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Paleobiology of *Argyrolagus* (Marsupialia, Argyrolagidae): an astonishing case of bipedalism among South American mammals

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Abstract

Argyrolagus constitutes, both for its craniodental and postcranial anatomy, one of the most notably specialized South American Neogene metatherians. Differentiating it from any other South American mammal, bipedal jumping has been proposed for *Argyrolagus*, even though this hypothesis was not supported by morphofunctional studies. Here, we describe the postcranium of *A. scaglai* (from the Pliocene of Argentina), perform a functional analysis, and interpret it against a varied background of locomotor adaptations of extant mammals. The configuration of joints, the degree of development and location of muscular insertions were mainly analyzed, and functional indices were evaluated. This study indicates that *Argyrolagus* had stabilized glenohumeral and humeroulnar joints, a great development of the arm retractors, flexors-extensors of the digits, pronator, and supinator muscles, low restrictive humeroradial joint, powerful extensor muscles of the hip, knee, and ankle, good development of the iliac muscle, and restrictive hind limb joints. Joint configurations are interpreted to be optimal to resist the impacts during jumping, avoiding dislocation, compatible with digging activity. A compromise between the capacities to dig and manipulate objects is inferred. It is concluded that *Argyrolagus* had bipedal jumping locomotion as well as good capacity to dig, constituting an astonishing case of convergence with the small bipedal rodents and small Australian macropodids. We suggest that bipedal jumping in Miocene and Pliocene argyrolagids should not be necessarily related to a particular arid environment. Finally, we evaluate the importance of postcranial features to understand the phylogenetic relationships of Argyrolagidae in a comprehensive phylogeny of Metatheria.

Keywords Metatheria · South America · postcranial anatomy · jumping locomotion

Introduction

Metatherians (marsupials plus their closest extinct relatives) constitute a minor component in the current terrestrial mammal faunas of South America (Tyndale-Biscoe 2005). They are represented by three main groups, the most diverse being

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the opossums (Didelphimorphia), which occupy diverse ecological niches, with diets ranging from carnivory to frugivory and substrate preferences including terrestrial, arboreal, and semiaquatic (Birney and Monjeau 2003; Jansa et al. 2014). The remaining extant Neotropical marsupials, the shrew opossums (Paucituberculata, Caenolestidae) and the "monito del monte" (Microbiotheria), are terrestrial insectivores and arboreal insectivore-frugivores, respectively (Kirsch and Waller 1979; Patterson 2007; Amico et al. 2009).

In contrast to the current relatively scarce representation, metatherians reached a wider ecological and taxonomical diversity during the Cenozoic of South America, as lineage diversification occurred in the main clades (Goin et al. 2016). Among the more notable examples of this radiation are the stem metatherian sparassodonts, with meso- to hypercanivorous species and body sizes ranging from that of a weasel to that of a spectacled bear (Prevosti and Forasiepi 2018), the frugivore to insectivore-frugivore polydolopid marsupials without extant counterparts (Sánchez-Villagra 2013), and the argyrolagoids, a lineage of rodent-like marsupials

(Zimicz 2011) whose more conspicuous and better known genus is *Argyrolagus* (Simpson 1970). Argyrolagoids include the Argyrolagidae, a clade grouping *Argyrolagus* and other genera such as *Microtragulus* and *Hondalagus* (Sánchez-Villagra et al. 2000; see Table 1), and some proposed basal argyrolagoids such as *Klhonia* and *Praedens* (Goin et al. 2010). The closest relationships of argyrolagids in the context of Marsupialia, and the monophyly of argyrolagoids, are yet under debate (see Beck 2017); they have been proposed as members of Polydolopimorphia (e.g., Goin et al. 2009) or, alternatively, as part of Paucituberculata (e.g., Sánchez-Villagra 2001). The origin of the argyrolagoids was probably associated with the profound climatic-environmental changes that occurred near the Eocene-Oligocene boundary. At that time metatherian assemblages of southern South America experienced a large taxonomic and ecological turnover known as Patagonian-Hinge (Goin et al. 2010, 2016), where different groups became extinct and others, such as argyrolagoids and paucituberculatans, radiated (Abello et al. 2018; Goin et al. in press). Argyrolagids diversified from the latest Paleogene giving rise to several genera and species that

are well recorded in mammal-bearing levels of the Mio-Pliocene of Argentina and Bolivia (Table 1).

Most argyrolagids are known by fragmentary cranial remains, as well as isolated teeth, from which it was possible to reconstruct their body size and diet (Zimicz 2011). *Argyrolagus* is the best known representative of the argyrolagids as specimens with nearly complete associated cranial and postcranial elements have been recovered. Therefore, besides diet and body size, other paleoecological hypotheses such as substrate usages and locomotor strategies have also been advanced (Simpson 1970; Straccia 1999; Abello and Candela 2017). Knowledge about its paleoecology stems from the influential work of Simpson (1970). In his study, Simpson (1970) noted strong morphological similarities between *Argyrolagus*, kangaroo rats (Heteromyidae), and jerboas (Dipodidae), concluding that they represented a striking example of evolutionary convergence. In this way, Simpson (1970) considered that *Argyrolagus* would have been a bipedal jumper, well adapted to live in open and semi-arid environments (Simpson 1970: 55). The adaptive convergence with bipedal rodents was also proposed in later works

