naturais, Porto Alegre, Brazil; MLP, Museo de La Plata, La Plata, Argentina; MMP, Museo Municipal de Ciencias Naturales Lorenzo Scaglia, Mar del Plata, Argentina; MPM, Museo Regional Provincial ‘Padre M. J. Molina’, Río Gallegos, Argentina; and YPM, Yale Peabody Museum, Princeton University, New Haven, USA.

The fossil Caviomorpha analysed comprise 26 specimens (Table 1). We described four bones of the appendicular skeleton (scapula, humerus, radius and ulna) (complementing anatomical descriptions of

Table 1. Fossil rodents analysed in this work.

Superfamily	Species	Collection number	
Cavioidea	<i>Neoreomys australis</i>	YPM VPPU 15104; YPM VPPU 15394; YPM VPPU 15960	
	<i>Neoreomys</i> sp.	MPM-PV 17446; MPM-PV 17449; MPM-PV 3520; MPM-PV 3521; MPM-PV 4342	
	<i>Eocardia excavata</i>	YPM VPPU 15211	
	<i>Eocardia fissa</i>	MPM-PV 3683	
	<i>Eocardia montana</i>	YPM VPPU 15385	
	<i>Eocardia perforata</i>	YPM VPPU 15463	
	<i>Schistomys ellipticus</i>	YPM VPPU 15648	
	<i>Schistomys erro</i>	YPM VPPU 15383	
	Chinchilloidea	<i>Perimys onustus</i>	MACN A 10158
		<i>Perimys puellus</i>	YPM VPPU 15284
		<i>Perimys scalaris</i>	YPM VPPU 15063
		<i>Perimys</i> sp.	MPM-PV 15040; MPM-PV 15053; MPM-PV 17443; MPM-PV 3684; MPM-PV 3689
Erethizontoidea		<i>Steiromys curtus</i>	MACN A 10055–10078
	<i>Steiromys duplicatus</i>	YPM VPPU 15156	
	<i>Steiromys</i> sp.	MPM-PV 17444; MPM-PV 17445	

Scott 1905) while comparing them with homologous elements of extant caviomorph rodents (Table 2).

We digitized the bones with a 3D NextEngine laser scanner and associated software Scanstudio version 2.0.2, which was also used for the first post-processing stage. The post-processing was continued in MeshLab version 1.3.3 (Cignoni *et al.* 2008) until clean meshes of right laterality (mirroring the left) were obtained. For creating figures, the Radiance scaling complement developed by Granier *et al.* (2012) for MeshLab was used for improving visualization of the convexities and concavities of the three-dimensional model, hence facilitating visualization of details. Three-dimensional scans allow reconstruction of the osseous elements by allowing combining fragments even from opposite sides (through mirroring) of the individual to create a complete skeletal element. Using this technique, left and right fragments of the same individual were used to generate a more complete piece of the radius of *Schistomys* YPM VPPU 15648 and the ulna of *Perimys* MPM-PV 1505, as shown in the descriptions.

Osteological terminology follows Rose & Chinery (2004) and Candela & Picasso (2008). The myological nomenclature, including attachment areas as well as general function for each muscle, is based on Woods (1972) and McEvoy (1982).

To perform functional analysis, we follow concepts defined by Bock & von Wahlert (1965) and

Table 2. Extant rodents analysed in this work.

Superfamily	Species	Substrate use	Collection number
Cavioidea	<i>Dasyprocta azarae</i>	Runner	CNP 790; CNP 896
	<i>Cuniculus paca</i>	Ambulatory	MMP Ma 22; MACN 49.396
	<i>Hydrochoerus hydrochaeris</i>	Ambulatory	MACN 31.18; MACN 43.43; MACN 14038
	<i>Pediolagus salinicola</i>	Runner	MLP 1081
	<i>Dolichotis patagonum</i>	Runner	MLP 208; MLP 252; MLP 236; MLP 275
	<i>Cavia aperea</i>	Ambulatory	MLP 15.II.96.49
Chinchilloidea	<i>Microcavia australis</i>	Ambulatory	MACN 34.7; MLP 7.IV.99.7
	<i>Chinchilla chinchilla</i>	Jumper	MACN 45.11; MACN 13037
	<i>Lagidium viscacia</i>	Jumper	MACN 44.25; MLP 29.XII.00.3; MLP 2021
Erethizontoidea	<i>Lagostomus maximus</i>	Digger	MLP 27.IV.95.1; MACN 48.85
	<i>Coendou spinosus</i>	Climber	MCN 2586; MCN 2680; MCN 2681
Octodontoidea	<i>Myocastor coypus</i>	Digger, swimmer	MLP 09.IX.97.02; MLP 1172
'Empty'	<i>Ctenomys australis</i>	Digger	MLP 7.XI.95.7

Source for substrate use: Nowak & Paradiso (1983); Candela *et al.* (2017).

discussed and expanded in Plotnick & Baumiller (2000) and more recently by Vizcaíno *et al.* (2016): trait is a part of an organism, including morphology, behaviour and physiology; form is the appearance, configuration, composition of a feature; function is what a trait does or how it works; faculty is what a trait is capable of doing in the life of an organism; biological role refers to how the organism uses a faculty during its life in the context of its environment. Therefore, first we describe the form, then model a function or functions, propose hypotheses about faculties, and speculate about biological roles (Plotnick & Baumiller 2000). In addition, the known substrate use of the extant sample is used in the comparisons as part of the palaeoecological analysis.

Results

Form

Scapula. – Recorded scapulae are very scarce and fragmented (Fig. 1), or absent, as in the case of *Schistomys*. The scapular blade has an almost complete preserved contour in only one specimen of *Eocardia* (Fig. 1B). In this genus, the supra and infraspinous fossae are equally developed and the scapular blade is elongated and narrow as in *Pediolagus* and *Dolichotis*. In *Perimys* (Fig. 1C), the scapular blade is more anteroposteriorly extended than in *Eocardia*, and the supraspinous fossa is twice as wide as the infraspinous fossa, at least in the

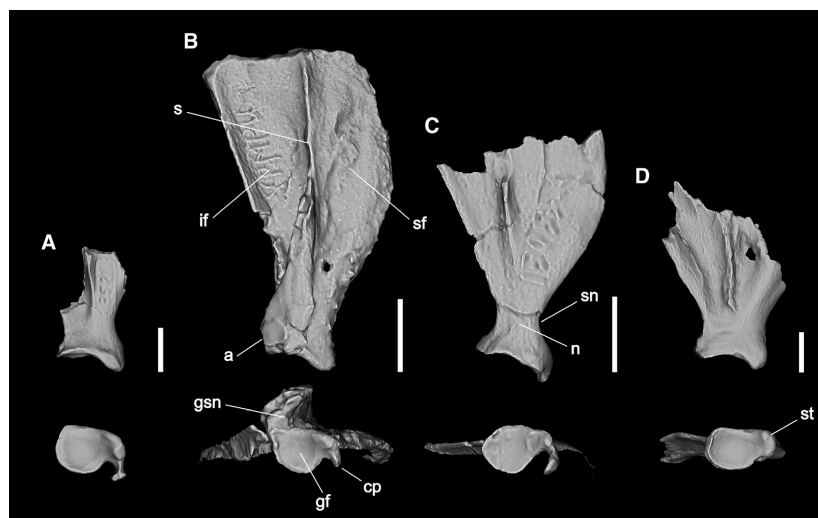


Fig. 1. Right scapulae of Santacrucian rodents in lateral and ventral view. A, *Neoreomys* MPM-PV 3521. B, *Eocardia* YPM VPPU 15211. C, *Perimys* MPM-PV 15053; D, *Steiromys* MPM-PV 17444. a, acromion; cp, coracoid process; gf, glenoid fossa; gsn, great scapular notch; if, infraspinatus fossa; n, neck; s, spine of the scapula; sf, supraspinatus fossa; sn, suprascapular notch; st, supraglenoid tubercle. Scale: 10 mm.

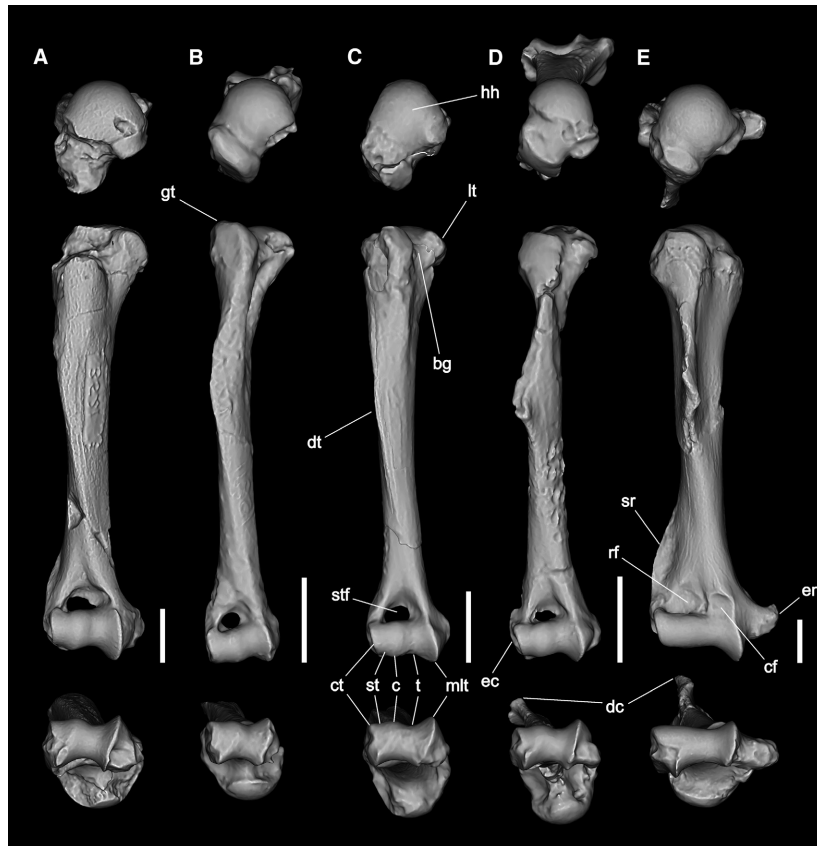


Fig. 2. Right humeri of Santacrucian rodents in proximal, anterior and distal view. A, *Neoreomys* MPM-PV 3521 (mirrored). B, *Eocardia* YPM VPPU 15211 (mirrored). C, *Schistomys* YPM VPPM 15648 (left and right combined). D, *Perimys* MPM-PV15053 (mirrored). E, *Steiromys* MACN A 10055–10078. bg, bicipital groove; c, capitulum; cf, coronoid fossa; ct, capitular tail; dc, deltopectoral crest; dt, deltoid tuberosity; ec, ectepicondyle; en, entepicondyle; gt, greater tuberosity; hh, humeral head; lt, lesser tuberosity; mlt, medial lip of the trochlea; rf, radial fossa; sr, supracondylar ridge; st, 'second trochlea'; stf, supratrochlear foramen; t, trochlea. Scale: 10 mm.

preserved portion. The difference in size between the supra- and infraspinous fossae is greater than in *Cuniculus*. In the rest of the Santacrucian rodents studied here, scapular blade remains are not complete enough to analyse these features.

The neck and the ventral portion of the scapular blade in *Steiromys* (Fig. 1D) are more robust than in the other Santacrucian rodents. In this genus, the supra- and infraspinous fossa have a sub-equal development. The spine of the scapula is not well preserved (with the exception of *Eocardia*). The ventral contact of the spine with the blade could reflect the size of the great scapular notch. This notch could have been larger in *Perimys* than in *Neoreomys* and *Steiromys*. In *Eocardia*, the great scapular notch is more pronounced than in *Cuniculus*, but less so than in *Cavia* or *Microcavia*. The acromion was observed only in *Eocardia*, and its preserved portion reaches the level of the glenoid fossa and presents a posterior expansion. The suprascapular notch of the scapula is deeper in *Perimys* than in the other genera. In *Steiromys*, this notch is almost absent.

The contour of the glenoid fossa is piriform in *Neoreomys*, *Eocardia* and *Perimys*, and oval in *Steiromys*. The supraglenoid tubercle is less developed in *Eocardia* and *Perimys* than in *Neoreomys* and *Steiromys*, and the last one exhibits the greater robustness of this tubercle.

The coracoid process is short in *Neoreomys* and *Eocardia* (as in *Cuniculus* and *Dolichotis*) and very elongated in *Perimys* (similar to *Lagostomus*). This process is not preserved in any specimen of *Steiromys*.

Humerus. – There is great morphological diversity among the humeri of Santacrucian rodents (Fig. 2). The general morphology of the humerus of *Eocardia* and *Schistomys* (Fig. 2B, C) is similar to that of *Dasyprocta*, whereas the humerus of *Neoreomys* (Fig. 2A) resembles that of *Cuniculus*. The humerus of *Perimys* (Fig. 2D) is similar but more slender than that of *Lagostomus*, and the one of *Steiromys* (Fig. 2E) resembles a more robust humerus of *Coendou*. In *Perimys*, *Eocardia* and *Schistomys*, the humerus shows similar robustness, while *Neoreomys*

and *Steiromys* present the most robust humeri, particularly the latter.

The humeral head is more lateromedially compressed in *Schistomys* and *Perimys* than in the remaining genera. In *Steiromys*, the head is hemispherical. In all the Santacrucian genera, the head is posteriorly oriented with respect to the proximodistal axis of the bone. In *Steiromys*, the posterior displacement of the head is less marked than in the other analysed genera. This genus presents, in addition, the greater lateromedial convexity of the humeral head. In *Neoreomys*, the greater tuberosity is not preserved in any of the analysed specimens. In *Eocardia*, the greater tuberosity is wide and high (exceeding the level of the head), as in *Dasyprocta*. In *Schistomys*, the preserved portion of this tuberosity has a shape and size similar to that of *Eocardia*. In *Perimys* and *Steiromys*, the greater tuberosity does not reach the proximal level of the head. In *Neoreomys*, *Schistomys* and *Perimys*, the lesser tuberosity reaches the level of the head (it is not preserved in *Eocardia*). In *Steiromys*, this tuberosity is markedly lower than the head.

Steiromys has the widest bicipital groove, while *Perimys* bears the narrowest, with the remaining genera presenting intermediate morphologies. In *Neoreomys*, *Eocardia* and *Schistomys*, the deltoid tuberosity occupies about two-thirds of the bone. In *Perimys* and *Steiromys*, the deltoid tuberosity extends reaching approximately the middle of the bone and forms a very pronounced deltopectoral crest (=deltoid crest). In the case of *Perimys*, this crest is oriented laterally and resembles, both in position and relative size, that of *Ctenomys*, *Myocastor* and *Lagostomus*. In *Steiromys*, the deltopectoral crest has a triangular shape in lateral view and is directed anteriorly, as in *Coendou*. The supracondylar ridge in *Eocardia* and *Schistomys* is not developed. In *Perimys*, it is very small, whereas in *Neoreomys*, it has a moderate development. In *Steiromys*, this ridge is highly developed and occupies the distal third of the bone.