Table 1 Temporal and geographical range of argyrolagid species

Species	Occurrence	Age	Main reference
Proargyrolagus bolivianus Wolff, 1984	Salla, Loaza, Bolivia.	Late Oligocene (Deseadan)	Sánchez-Villagra and Kay 1997; Kay et al. 1998
P. argentinus Goin and Abello, 2013	Gran Barranca, Chubut, Argentina.	Early Miocene (Colhuehuapian)	Goin and Abello 2013; Dunn et al. 2013
Anargyrolagus primus Carlini et al., 2007	Gaiman, Chubut, Argentina.	Early Miocene (Colhuehuapian)	Carlini et al. 2007; Kay et al. 2008
Microtragulus argentinus Ameghino, 1904	Monte Hermoso, Buenos Aires, Argentina.	Early Pliocene (Montehermosan)	Simpson 1970; Tomassini et al. 2013
M. reigi Simpson, 1970	Chapadmalal-Miramar region, Buenos Aires, Argentina.	Late Pliocene-Early Pleistocene (Chapadmalalan to Uquian)	Simpson 1970; Cione et al. 2015
M. catamarcensis Kraglievich, 1931	Andalhuala, Catamarca, Argentina.	Late Miocene (Huayquerian)	Simpson 1970; Bonini 2014
M. bolivianus Hoffstetter and Villarroel, 1974	Vizcachani, Bolivia; San Roque, Jujuy; Argentina	?Early Pliocene – Early Pleistocene Montehermosan to Uquian)	Hoffstetter and Villarroel 1974; Babot and García-Lopez 2016
***Microtragulus* sp.**	North of Tucumán, Argentina	?Late Miocene	García-López and Babot 2015
Argyrolagus scagliai Simpson, 1970	Chapadmalal-Miramar region, Buenos Aires, Argentina.	Pliocene (Chapadmalalan)	Simpson 1970; Cione et al. 2015
A. rusconi Goin et al., 2000	Cerro Azul, La Pampa, Argentina.	Late Miocene (Huayquerian)	Goin et al. 2000; García-López and Babot 2015
A. parodii Ameghino, 1904	Miramar?, Buenos Aires, Argentina.	Chapadmalalan? (see Simpson 1970)	Simpson 1970
A. palmeri Ameghino, 1904	Monte Hermoso, Buenos Aires, Argentina.	Early Pliocene (Montehermosan)	Simpson 1970; Tomassini et al. 2013
***Argyrolagus* sp.**	Río Quequén Salado (Cascada Grande), Buenos Aires, Argentina	Early Pliocene (Montehermosan)	Pardiñas et al. 2017; Beilinson et al. 2017
***Argyrolagus* sp.**	Caleufú, La Pampa, Argentina	?Late Miocene	Abello et al. 2002
Hondalagus altiplanensis Hoffstetter and Villarroel, 1988	Quebrada Honda, Bolivia.	Middle Miocene (Laventan)	MacFadden et al. 1990; Sánchez-Villagra et al. 2000

(Mares 1985, 1993a, b; Straccia 1999). Regarding the diet of *Argyrolagus*, there is general agreement that it included seeds as well as other nutritious plant parts (Simpson 1970; Zimicz 2011). In relation to locomotor behavior, a jumping locomotion was proposed based on the overall morphological similarity with the noted bipedal rodents (Simpson 1970; Straccia 1999). However, despite that this inference has been largely accepted (Wolff 1984; Emerson 1985; Mares 1985, 1993a, b; Sánchez-Villagra 2001; Babot and García-López 2016), to date no detailed morphofunctional analysis of the postcranium has been performed, nor has an analysis of the forelimb form and function been carried out in order to evaluate their ecological role. Therefore, so as to reach a deeper understanding of the paleoecology of *Argyrolagus*, and to evaluate its significance in the environmental context of Neogene units of southern South America, we performed a detailed study of its postcranium, based on both published and unpublished specimens coming from Pliocene mammal-bearing units from Argentina. In addition, taking into account that the relationships of argyrolagids among marsupials are contentious, we assessed the phylogenetic information content of *Argyrolagus* postcranium in a comprehensive phylogeny of Metatheria.

Material and Methods

Materials

Most of the current knowledge of the postcranium of *Argyrolagus* and *Microtragulus* (see Table 1) is based on the specimens presented by Simpson (1970) and Babot and García-López (2016). Original description of the postcranium of *Argyrolagus* was based on the postcranial skeleton of the MMP 785-S, the type material of *A. scagliai* (Simpson 1970) (Online Resource 1). Since that original study, MMP 785-S has deteriorated with several bones lost or damaged, and bones that probably do not belong to this specimen are currently under this collection number. The current composition of MMP 785-S is detailed in Online Resource 1. In addition to the study of the type specimen, we reported a new specimen, MLP 91-IV-1-85, which currently represents the second most complete specimen referable to *Argyrolagus* (Online Resource 1). Another specimen, MLP 87-XIII-II-1 assigned by us to *Argyrolagus* (Online Resource 1), is also analyzed. Comparisons within argyrolagids were made with *Microtragulus*, the remaining argyrolagid genus for which postcranial remains are known (on the validity and usage of this generic name, see taxonomic discussion in Simpson 1970: 4-6, and Babot and García-López 2016). The species *Microtragulus reigi* and *Microtragulus bolivianus* (Simpson 1970; Babot and García-López 2016), known by associated cranial and postcranial bones, were included in this study.

Methods

Morphofunctional Analyses Comparative studies were based on first hand observation of the postcranium of nine extant species (Online Resource 1) from several families (Didelphidae, Microbiotheriidae, Potoroidae, Thylacomyidae, Pseudocheiridae, and Phalangeridae), belonging to most of the higher taxa of both "Ameridelphian" and Australidelphian marsupials (Nilsson et al. 2004; Beck et al. 2014; Gallus et al. 2015). These extant species exhibit a wide array of locomotor behaviors (e.g., climbing, bipedal jumping, halfbounding, bounding, and digging) and substrate preferences (e.g., terrestrial, arboreal, and scansorial), and occur in diverse habitats (Online Resource 2). Data on these ecological characteristics were taken from different bibliographic data (Online Resource 2). Postcranial anatomy of other extant marsupials was evaluated from bibliographic sources (e.g., Osgood 1921; Hopwood and Butterfield 1976; Szalay 1994; Argot 2001, 2002; Szalay and Sargis 2001; Warburton et al. 2011, 2012, 2013, 2015). Following previous studies (e.g., Simpson 1970) that hypothesized bipedal jumping locomotion for *Argyrolagus*, we emphasized comparisons with the marsupial *Potorous tridactylus*, the heteromyid *Dipodomys*, and other small bipedal rodents (Howell 1932; Simpson 1970; Emerson 1985; Candela and Picasso 2008). We performed a qualitative morphofunctional analysis, emphasizing the study of joint' traits with functional significance, the inferred postcranial muscle development and their mechanic advantages. In addition, we calculated some functional indices that are indicative of substrate use and locomotor behavior in mammals (Elissamburu and Vizcaíno 2004; Samuels and Van Valkenburgh 2008; Warburton et al. 2013): SMI, shoulder moment index; HRI, humerus robustness index; EI, epicondyle index; IFA, index of fossorial ability; URI, ulna robustness index (Online Resource 3). Summarizing, we scrutinized the anatomical variation within the sample examined, and evaluated the possible functional relationships between anatomy and compatible movements, in association with the locomotor behavior and substrate preference of extant models analyzed.