While the ectepicondyle is incipient in all fossil genera, the entepicondyle shows different degrees of development. In *Eocardia*, it is poorly developed, and in *Schistomys*, it is more protruded. In *Neoreomys* and *Perimys*, the entepicondyle is more developed than in the former genera, being similar to that of *Cuniculus* and *Dasyprocta*. *Steiromys* has the most medially extended entepicondyle among Santacrucian rodents, being almost as long as half the trochlea length (which is longer than that of *Ctenomys* and *Coendou*). The olecranon fossa is perforated in all genera (=supratrochlear foramen), excepting *Steiromys* in which it is shallow. The radial and coronoid fossae are only differentiable in

Steiromys. In the other genera, both fossae converge in a larger fossa that connects through a supratrochlear foramen with the olecranon fossa.

The distal articular surface shows a very similar morphology in *Neoreomys*, *Eocardia*, *Schistomys* and *Perimys*. In these four genera, this surface is lateromedially short and proximodistally high, with an inclined (anteromedial–posterolateral) plane of articular rotation (as in *Dolichotis*, *Pediolagus* and extant chinchillids). In addition, in these genera, the capitulum has a very marked capitular tail that generates a small ‘second trochlea’. In *Steiromys*, the distal articular surface is more extended lateromedially than in the other genera and the capitular tail is incipient. The medial lip of the trochlea in *Neoreomys*, *Schistomys*, *Perimys* and *Steiromys* is much protruded distally, farther than in *Eocardia*.

Radius. – Only the radii of *Neoreomys*, *Eocardia* and *Perimys* (Fig. 3) have a complete diaphysis preserved. In all three cases, the diaphysis is similarly curved, bending anteriorly and hence having a posterior concavity. The stouter radius is that of *Neoreomys* (Fig. 3A), which resembles that of *Cuniculus*. *Perimys* (Fig. 3D) has the most slender radius, and its morphology is more similar to that of *Dasyprocta*. The radius of *Eocardia* (Fig. 3B) is intermediate in robustness between *Neoreomys* and *Perimys*, being slightly straighter than in the latter. In all genera, the cross-section of the diaphysis is oval (expanded lateromedially) in its proximal portion, sub-circular in its middle portion and slightly sub-triangular in its distal portion.

The radial head of *Neoreomys* is very elongated lateromedially. In *Perimys*, and to a lesser extent in *Schistomys* (Fig. 3C), the radial head is also lateromedially elongated, but to lesser extent than in *Neoreomys*. In *Eocardia*, the radial head is less extended lateromedially, and it shows a sub-rectangular contour. The radial head of *Steiromys* (Fig. 3E) has an oval outline. In accordance with the capitular tail present in the humerus, the radial heads of *Neoreomys*, *Schistomys* and *Perimys* have a differentiated lateral expansion (=capitular tail facet). In *Neoreomys*, *Schistomys* and *Perimys*, a medial expansion articulates with the medial facet of the trochlea (=trochlear facet). Both expansions are less marked in *Eocardia*. The posterior border of the radial head in *Eocardia* and *Schistomys* is slightly convex. In *Neoreomys* and *Perimys*, this edge is slightly sigmoid, whereas it is markedly convex in *Steiromys*. The bicipital tuberosity is well marked and protruded only in *Steiromys*.

The distal epiphysis (not preserved in *Eocardia*, *Schistomys* and *Steiromys*) is very robust in



Fig. 3. Right radii of Santacrucian rodents in proximal, medial, posterior and distal view. A, *Neoreomys* MPM-PV 3521 (mirrored). B, *Eocardia* YPM VPPU 15211 (mirrored, with ulna). C, *Schistomys* YPM VPPU 15648. D, *Perimys* MPM-PV 17443 (mirrored). E, *Steiromys* MACN A 10055–10078 (mirrored). bt, bicipital tuberosity; cf, carpal facet; ctf, capitular tail facet; f, fovea; rh, radial head; sp, styloid process; tf, trochlear facet. Scale: 10 mm.

Neoreomys, and more slender in *Perimys*. The carpal facets are complex (with convexities and concavities) in both *Neoreomys* and *Perimys*, with a morphology very similar to that present in *Cuniculus* and *Dasyprocta*. In the two genera, the styloid process is very robust and extended anteroposteriorly.

Ulna. – The complete diaphysis of the ulna (Fig. 4) is preserved only in *Eocardia*, although that of *Perimys* can be reconstructed from fragments of different laterality (see Materials and Methods). In these two genera, the diaphysis is sigmoidal in lateral view, with an anterior convexity in its medio-distal portion and a posterior convexity in its medioproximal portion (more noticeable in *Perimys*), similar to what occurs in most extant rodents. The diaphysis of the other genera is fragmentary. From the preserved portion, it can be interpreted that the *Neoreomys* diaphysis (Fig. 4A) is sigmoidal, similar to those of *Eocardia* and *Perimys* (Fig. 4B, D). *Schistomys* and *Steiromys* (Fig. 4C, E) show a straighter diaphysis, but the latter has a more pronounced posterior convexity in the proximal segment.

The olecranon was not preserved in either *Neoreomys* or *Schistomys*. In *Eocardia* and *Perimys*, it is broad, quadrangular and robust, similar to those of *Cuniculus* and *Dasyprocta*, and shorter than those of *Cavia*, *Myocastor*, and *Lagostomus*. *Steiromys* also has a square-shaped and robust olecranon, but

relatively shorter than that of *Eocardia* and *Perimys*, inclined anteriorly respect to the proximodistal axis of the bone.

The trochlear notch in all genera except *Steiromys* is oblique with respect to the proximodistal axis of the ulna. In *Steiromys*, it is mostly coincident with this axis, as in *Coendou*. Only *Steiromys* has a highly developed lateral coronoid process. In the other genera, this process is incipient. A less developed medial coronoid process is seen in *Perimys*, and it is slightly more developed in *Neoreomys*, *Eocardia* and *Schistomys*. *Steiromys* has a very large medial coronoid process, lateromedially expanded and forming a platform that would have fitted into the coronoid fossa of the humerus during flexion.

The radial notch is slightly oblique to the diaphyseal major axis in *Neoreomys*, but mostly perpendicular in all other genera. It is slightly concave on the transverse plane in *Neoreomys*, *Eocardia* and *Schistomys*, flat in *Perimys* and very concave in *Steiromys*. The styloid process is elongated anteroposteriorly in *Eocardia* and sub-cylindric in *Perimys* (this process is not preserved in the other genera).

Function

Scapula. – Some of the classic functional interpretations of scapular features are focused on the size and orientation of the acromion and metacromion

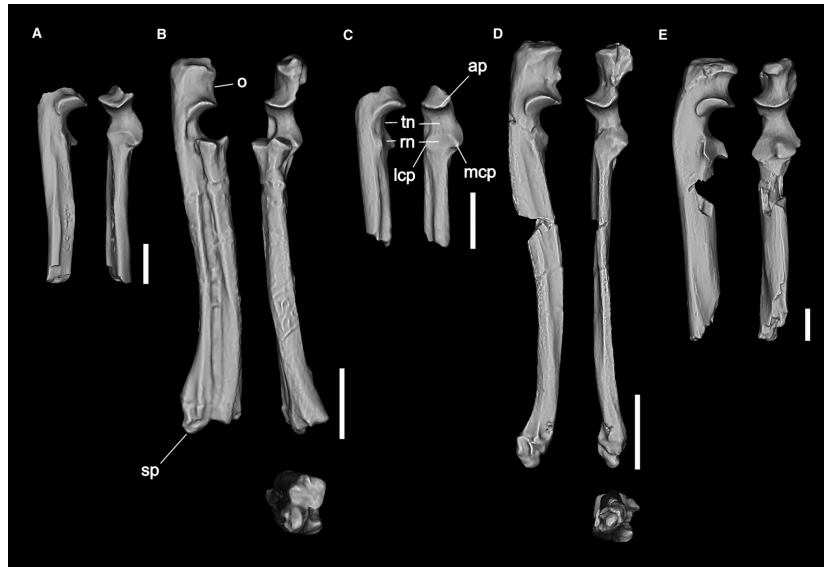


Fig. 4. Right ulnae of Santacrucian rodents in lateral, anterior and distal view. A, *Neoreomys* YPM VPPU 15394 (mirrored). B, *Eocardia* YPM VPPU 15211 (mirrored, with radius). C, *Schistomys* YPM VPPU 15648. D, *Perimys* MPM-PV 15053 (left and right combined). E, *Steiromys* MACN A 10055–10078 (mirrored). ap, anconeal process; lcp, lateral coronoid process; mcp, medial coronoid process; o, olecranon; rn, radial notch; sp, styloid process; tn, trochlear notch. Scale: 10 mm.