Measurements on limb bones were either standard postcranial measurements or with functional relevance (Online Resource 3). All measurements were made with a digital caliper, and a stereoscopic microscope (Nikon SMZ 1000) using an ocular micrometer. The myological nomenclature and muscular systems were based on Argot (2001, 2002) and Szalay and Sargis (2001) for Didelphimorphia, Microbiotheria, and Paucituberculata, and on Warburton et al. (2011, 2012, 2013, 2015) and Hopwood and Butterfield (1976) for macropodids and peramelids. The osteological nomenclature follows mainly Szalay (1994), Argot (2001, 2002), Szalay and Sargis (2001), and Abello and Candela (2010).

Phylogenetic Analyses The relationships of the argyrolagids *Proargyrolagus*, *Argyrolagus*, and *Microtragulus* were analyzed in a comprehensive phylogenetic dataset of metatherians, modified from Beck et al. (2014) and Beck (2017). We combined data from the morphological Matrix B of Beck (2017) and from five nuclear protein-coding genes (APOB, BRCA1, IRBP, RAG1, and VWF) used in the analysis of Beck et al. (2014) and Beck (2017). The original morphological matrix, which included 41 taxa and 273 morphological cranial and postcranial characters, was modified by the addition of *Microtragulus* and scoring changes in *Argyrolagus*, *Proargyrolagus*, and *Palaeothentes* (Online Resource 4 and 5). The new data matrix was analyzed under equally weighted maximum parsimony using TNT v.1.5-beta (Goloboff et al. 2008). To explore the phylogenetic signal of the *Argyrolagus* postcranial anatomy, two separate analyses were conducted, one using morphological data alone, and another based on the combined molecular and morphological data. In each analysis, optimal trees were searched departing from 500 random addition sequences followed by Tree Bisection Reconnection (TBR) branch swapping (saving ten trees per replication). The most parsimonious trees found in the replicates were subject to a final round of TBR. As originally proposed (Beck 2017), 49 characters (see Online Resource 5) were considered additive during the searches.

Institutional Abbreviations MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; MLP, Museo de Ciencias Naturales de La Plata, La Plata, Argentina; MMP, Museo Municipal de Ciencias Naturales "Lorenzo Scaglia," Mar del Plata, Argentina; QM, Queensland Museum, Brisbane, Australia.

Functional Indices HRI, humerus robustness index, the transverse diameter of the humerus divided by functional length of the humerus; EI, epicondyle index, the epicondylar width of the humerus divided by functional length of the humerus; IFA, index of fossorial ability, is the length of the olecranon process divided by the functional ulna length; URI, ulna robustness index, the transverse diameter of the ulna divided by the functional ulna length. Morphological measurements of humerus and ulna were taken as proposed by Elissamburu and Vizcaíno (2004: fig.1).

All data generated or analyzed during this study are included in this published article [and its supplementary information files].

# Comparative Description

Scapula

The left scapula of MMP 785-S only preserves the proximal end. The outline of the articular surface is teardrop-shaped (Fig. 1a) and, as well as the neck, is narrow. The scapular

coracoid process is a small protuberance not well differentiated from the border of the glenoid fossa, suggesting a moderate development of the coracobrachialis and the short head of the biceps brachii muscles, both of them originating from the distal tip of this process (Argot 2001; Sargis 2002a).

Humerus

The humerus is short (40 % of the femur length), similar to the proportions seen in the macropodids *Bettongia* and *Potorous,* and in the rodents *Dipodomys* and *Jaculus* (Table 1, Online Resource 3). Currently, the most complete humerus referable to *Argyrolagus* is the right humerus of MLP 91-IV-1-85 (Fig. 1b, d, h). The humeral head is mediolaterally compressed, "beaked," and slightly higher than the humeral tuberosities (Fig. 1b, h). The lesser tuberosity was lost, but based on specimen MMP 395-M (Fig. 1c, e-g, j) tentatively referred to *Microtragulus* by Simpson (1970: 28), it could be speculated that the lesser tuberosity in *Argyrolagus* was similar in size to the greater tuberosity but more protruding than it (Fig. 1j). The robust greater tuberosity and the protruding lesser tuberosity indicate wide insertion areas for the infra- and supraspinatus muscles on the first, and subscapularis on the second (Fig. 1c, e). The proximal half of the shaft is posteriorly curved, probably associated with the extreme development of the deltopectoral crest (Fig. 1b, d), and has on its medial aspect a well-marked relief for the teres major and latissimus dorsi muscles (Fig. 1h). In relation to humerus length, the deltopectoral crest is relatively short (46 % of humerus length; see SMI, Table 1, Online Resource 3) and restricted to the proximal half of the humerus. *Argyrolagus* differs from the remaining compared sample in that the

Fig. 1 Forelimb anatomy of *Argyrolagus* showing reconstructed areas of muscular origins and insertions discussed in the text. Scapula and humerus of *Argyrolagus* spp. (MLP 91-IV-1-85 and MMP 785-S) and humerus of ?*Microtragulus* (MMP 395-M): **a**, fragment of left scapula (MMP 785-S) in proximal view; **b**, **d**, and **h**, right humerus (MLP 91-IV-1-85) in lateral (b), anterior (d), and medial (h) views; **c**, **e**, **f-g**, and **j**, right humerus (MMP 395-M) in lateral (c), anterior (e), posterior (f), medial (g), and distal (j) views; **i**, **k**, and **l**, distal fragment of left humerus (MLP 91-IV-1-85) in distal (l), posterior (k), and anterior (l) views. **Abbreviations**: A, anconeus muscle; **BR**, brachioradialis muscle; **c**, capitulum; **cf**, coronoid fossa; **cle**, capitulum lateral extension; **cp**, coronoid process; **dc**, deltopectoral crest; **DPA**, deltoideus pars acromialis muscle; **DPS**, deltoideus pars spinalis muscle; **dsh**, deltopectoral shelf; **e**, entepicondyle; **ec**, ectepicondylar crest; **ECR**, extensor carpi radialis muscle; **gtu**, greater tuberosity; **hh**, humeral head; **IS**, infraspinatus muscle; **ltu**, lesser tuberosity; **of**, olecranon fossa; **PE**, pectoral muscles; **pec**, proximal projection of the **ec**; **plct**, posterolateral crest of the trochlea; **pmct**, posteromedial crest of trochlea; **PT+E**, pronator teres + extensor muscles; **SB**, subscapularis muscle; **scp**, scapular coracoid process; **sf**, supracondyloid foramen; **sr**, supracondyloid ridge; **SU**, supraspinatus muscle; **t**, trochlea; **TBcl**, triceps brachii caput laterale muscle; **tl**, tricipital line; **TM+LD**, teres major muscle + latissimus dorsi muscles
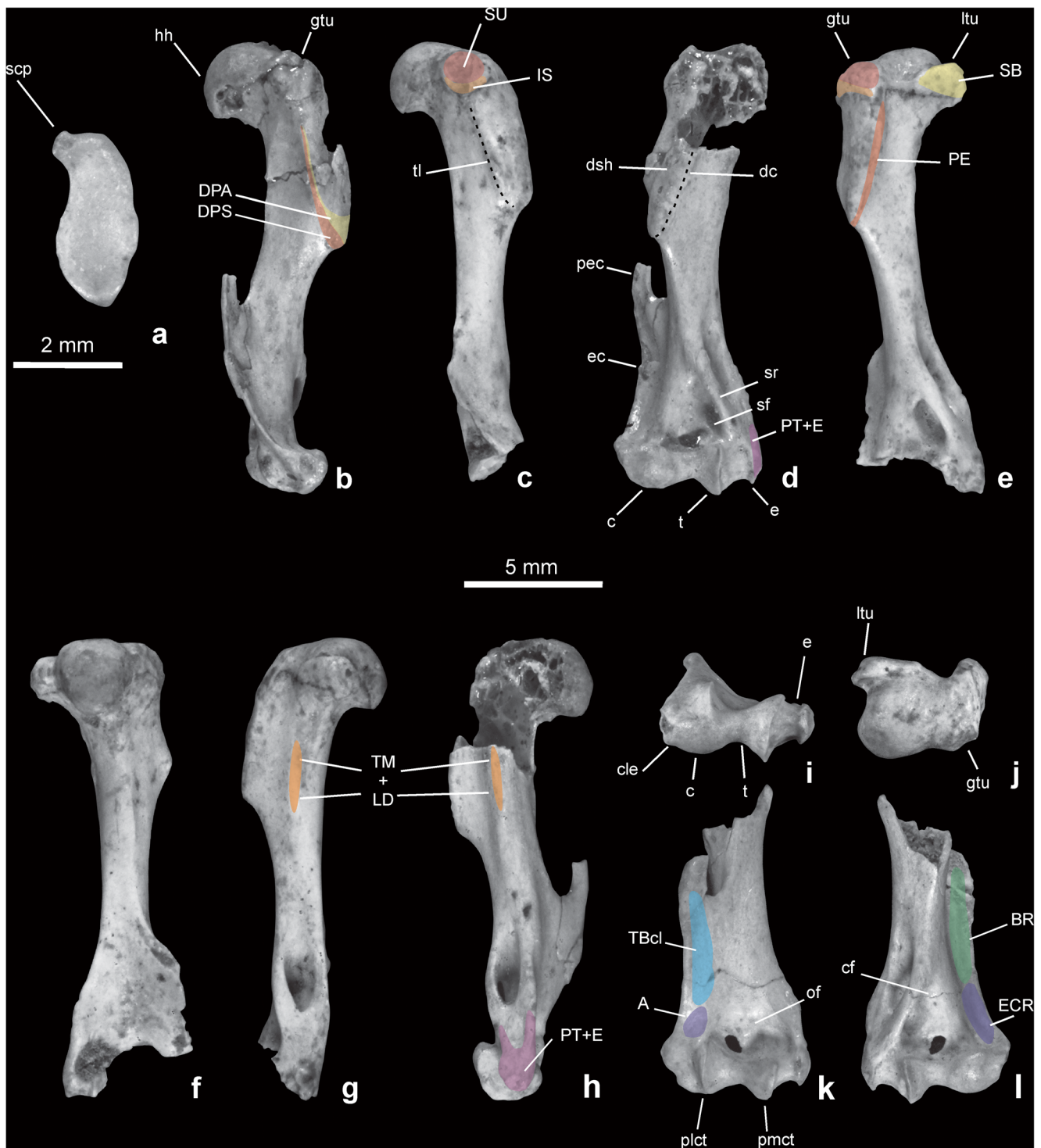
deltopectoral crest is stronger (i.e., more robust and salient along its extension), indicating well-developed pectoral muscles. In addition, the deltopectoral shelf (area delimited medially by the deltopectoral crest and laterally by the tricipital line; Fig. 1b-d) is quite wide suggesting a large insertion area for the M. deltoideus pars spinalis and pars acromialis (Fig. 1b). A similar deltopectoral shelf is present in