(Seckel & Janis 2008; Morgan 2009). In the case of the taxa studied in this work (and in most studies including fossil remains), the preservation of these structures is insufficient to make many functional inferences. Consequently, only the best-preserved characteristics were described and used herein for the functional interpretations, such as the robustness and the height/width proportion of the blade, among others. *Steiromys* has the most robust scapula of all analysed, indicating great development of all associated musculature.

Given that the scapula is not attached to the axial skeleton, simply being embedded in the axial musculature, it is displaced along with the limb during locomotion. Consequently, limb displacement during stride is strongly influenced by the rotation of the scapula, which pivots on its vertebral border and represents the most proximal element of the arc of movement (see Fischer *et al.* 2002). For this reason, the height/width proportion of the scapula provides information about the importance of this bone in the total length of the limb and in the stride. A proximodistally enlarged (high) blade provides further elongation of the limb and consequently a longer stride, when compared with a short (low) scapula. In *Eocardia*, the lamina is higher with respect to its width than in the other taxa analysed and would indicate a greater contribution of the scapula to stride length in this genus.

In turn, the height/width proportion is also related to the available area for insertion and origin of the musculature associated with the peripheral

areas of the scapula. A proximodistally low and anteroposteriorly broad scapula has a longer vertebral border than a high scapula. An enlargement of this edge could increase the mechanical advantage of the musculature that stabilizes and resists the rotation of the scapula like the *mm. serratus anterior* and *rhomboides* (Sargis 2002). In this sense, *Eocardia* would show comparatively poor development of this musculature.

The supraspinous fossa provides the most important origin area for the *m. supraspinatus*, extensor of the shoulder joint. This muscle allows limb protraction, arm elevation and also prevents proximal humeral dislocation. Among the genera studied here, *Perimys* has the largest supraspinous fossa with respect to the infraspinous counterpart (Fig. 1C), suggesting great development of the *m. supraspinatus*.

A larger and wider scapular notch would allow a greater development of the *m. infraspinatus* (Morgan 2009) which, in addition to its function as retractor of the arm, acts as a stabilizer of the shoulder joint, providing greater resistance to dislocation under great efforts. Among the genera analysed, *Perimys* may have had the larger scapular notch, and therefore the greatest development of the *m. infraspinatus*.

The supraglenoid tubercle represents one of the areas of origin of *m. biceps brachii*, a muscle involved in flexion of the forearm at the elbow joint, and also recruited in supination. This tubercle is more developed in *Steiromys* (Fig. 1D) than in the other genera, indicating a very developed *m. biceps brachii* and hence a powerful forearm flexion.

Humerus. – The position of the humeral head with respect to the proximodistal axis of the humerus is a feature that is difficult to interpret. A head with greater posterior displacement may indicate greater restriction in the elevation of the limb above the body in the anteroposterior plane. Among the taxa analysed, *Steiromys* has the most proximally located humeral head (Fig. 2E), a feature consistent with a greater anterior mobility for elevation of the humerus. In contrast, the other genera would have had more restricted humeral elevation.

The position of the tuberosities with respect to the head is an indicator of freedom of movement at the glenohumeral joint (see Argot 2001; Candela & Picasso 2008). These tuberosities are very low in *Perimys* and *Steiromys*, allowing a very wide articulation of the humerus with the scapula. In *Eocardia*, on the other hand, the shoulder joint would have been more restricted in mobility.

The depth of the bicipital groove, through which the *m. biceps brachii* tendon moves, may indicate the use or potency of *m. biceps brachii* (Taylor 1974). This groove is well defined in all studied caviomorphs, but it is markedly wider in *Steiromys*, which would indicate a greater development of this muscle in this genus, as suggested by the supraglenoid tubercle.

A distal projection of the deltoid tuberosity increases the lever arm and area of insertion for the *m. deltoideus*. This muscle consists of two (Evans & de Lahunta 2012) or three (McEvoy 1982) bellies depending on the presence or absence of a clavicle. The *m. clavodeltoideus* (which originates in the clavicle) participates in the adduction and internal rotation of the humerus, the *m. acromiodeltoideus* in the extension and abduction of the humerus and the *m. spinodeltoideus* in the flexion and external rotation of the humerus (McEvoy 1982). In *Neoreomys*, *Eocardia* and *Schistomys*, the deltoid tuberosity occupies about two-thirds of the bone length (Fig. 2A–C), indicating greater mechanical advantage for the action of the *m. deltoideus* than in *Perimys* and *Steiromys*.

In cases in which a deltopectoral crest is present, the insertions of the *mm. deltoideus* and *pectoralis major* are projected anteriorly. This crest can be seen in *Perimys* and *Steiromys* (Fig. 2D, E). The protrusion of the deltopectoral crest increases the moment arm for external rotation of the humerus by the *m. deltoideus* (mainly *m. spinodeltoideus*, McEvoy 1982) and for internal rotation by the *m. pectoralis major*. In *Steiromys*, this crest is very prominent anteriorly, as in extant porcupines. In *Perimys*, the deltopectoral crest, in addition to being anteriorly protruded, is lateralized (resulting in an anterolateral projection). This contrast in the orientation of the deltopectoral crest can be interpreted as involving different

mechanical advantages for the external and internal rotation of the humerus. The anterior protrusion of this crest in *Steiromys* could be associated with greater mechanical advantage for internal rotation of the humerus by the *m. pectoralis major* rather than to the action of the *m. spinodeltoideus* (Fig. 5A, C). In contrast, the anterolateral protrusion of this crest in *Perimys* could be more associated with greater mechanical advantage for the external rotation of the humerus by the *m. spinodeltoideus* than with the action of the *m. pectoralis major* (Fig. 5B, D).

The supracondylar crest is the area of origin of the extensors of the manus and *m. brachioradialis* (only present in Erethizontidae among the Hystricognathi; Woods 1972). The *m. brachioradialis* would act as a supinator of the forearm as well as forearm retractor, turning the palmar side of the manus medially (McEvoy 1982). In *Steiromys*, this crest is very developed, suggesting forceful forearm retraction and perhaps also supination capabilities (Candela & Picasso 2008). This crest has almost no development in the other taxa analysed.

The entepicondyle is the area of origin for the flexors of the manus and the *m. pronator teres* (Woods 1972; Evans & de Lahunta 2012). The medial protrusion of this feature results in increased mechanical advantage for these muscles, resulting in forceful flexion of the manus, digit prehension and supination. The epicondyle has an extreme medial development in *Steiromys* that would be related to powerful flexion of the manus and digits (Candela & Picasso 2008). In *Neoreomys* and *Perimys*, the entepicondyle is also very developed (Fig. 2A, D), although to a lesser extent than in *Steiromys* (Fig. 2E).