Microtragulus (Babot and García-López 2016: fig. 5), *Macrotis*, and *Potorous*. The distal half of the humerus is better known from MLP 91-IV-1-85 than from MMP 785-S specimens (Fig. 1d, i, k-l). The ectepicondylar crest is wider than all compared taxa, except *Potorous*, and its proximodistal length in relation to the length of the humerus is longer than any other species compared (HL/ELH=1.9; Table 1, Online

Resource 3). In addition, it has a large proximal projection (proximal process on the supinator ridge, Flores 2009; Fig. 1b, d, h, k-l) similar to that developed in *Microtragulus* (Babot and García-López 2016: fig. 5). By this morphology, the ectepicondylar crest offers broad surfaces of attachment for the triceps brachii caput laterale and anconeus muscles posteriorly, and brachioradialis and extensor carpi radialis, anteriorly (Fig. 1k-l). The supracondyloid ridge is not antero-laterally positioned as it is in most of the compared species, but it is located on the anterior humerus face forming the superficial wall of a large supracondyloid foramen (Fig. 1d). The entepicondyle is moderately salient and separated from the posteromedial crest of the trochlea by a wide sulcus (Fig. 1d, i, k). On the anterior face of the entepicondyle there is a well-delimited scar indicating the origin of the pronator teres muscle (Fig. 1d, h). The capitulum and trochlea are high, deep, and equally extended proximally (Fig. 1d, k, l) as occurs in *Macrotis*. The morphological proportions among the capitulum and trochlea differ from that shown by *Dromiciops* and *Trichosurus* in which the capitulum is higher and deeper than the trochlea. The capitulum is cylindrical (i.e., mediolaterally elongated) and the lateral extension of its articular surface is poorly developed (Fig. 1i). As in *Macrotis*, trochlear postero-lateral and posteromedial crests are strong (Fig. 1k). The olec-ranon fossa is wide, deep, and perforated (Fig. 1k). In anterior view, there is a well-developed coronoid fossa, similar to that present in *Macrotis* (Fig. 1l). With the exception of the humeral proximal end, which is not preserved in the humerus certainly referred to *Microtragulus* (Babot and García-López 2016: fig. 5), the remaining humeral structures are similar to those described for *Argyrolagus*.

Ulna

The proximal portion of the ulna is straight, as those of *Macrotis* and *Potorous* (Fig. 2b). The prominent coronoid and ulnar proximal processes shape a deep trochlear notch (Fig. 2a-b; UTNI= 1.79, Table 1, Online Resource 3) which is, in medial view, less open than that of *Dromiciops*, *Didelphis*, and *Trichosurus*, and resembles that of *Potorous* and *Macrotis*. The ulnar proximal trochlear crest is mediolaterally broad, more than in all species compared, and has its lateral and medial wings subequal in length, and con-cave and convex shaped, respectively (Fig. 2c). The ulnar distal trochlear crest is mediolaterally roughly as wide as the proximal trochlear crest. The radial notch is concave and faces more laterally than anteriorly (Fig. 2a, c), as occurs in *Macrotis* and *Potorous*. The proximal and medial portions of the ulna have strongly marked surfaces for various muscle attachments. The olecranon process is as long as the trochlear notch length and quite deep, allowing wide insertions areas for all triceps heads (triceps brachii caput longum, caput mediale, and caput laterale) (Fig. 2a, b). Medially, it shows a deep fossa

for the flexor digitorum profundus (Fig. 2b). In lateral view, it has a moderate fossa, and a posterolateral ridge, which indi-cates the insertion area of the anconeus (Fig. 2a). In anterior view, there is a well-marked insertion area for the brachialis + biceps brachii (Fig. 2c). In lateral view, the shaft of the ulna, distal to the radial notch, has a deep fossa that indicates that the abductor pollicis longus muscle was well developed (Fig. 2a). Towards the distal end, the ulnar shaft becomes quite narrow, particularly in an anteroposterior direction, resem-bling that of *Macrotis* and *Potorous*. In this trait, the ulna of *Argyrolagus* differs from species such as *Didelphis*, *Trichosurus*, and *Pseudocheirops*, which have distal ulnar shafts anteroposteriorly broader. On the medial face of the preserved distal portion, there is a crest that would indicate the origin of the pronator quadratus (Fig. 2c). The ulnae of MLP 91-IV-1-85 lack the more distal end, thereby the mor-phology of the styloid process is unknown. In those compa-rable characters (most of the shaft and proximal portion), the ulna of *Argyrolagus* is quite similar to that of *Microtragulus* (Babot and García-López 2016: fig 5).

Radius

In proximal view, the radial head is subcircular (Fig. 2f). On the rim of the radial head there is a central process and an extended radioulnar articular facet (Fig. 2d, e). The radius shaft is bowed anteroposteriorly (convex anteriorly; Fig. 2e). Similar to *Potorous* and *Macrotis*, the bicipital tuberosity is both more proximal and more sharply delineated than in *Didelphis* and *Pseudocheirops* (Fig. 2d). Below this tuberos-ity, a sharp and prominent radial ridge is extended along the shaft, particularly on its distal half. This crest is delimited by the origin area of the flexor digitorum profundus medially and abductor pollicis longus laterally (Fig. 2d). Anteriorly, there is a strong scar, approximately on the point of maximum shaft convexity, which could correspond with the beginning of the insertion of the pronator teres (Argot 2001; Fig. 2e). As in *Potorous* and *Macrotis*, the distal end of the radius is mediolaterally wide, and has a moderately developed and distally extended styloid process. The distal articu-lar surface for the scaphoid is transversely broad and concave. The grooves for the tendons of extensor digitorum communis and extensor carpi radialis are well delimited (Fig. 2e).

Phalanges

The ungual phalanges of the hand (known for specimens MMP 785-S and MLP 91-IV-1-85) are mediolaterally com-pressed and elongated. In lateral view, the phalangeal shafts are dorsoventrally shallow, the tips are pointed, and the dorsal margins are convex, extended in an unbroken manner from the tip to the extensor tubercle. The flexor tubercles are

Fig. 2 Forelimb anatomy of *Argyrolagus* showing reconstructed areas of muscular origins and insertions discussed in the text. Ulna and radius of *Argyrolagus* sp. (MLP 91-IV-1-85): **a-c**, left ulna in lateral (a), medial (b), and anterior (c) views; **d-f**, left radius in posterior (d), lateral (e), and distal (f) views. **Abbreviations: A**, anconeus muscle; **APL**, abductor pollicis longus muscle; **BRA+BI**, brachialis + biceps brachii muscles; **bt**, bicipital tuberosity; **cp**, coronoid process; **FDP**, flexor digitorum profundus muscle; **of**, olecranon fossa; **op**, olecranon process; **PQ**, pronator quadratus; **PT**, pronator teres; **rcp**, radial central process; **rgecr**, radial groove for the extensor carpi radialis; **rn**, radial noth; **rr**, radial ridge; **ruaf**, radioulnar articular facet; **st**, styloid process; **TB**, triceps brachii caput laterale, longum and mediale muscles; **tn**, trochlear notch; **udtc**, ulnar distal trochlear crest; **upp**, ulnar proximal process; **uptc**, ulnar proximal trochlear crest
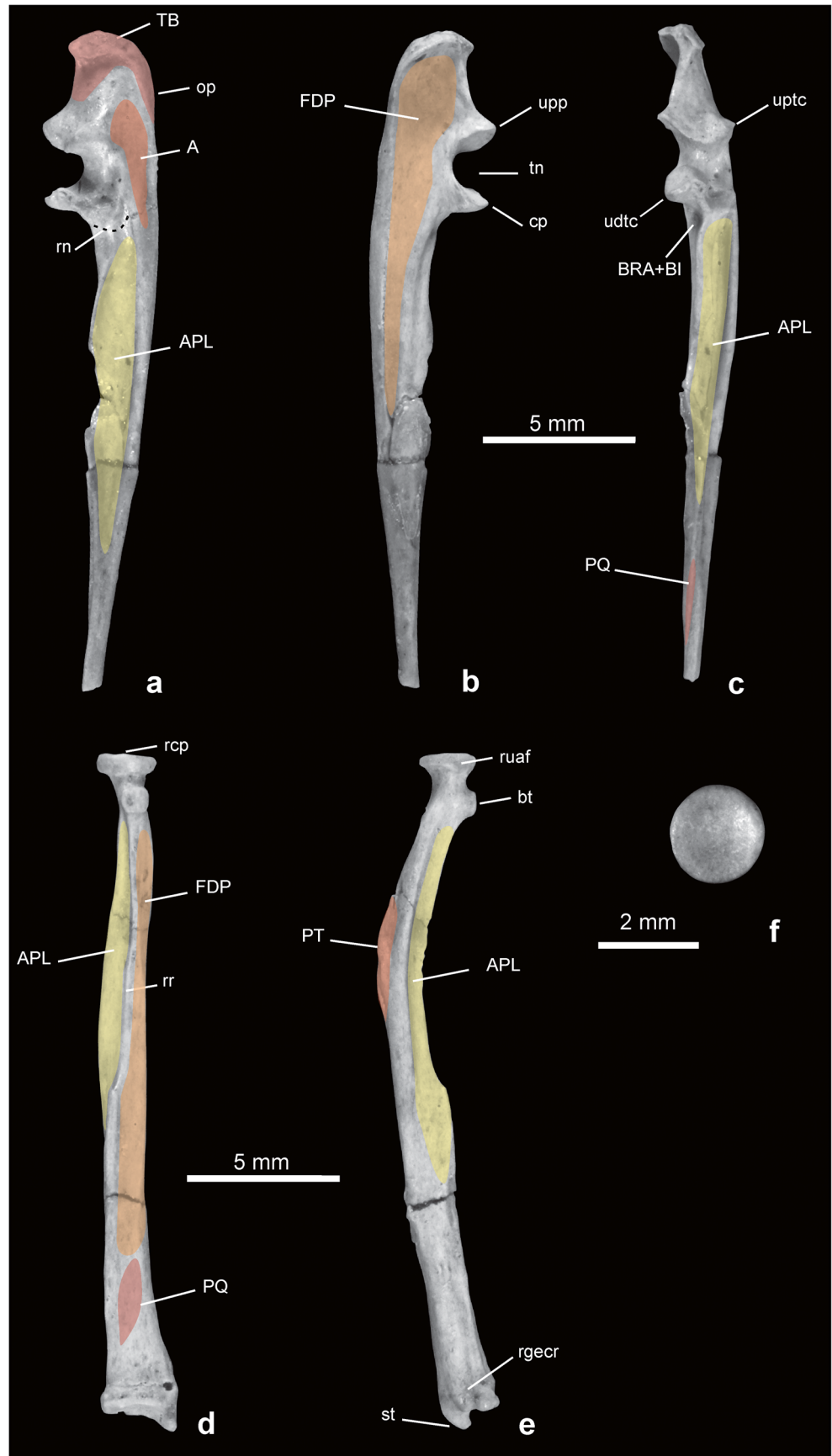
mediolaterally constricted and larger (more elongated) than the extensor tubercles, which are small but well differentiated. The articular surface for the middle phalanx is strongly concave. In their general morphology, the ungual phalanges of *Argyrolagus* are quite similar to those described for *Microtragulus* (Babot and García-López 2016: 14, fig. 7).