The olecranon fossa is the region where the *m. anconeus* process and the olecranon of the ulna are lodged when the limb is extended. A shallow fossa would indicate incomplete extension of the forearm, limited stability of the elbow joint and relative mobility during extension, as well as a frequently flexed posture. A deep fossa would accommodate the anconeal process to a greater extent, providing not only greater stability when elbow joint is at full extension, but also allowing a greater degree of forearm extension (Argot 2001; Candela & Picasso 2008). When the fossa is perforated, it permits a greater arc of movement of the forearm, as there is more space for the anconeal process when the forearm is fully extended (Taylor 1974). This feature can be observed in *Neoreomys*, *Eocardia*, *Schistomys* and *Perimys* (Fig. 2A–D), suggesting they would have had ample, stabilized forearm extension. On the contrary, the shallow fossa of *Steiromys* (Fig. 2E), lacking a supra-trochlear foramen, indicates this genus would not have had a complete extension of the elbow, showing

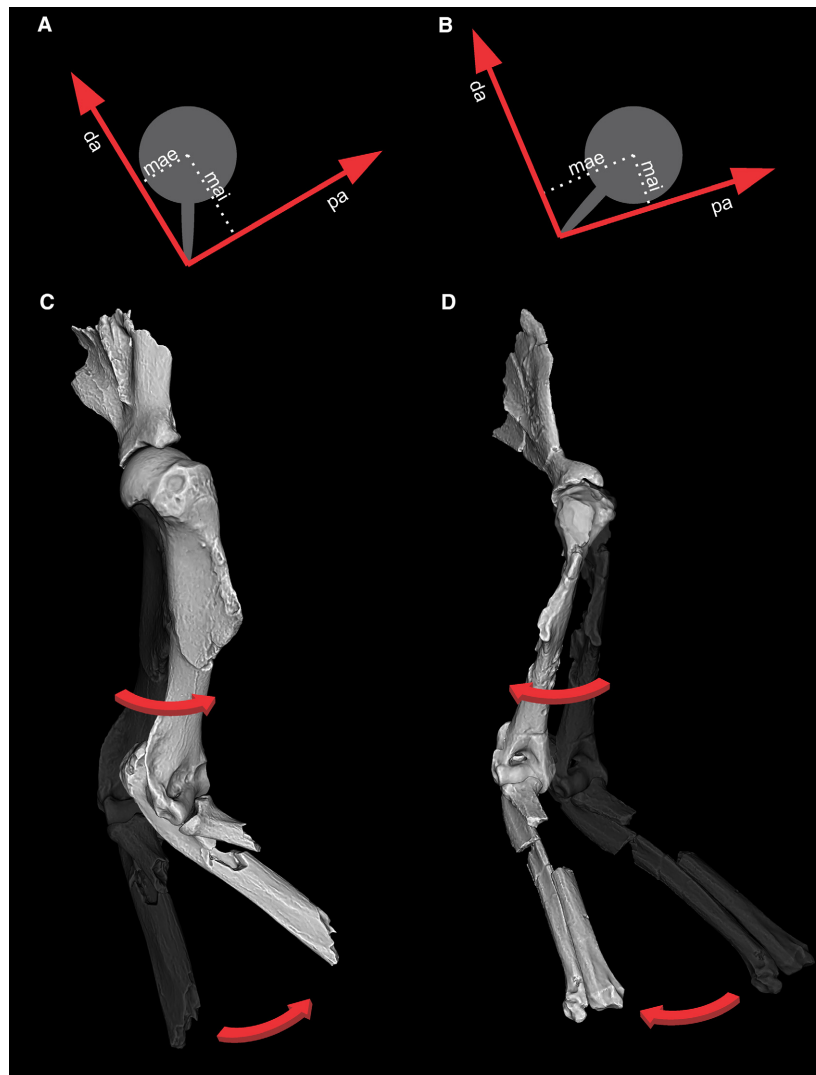


Fig. 5. Schematic transversal cuts of right humerus at the deltopectoral crest level and articulated forelimb showing differences in moment arm for internal and external rotation of the humerus in relation to deltopectoral crest orientation. A, C, *Steiromys*. B, D, *Perimys*. da, *spinodeltoideus* line of action; pa, *pectoralis major* line of action; mae, moment arm for external rotation of the humerus; mai, moment arm for internal rotation of the humerus. Orientation: medial to the right and lateral to the left. [Colour figure can be viewed at wileyonlinelibrary.com]

some lateral mobility in this joint and a frequently flexed posture (see Candela & Picasso 2008).

The distal articular surface can be divided into a capitulum and a trochlea. The morphology of the capitulum has been used to infer the ability of the forearm for pronation/supination (Szalay & Dagosto 1980; Gebo & Sargis 1994; Sargis 2002; Candela & Picasso 2008). The absence of a capitular tail would allow rotation of the radius, necessary for the supination of the forearm. On the contrary, a well-developed capitular tail would be effective in maximizing the correspondence between facets and providing stability in this articulation (Candela & Picasso 2008), but restricting rotatory movements of the radius on the capitulum. In this regard, *Steiromys* has

a capitular morphology that would have allowed broad movements of the radial head, without obstruction of pronation/supination. Conversely, *Neoreomys*, *Eocardia*, *Schistomys* and *Perimys*, bearing a large capitular tail (Fig. 2A–D), would have optimized the stability of parasagittal movements resulting in a decrease in mobility. A slightly protruded medial lip of the trochlea would allow a greater freedom of mediolateral movement at the level of the elbow joint. In contrast, a highly anterodistoposteriorly expanded medial lip of the trochlea (deep trochlea) would help resist mediolateral forces at the level of the elbow and restrict movement to the parasagittal plane (Schmitt 2003). A deep trochlea maximizes the stability of the elbow

joint because of the greater congruence between the articular surfaces of the humerus and ulna (Jenkins 1973). Hence, and based on its presence in all rodents studied (but to a lesser extent in *Eocardia*), they would present a markedly stabilized elbow joint.

Radius. – As for the humeral capitulum, the radial head morphology has been proposed as an indicator of the freedom of movement of the radius (pronation & supination) at the elbow (Szalay & Dagosto 1980; Sargis 2002; Candela & Picasso 2008). When there is supination, the radial head rotates over the humerus, and its posteromedial border travels through the radial notch of the ulna. Supination is favoured if the curvature of the radial head is uniformly convex across the ulnar articular surface (Argot 2001; but see Toledo *et al.* 2013). While *Neoreomys*, *Eocardia*, *Schistomys* and *Perimys* show a flat or sigmoidal posterior border of the radial head in proximal view (Fig. 3A–D), greatly restricting their supination capacity, *Steiomys* has a simple, uniformly convex posterior edge (Fig. 3E), which would indicate broad freedom of movement (Candela & Picasso 2008).

The bicipital tuberosity of the radius, where the radial head of the *m. biceps brachii* is inserted (McEvoy 1982), is markedly more developed in *Steiomys* than in the other caviomorphs studied. In *Steiomys*, development of the *m. biceps brachii* as indicated by its greater bicipital tuberosity suggests a powerful flexion and supination of the forearm (Candela & Picasso 2008).

The carpal joint facet of *Perimys* is slightly more complex than that of *Neoreomys*, so it would have a more restrictive articulation with the carpus.

Ulna. – In *Steiomys*, there is a pronounced proximal convexity of the diaphysis, posterior to the trochlear notch (Fig. 4E). The combined actions of the flexor and extensor muscles during ontogeny would increase the degree of convexity of the posterior border of the olecranon (Argot 2001). Therefore, it can be interpreted that in *Steiomys*, there is a combination of great efforts produced by these two muscle groups.