Pelvis

The pelvis of 785-S comprises the right complete ilium, acetabulum, and dorsal and posterior rami of the right ischium (Fig. 3a-c). The left pelvis only preserves the acetabulum and fragmentary ilium and ischium. Neither the pubis nor the pelvic symphysis are preserved (Fig 3a). The iliac wing is longer than the dorsal ramus of the ischium (Fig. 3b; see IRI Table 1, Online Resource 3), being relatively shorter than that of *Dromiciops*, *Didelphis*, and *Trichosurus*, and longer than that of *Macrotis* and *Potorous*; the iliac wing of *Argyrolagus* shows an intermediate condition. Similar to *Macrotis* and *Potorous*, the iliac wing of *Argyrolagus* is outwardly flared (Fig. 3a) and the sacroiliac joint is posteriorly well placed in relation to the anterior end of the ilium. The gluteal fossa, which is the area of attachment of the gluteus medius and profundus, is broader and deeper than the iliac fossa, the origin area of the iliacus muscle (Fig. 3b). Anterodorsal to the acetabulum, there is a well-marked origin area for the gluteus minimus (Fig. 3a-b). Next to it, and cranial to the acetabulum in the proximal end of the acetabular border, there is a well-developed tuberosity (rectus tubercle, Fig. 3b) for the rectus femoris origin. There is no evidence of an iliopectineal process. The acetabulum is somewhat ovate and deep, and faces ventrolaterally (Fig. 3b-c). Its dorsal border is slightly concave (Fig. 3a). Lobes of the articular facet are broad and have salient borders, especially the posterior one (Fig. 3b), as occurs in *Potorous*. The posterior ramus of the ischium is laterally extroverted (Fig. 3a) and has a robust ischiatic spine for the origin of the hamstring muscles: biceps femoris and semitendinosus.

Femur

All femurs included in specimen MMMP 785-S are fragmentary. None of them have a complete greater trochanter. However, by the preserved parts and femurs described and figured by Simpson (1970: 29, fig. 13 A-B), it can be inferred that it was robust and higher than the femoral head (Fig. 4a-b), which is hemispherical and its articular surface lightly extends dorsally onto the femoral neck (Fig. 4c), as occurs in *Potorous*. Distal and lateral to the greater trochanter, there is a salient crest that probably corresponds to the insertion area of the gluteus superficialis (Fig. 4a). The trochanteric fossa is short (Fig. 4b). The lesser trochanter, which is the insertion area of the iliopsoas complex, is distally extended, salient, and

posteromedially oriented (Fig. 4a-c). Like *Potorous* and *Macrotis*, as well as *Metachirus* among didelphids, the distal femur is anteroposteriorly deep, and the lateral and medial articular condyles are subequal (Fig. 4d-e). The femoral groove for the tendon of the quadriceps femoris is proximally extensive and well delimited by two parallel crests (Fig. 4e).
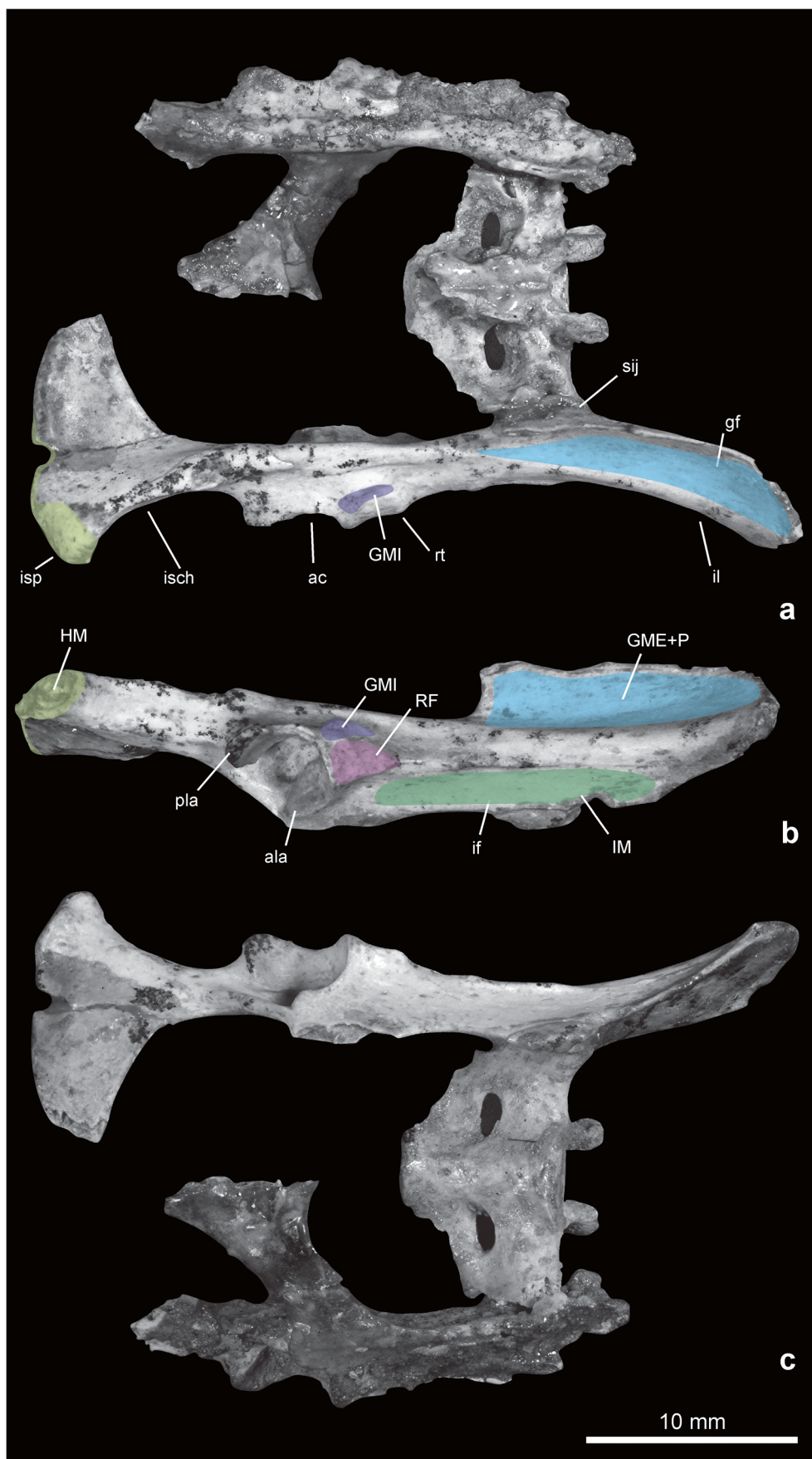
Tibio-fibula