The olecranon provides the insertion area for the *m. triceps brachii*, extensor of the forearm. A long olecranon in relation to the total length of the ulna increases the out-lever arm of this extensor muscle, favouring the output force (Smith & Savage 1956). A proportionally shorter olecranon, on the other hand, decreases the in-lever arm of this muscle, favouring the output speed. The extension of the olecranon would also increase the mechanical advantage of the *m. anconeus* to stabilize the elbow joint (Toledo

et al. 2013). *Steiomys* has a very robust but short olecranon, indicating a substantial development of *m. triceps brachii* (Candela & Picasso 2008). This configuration may indicate that the *m. triceps brachii* is more likely used during elbow stabilization rather than as a powerful forearm extensor. *Eocardia* and *Perimys* have an olecranon of intermediate length compared with the extant sample, suggesting a moderate force of extension of the forearm.

The proximal facet, formed by the trochlear and radial notch, provides valuable information on the relationship of the ulna to the humerus and radius (Muñoz *et al.* 2017). A mediolaterally broad medial coronoid process, when compared with the radial notch, can perform a greater function of weight support of the body, releasing the radius from loads, a remarkable feature in the Erethizontidae compared to the rest of the Hystricognathi (Candela & Picasso 2008). The anterior extension of the coronoid process also ensures stability of the joint with the humerus in animals in which the forearm extension is not usually complete (Szalay & Sargis 2001). *Steiomys* has the largest anterior and medial extension of the medial coronoid process, which would allow relatively free rotational movements of the radius. If the radial notch was more distant from the axis of the ulna, the freedom of movement for supination would be greater (Taylor 1974). *Neoreomys*, *Eocardia*, *Schistomys* and *Perimys* have a very small concave radial notch, aligned with the proximodistal axis of the ulna, similar to what is observed in the extant Caviioidea, in which the radius is anterior to the ulna and has great participation in weight support but restricted supination (Candela & Picasso 2008). *Steiomys* has the most lateralized radial notch among the analysed taxa (Fig. 4E), which would give more freedom of movement to the radius (but see Muñoz *et al.* 2017).

The styloid process is the ulnar structure articulating with the carpus. The shape and dimension of this structure are varied and difficult to interpret. *Eocardia* has a anteroposteriorly broad styloid process (Fig. 4B) and, therefore, greater ulna-carpal contact than *Perimys*. This could be related to greater load transmission or greater mobility between ulna and cuneiform in the former than in the latter.

Discussion

Faculty

Shoulder joint. – A proximodistally high and anteroposteriorly narrow scapula is present in

walking or running species, and a proximodistally short and anteroposteriorly broad form is present in climbing species (Taylor 1974; Argot 2001; Sargis 2002). However, this association could be too simplistic, as most of the studies evaluating it focused on differences between terrestrial *versus* arboreal forms (substrate preference), without considering other substrate uses or habits (e.g. diggers with short and wide blades; see Morgan 2009).

A relatively longer vertebral border was reported for both diggers (Morgan 2009) and climbers (Taylor 1974). On the contrary, the high and narrow blade present in *Eocardia* is similar to that of the scapula present in extant runners (e.g. *Dolichotis*). This limb configuration and the associated increase in stride length are optimal for running at high speeds.

The robust scapula of *Steiromys* is in agreement with the great development of the musculature that is proposed for the majority of the remaining bones of this genus and the necessary force for the climbing habits proposed by Candela & Picasso (2008).

With regard to the relative size of the supraspinous fossa and the consequent importance of the *m. supraspinatus*, Sargis (2002) argued that the functions of this muscle are more demanding in arboreal mammals, since they raise the arm over their heads more frequently than terrestrial mammals. On the other hand, Morgan (2009) discussed that a greater development of the *m. infraspinatus*, given by the space provided by the great scapular notch, would represent an advantage in diggers like *Ctenomys* and also found a strong influence of the common evolutionary history of the major lineages of caviomorphs on scapular shape. The great scapular notch present in *Perimys*, and the corresponding great development of the *m. infraspinatus* inferred, would have been advantageous for digging, an activity that generates great efforts in the articulation of the shoulder. However, the difference in size between the supra and infraspinatus fossa is difficult to interpret because of the varied demand of muscle groups associated with a great diversity of movements (Argot 2001). In a study on Primates, Larson (2015) attributed the differences between the relative sizes of *m. supraspinatus* and *m. infraspinatus* to the angular changes in the scapula and their position with respect to the thorax rather than to locomotor differences. Taking into account all these arguments, it is difficult to evaluate the significance of the great development of *m. supraspinatus* inferred in *Perimys*.

Taylor (1974) found that the more cursorial species of viverrids (Carnivora) have the most posteriorly displaced heads, and related this feature to the greater development of the greater tuberosity and a rapid forward swinging of the forelimb. The position

of the humeral head with respect to the proximodistal axis of the humerus in caviomorph rodents was analysed by Candela & Picasso (2008). These authors did not observe a strict relationship of this feature with a type of locomotion; nevertheless, they found that terrestrial rodents present, for the most part, a more overturned head than the arboreal ones. The slightly posteriorly displaced heads of *Steiromys*, and the greater anterior mobility associated with it, would be concordant with the morphology necessary to climb, but does not exclude other habits.

Low tuberosities and wide mobility of the glenohumeral joint have been related to arboreality (Argot 2001; Sargis 2002; Candela & Picasso 2008), but there are also many mammals with low tuberosities that do not climb, such as *Myocastor* (ambulatory, swimmer, digger), *Ctenomys* (digger), *Lagidium* (jumper). The low tuberosities, and therefore the wide freedom of movement of *Perimys* and *Steiromys*, could be related to the activity of climbing, although as has been pointed out, this would not be an exclusive relationship. In contrast, the high tuberosities (especially the greater) and therefore the restriction of the forelimb to parasagittal movements found in *Eocardia* are more compatible with running.

The increase in the lever arm for the *m. deltoideus*, given by a distal extension of the deltoid tuberosity, generates a powerful shoulder flexion that is advantageous for various activities, such as running, climbing, swimming and digging. The extent of this tuberosity observed in *Neoreomys*, *Eocardia* and *Schistomys* is similar to that present in runners like *Dasyprocta* and *Pediolagus* and to that of an occasional digger like *Cuniculus*. Analysing this characteristic in the context of the other bones could help to discern between these activities. In *Perimys*, the deltopectoral crest is identical to that found in the diggers *Ctenomys* and *Lagostomus*, as well as in *Myocastor*, which, in addition to dig, swims frequently. The advantage in the external rotation of the humerus inferred for *Perimys*, given by the lateral protrusion of the deltopectoral crest, could be related to a lateral movement of the forearm to remove the extracted sediment when digging. In contrast, the advantage in the internal rotation of the humerus inferred for *Steiromys* would assist the adduction of the forearm to help the animal cling when climbing. This interpretation for *Steiromys* is compatible with that made by Candela & Picasso (2008) (see also McEvoy 1982).

Elbow joint. – With respect to the differences observed in the bicipital groove, the greater development of the *m. biceps brachii* indicated for *Steiromys* can be related to the ability to climb, as it is one of

the activities that more strongly needs the use of this muscle. Taylor (1974) observed this groove is better delimited in climbers.

A shallow olecranon fossa (indicative of poor extension of the forearm) is generally associated with arboreal forms, whereas a deep and perforated fossa (characteristic of forelimbs with great extension of the forearm) is associated with terrestrial forms (Taylor 1974; Argot 2001). However, Sargis (2002) related a perforated pit with a digging habit because it would involve a repeated and powerful extension of the forearm. The great extension of the forearm of *Neoreomys*, *Eocardia*, *Schistomys* and *Perimys* interpreted from their olecranon foramen could then be related to a running habit, as well as the capacity to dig. *Steiomys* would probably have had a stance more similar to that of an ambulatory mammal or climber, with a semi-flexed forelimb.

It has been inferred that the protrusion of the medial lip of the trochlea would be indicative of greater stability in the elbow. Stability can be beneficial in more than one context. In *Steiomys*, the protrusion of the medial lip could maintain the integrity of the joint when pronating/supinating the forearm; in other rodents, which also possess the 'second trochlea', it could contribute to the restriction of movement of the forearm to the sagittal plane, as in other extant running mammals.

Sargis (2002) found no relationship between substrate preference and the shape of the trochlear notch in tupaiids. Argot (2001) found a relationship between a smooth and an open trochlear notch (which would provide greater mobility) and arboreal marsupials, while a deep (more stable) trochlear notch is present in the terrestrial ones. The general conformation of the trochlear notch seems to be an indicator of the degree of stability of the elbow joint, but it cannot be unequivocally associated with a particular substrate use (Szalay & Sargis 2001). This relationship between the opening of the trochlear notch and the locomotor habit is not observed between the rodents used as a comparison sample in this work. In this sample, the runners have the open trochlear notch, with a reduced medial coronoid process and the radius occupying the place of support of the weight. The large coronoid process of *Steiomys* and the radial mobility involved could be of importance for climbing.

The proximal convexity of the ulnar diaphysis is explained by the combination of the flexor and extensor muscles acting together when climbing and is associated with arboreal species (Argot 2001). This curvature, present in *Steiomys*, supports its proposed climbing habits (Candela & Picasso 2008). Vizcaíno *et al.* (1999) used the relative length of the olecranon

to characterize extant armadillos in relation to their digging capabilities. They found correlation between the relative development of the olecranon process and the tendency towards fossoriality, interpreting it as an increase in the mechanical advantage of *m. triceps brachii*. However, a relatively long olecranon, and consequently a great force of extension of the forearm, is not only connected to the act of digging. There are several uses of substrate for which it is advantageous to have a powerful forearm extension, which include digging, swimming and climbing (Vizcaíno *et al.* 1999; Elissamburu & Vizcaíno 2004; Toledo *et al.* 2013). Therefore, this feature has to be specially considered in the context of other morphological features. In *Eocardia* and *Perimys*, the olecranon is similar and not strongly associated with a particular activity. Candela & Picasso (2008) associated the short but robust olecranon of *Steiomys* with a frequently flexed position of the forelimb and proposed that the short lever arm of the *m. triceps brachii* is compensated by the great volume of this muscle.

Taylor (1974) noted the *m. triceps brachii* could counteract body weight in head down arboreal descents. However, Sargis (2002) observed a shorter olecranon in arboreal rather than in the terrestrial forms, indicating that the longer olecranon would be more related to digging habits (see Hildebrand 1985). Argot (2001) and Sargis (2002) proposed that the short olecranon in the arboreal species would probably be related to the fact that these taxa generally do not require powerful extensors because they present a semi-flexed position during locomotion. *Eocardia* has a relatively short olecranon in relation to the total length of the ulna, similar to that found in running forms. The great development of the *m. triceps brachii* in *Steiomys*, indicated by the robust (although short) olecranon, is interpreted by Candela & Picasso (2008) as an advantage in extending the front leg to reach new supports, facilitating directional changes associated with arboreal locomotion (see Argot 2001). *Perimys* has a somewhat long olecranon in relation to the total length of the ulna, providing great mechanical advantage for the *m. triceps brachii*, which, as explained, could be associated with climbing, digging or swimming habits. It is difficult to interpret the relative length of the olecranon by itself and should be considered in the context of the other postcranial features.

Taking into account the morphology of the capitulum, *Steiomys* may have had good pronation/supination capacity. The preponderance of parasagittal movements given by the large capitular tail of *Neoreomys*, *Eocardia*, *Schistomys* and *Perimys* could be related to a running or digging habit. Pronation and supination fulfil the biological role of

positioning the manus in different orientations when climbing (Toledo *et al.* 2013). This ability to pronate/supinate the forearm is found in climbing mammals (Argot 2001; Sargis 2002; Candela & Picasso 2008). However, the significance of the morphology of the capitulum (and also of the radial head) with respect to pronation/supination ability is unclear (Toledo *et al.* 2013).

McEvoy (1982) proposed that *m. brachioradialis* (with its origin in the supracondylar crest), acting as supinator of the forearm, would orient the plantar side of the manus towards the surface of the arboreal substrate and assist in flexion of the elbow when climbing. Candela & Picasso (2008) inferred a similar function and faculty in *Steiromys*.

The mechanical advantage for the flexor musculature of the manus given by the medial protrusion of entepicondyle is important for both climbing (Taylor 1974; McEvoy 1982; Candela & Picasso 2008) and digging (Taylor 1974; Hildebrand 1985; Sargis 2002). The extreme development of the entepicondyle in *Steiromys*, along with the associated powerful flexion of the manus, would be related to the need for apprehension necessary when climbing (Candela & Picasso 2008). In turn, considering the rest of their morphology, in *Neoreomys* and *Perimys*, this feature may probably have been more related to occasional digging (as in *Cuniculus*).

In climbing species, the proximal facet of the radius is relatively simple and slightly concave as it articulates with a relatively simple capitulum (Taylor 1974). The increased rotational capacity proposed for *Steiromys* might have been advantageous for climbing. The poor rotational capacity inferred for *Neoreomys*, *Eocardia*, *Schistomys* and *Perimys* would have been more compatible with a running or digging habit.

A deep radial notch is related to a rigid forearm as found in running animals, whereas a more open radial notch would allow greater rotational movement and would be more suitable for climbing animals (Taylor 1974). The almost flat radial notch and its anterior position in the ulna of *Neoreomys*, *Eocardia*, *Schistomys* and *Perimys* determine the radius as the main support of the weight in the forearm, which, together with the limited movement of pronation/supination, is characteristic features of running forms or at least not-climbers. The lateralized and concave radial notch present in *Steiromys* and the greater freedom of movement that this entails are expected in species with climbing habits, but not exclusively. The strong flexion and supination inferred for the forearm of *Steiromys* from the great bicipital tuberosity would be optimal to climb, as suggested by (Candela & Picasso 2008).

Wrist joint. – In a study of squirrel wrist, Thorington & Darrow (2000) found that this articulation is more stable in flying squirrels (proximal row of carpal bones functioning as a single unit) than in the rest of them, probably increasing the stability of the joint in the former. The rigid articulation of the radius with the carpus in *Perimys* (and to a lesser extent in *Neoreomys*) inferred from the complex carpal joint facet could increase the stability of this joint and could be related to a digging activity. A rigid articulation could have allowed a transmission of forces through the arm to scratch the sediment, offering protection against a possible dislocation.

With respect to the styloid process of the ulna, Szalay & Sargis (2001) proposed a relationship of mobility *versus* stability between the different forms of this trait: a wide process with a large contact in the ulnar-cuneiform joint would be related to an arboreal mode of life, whereas a styloid process considerably narrowed into a tip with a relatively small ulno-cuneiform joint would be related to a more terrestrial habit. Following Szalay & Sargis (2001), the more narrowed styloid process of *Perimys* would imply a more stable articulation related to terrestriality than that in *Eocardia*. In turn, Toledo *et al.* (2013) relate the robustness of this process with great mechanical loads transmitted between the ulna and the cuneiform. In this context, the ulno-cuneiform joint of *Eocardia* would be stronger than the one of *Perimys*. Nevertheless, this is a difficult trait to evaluate and there is no consensus for its interpretation.

Functional characterization and proposed faculty for each taxa

In sum, the functional evaluation of a set of traits allows understanding what activities each taxon was capable of performing in their life. For a more complete characterization, it is necessary to analyse both limbs; therefore, this work will be complemented with a study of the hindlimb of these rodents. The following is a synthesis of the functional analysis of the forelimb (Fig. 6).

Neoreomys would have been capable of strong abduction and/or flexo-extension of the humerus, moderate flexion of the manus, complete and stabilized extension of the forearm, a stable articulation of the elbow resistant to mediolateral forces and with a parasagittal restriction, and the radius as the main weight support in the forearm. Therefore, *Neoreomys* may have been ambulatory, and an occasional runner. This hypothesis is in partial agreement with Candela *et al.* (2012), who proposed *Neoreomys* was ambulatory similar to *Cuniculus* and may have had swimming abilities.

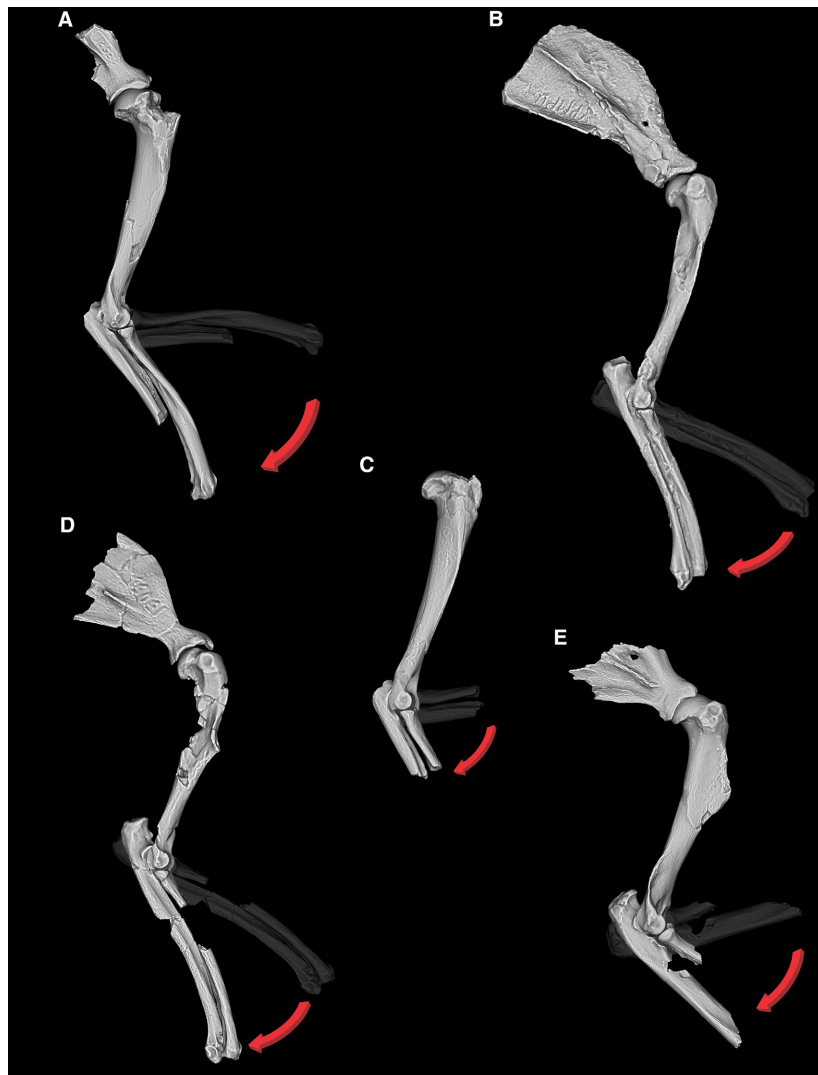


Fig. 6. Right articulated forelimb of Santacrucian rodents reconstructed with combined specimens and laterality at the maximum extension. A, *Neoreomys*. B, *Eocardia*. C, *Schistomys*. D, *Perimys*. E, *Steiromys*. [Colour figure can be viewed at wileyonlinelibrary.com]

Eocardia had a wide stride, a glenohumeral joint restricted to the parasagittal plane, complete and stabilized forearm extension, elbow joint stabilized and optimized for parasagittal movements, an elbow joint resistant to mediolateral forces with parasagittal movement restriction and moderate extension of the forearm. Consequently, *Eocardia* is interpreted as a runner. Candela *et al.* (2012) likewise interpreted *Eocardia* as a runner, although to a lesser degree than *Pediolagus* and *Dolichotis*.

Schistomys had complete and stabilized extension of the forearm, an elbow joint stabilized and optimized for parasagittal movements, with an interpretation in this case equivalent to that performed for *Eocardia*, that of a runner.

Perimys had a very stable shoulder joint, strong external rotation of the humerus, rigid radial-carpal

articulation and moderate forearm extension. *Perimys* is interpreted as a digger or an occasional digger.

Steiromys had a highly mobile glenohumeral joint, strong forearm flexion, strong internal rotation of the humerus and consequently a strong adduction of the forearm, strong supination of the forearm and, therefore, the ability to orient medially the palmar side of the manus, strong flexion of the manus, incomplete extension and some lateromedial mobility of the forearm. These characters are compatible with a climbing habit, supporting the hypothesis of Candela & Picasso (2008).

Biological role

The inferences about the functional morphology of the genera studied here enabled us to hypothesize

about how these traits functioned during the life of an organism (faculty). As not all animals use their faculties in the same way (Vizcaíno *et al.* 2016) during their life in the context of their environment (biological role), the functional hypotheses outlined here must be considered along with other characteristics of their palaeobiology. For example, if a running habit is inferred for a species in a study of the appendicular skeleton and masticatory anatomy suggest that the animal is carnivorous, it could be speculated that the faculty of running would have been used during hunting and food capture. Consequently, the inferred faculties for the Santacrucian rodents, interpreted as herbivorous (Candela *et al.* 2012), would be related mainly to escaping from predators, construction of shelter and searching for food.

Neoreomys would have had an ambulatory habit and could have secondarily been a runner. Candela *et al.* (2012) reported for *Neoreomys* a diet similar, but of greater hardness, to that of *Dasyprocta* (fruits, seeds, shoots and leaves) that they could have consumed in mixed or closed environments. *Neoreomys* could have used its running ability to escape from predators. *Eocardia* would have been a fast runner and would have been able to escape predators in this way in open environments where it could have grazed (with a diet consisting of abrasive foods and herbs as well as leaves of shrubs and trees, similar to the diet of *Pediolagus* and *Dasyprocta*; Candela *et al.* 2012). The interpretations of substrate use and biological role for *Schistomys* are the same as for *Eocardia*. There are no dietary hypotheses for *Schistomys*, but it could have probably been similar to *Eocardia* as they have very similar cranial and dental structure. *Eocardia* and *Schistomys* would have been the most agile genera among the Santacrucian rodents. There is not a diet hypothesis for *Perimys* either, which was interpreted here as a digger, and could have dug to create burrows in the substrate or to get food. *Steiromys* would have been a climber and could have used trees as a shelter and food source, as their diet may have included bark, seeds and hard leaves (Candela *et al.* 2012).

The high morphological disparity of the forelimb of Santacrucian rodents would reflect high ecological diversity. This diversity, interpreted here as disparate substrate uses, would indicate a differential use of space and could have diminished competition. The interpretations made in this work will be complemented with a functional analysis of the hindlimb, which will provide understanding for the whole locomotor apparatus.

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