Currently, there is not a whole preserved tibio-fibula as was originally described by Simpson (1970: 30). Instead there are several proximal and distal parts corresponding to specimen MMMP 785-S and an almost complete left tibio-fibula of MLP 91-IV-1-85 (Online Resource 1). In *Argyrolagus*, the fibula is quite reduced and fused to the tibia along its distal half conforming a unit, the tibio-fibula (Fig. 4f-h), which is markedly longer (approximately 30 %) than the femur (see Table 1, Online Resource 3). The proximal surface of the tibia is triangular in outline, with a tibial tuberosity, being the point of the insertion for the tendon of the quadriceps femoris prominent (TPDI: 25-31; see Table 2, Online Resource 3; Fig. 4i). The articular surface of the medial condyle is relatively more concave than that of the lateral condyle (Fig. 4g-h). The lateral condyle is a bit wider than the medial, and, in contrast to it, its posterior edge is not rounded but is quite straight, being the area of proximal articulation with the fibula. The condyles are separated by a well-developed intercondylar eminence (Fig. 4i). The tibial crest is proximally restricted and quite salient (Fig. 4f-g) as occurs in saltatorial *Potorous*. Its medial aspect, and the medial surface of the tibia, probably provided insertion, partially or completely, to the gracilis, semimembranosus, and semitendinosus via the crural fascia, as occurs in several marsupials (Hopwood and Butterfield 1976; Argot 2002; Warburton et al. 2015). The tibial crest is markedly concave laterally (Fig. 4g) in order to accommodate the tibialis anterior, which could have extended its origin on the also concave proximal lateral half of the shaft (proximal lateral fossa of the tibia sensu Warburton et al. 2012) (Fig. 4f-g). As in *Macrotis lagotis*, the posterior aspect of the tibia is marked by a medial crest (Fig. 4h) for the insertion of the popliteus (Warburton et al. 2015). Medial to this crest, there is a concave surface of the tibia identified as the origin area of the flexor digitorum profundus. As was noted by Simpson (1970: 30), and as can be inferred from the most complete known remains (MLP 91-IV-1-85 and MMMP 785-S; Fig. 4f-h, j-k), the distal half of the tibia and fibula are completely fused with each other (Fig 4l), and the part of the fibula above its fusion with the tibia is about 50 % of the total tibia length. Even though bony fusion of the lower ends of the tibia and fibula is present in some bilby and bandicoot species (Barnett and Napier 1953a), the extensive fusion among both bones in *Argyrolagus* is unique among

Fig. 3 Anatomy of the pelvis of *Argyrolagus* showing reconstructed areas of muscular origins and insertions discussed in the text. Pelvis of *Argyrolagus scagliai* (MMP 785-S): **a**, dorsal, **b**, lateral, and **c**, ventral views. **Abbreviations: ac**; acetabulum; **ala**, anterior lobe of articular facet of acetabulum; **gf**, gluteal fossa; **GME+P**, gluteus medius + profundus muscles; **GMI**, gluteus minimus muscle; **HM**, hamstring muscles; **if**, iliac fossa; **il**, Ilium; **IM**, iliopsoas muscle; **isch**, ischium; **isp**, ischiatic spine; **pla**, posterior lobe of articular facet of acetabulum; **RF**, rectus femoris; **rt**, rectus tubercle; **sij**, sacroiliac joint

Fig. 4 Hind limb anatomy of *Argyrolagus* showing reconstructed areas of muscular origins and insertions discussed in the text. Femur and tibio-fibula of *Argyrolagus* spp. (MLP 91-IV-1-85 and MMP 785-S): **a**, left femur (MMP 785-S) in anterior view; **b-c**, proximal fragment of right femur (MMP 785-S) in posterior (b) and proximal (c) views; **d-e**, distal fragment of right femur (MMP 785-S) in posterior (d), and anterior (e) views; **f-h**, left tibio-fibula (MLP 91-IV-1-85) in lateral (f), anterior (g), and posterior (h) views; i, fragment of proximal left tibio-fibula (MMP 785-S) in proximal view; **j-k**, fragment of distal left tibio-fibula (MMP 785-S) in posterior (j), and distal (k) views. **Abbreviations: Atil**, lateral astragalotibial facet; **CaFi**, calcaneofibular facet; **eg**, extensor groove; **f**, fibula; **FDPt**, flexor digitorum profundus (tibial) muscle; **fg**, femoral groove; **fh**, femoral head; **gf**, groove for flexors; **GS**, gluteus superficialis muscle; **gt**, greater trochanter; **ie**, intercondylar eminence of tibia; **IM**, iliopsoas muscle; **lacf**, lateral articular condyle of femur; **lact**, lateral articular condyle of tibia; **lt**, lesser trochanter; **ltu**, lesser tuberosity; **macf**, medial articular condyle of femur; **mact**, medial articular condyle of tibia; **mtm**, medial tibial malleolus; **P**, popliteus; **pmt**, posterior medial crest of the tibia; **TA**, tibialis anterior muscle; **tc**, tibial crest; **tf**, trochanteric fossa; **tt**, tibial tuberosity

metatherians and similar to that developed in many small placentals such elephant shrews, jerboas, and tarsiers (Barnett and Napier 1953b). The distal tibia and fibula of extant metatherians can be closely bounded together, yet both bones are distinct and separate, having a synovial tibiofibular joint or, less common, a syndesmosis between them (macropodids, didelphids, marmosines, and peramelids; Barnett and Napier 1953a; Argot 2002; Szalay 1994). Simpson (1970: 30) described that tibia and fibula of *A. scagliai* as also fused proximally. Currently, the fibula is only preserved in MLP 91-IV-1-85, where its proximal end is seriously damaged, preventing us from corroborating Simpson`s observation (Fig. 4g-h). The fibular shaft is slender and becomes thicker proximally. Differing from all compared species, the medial surface of the fibula is quite concave (Fig. 4h) for the origin of the flexor digitorum profundus (sensu Warburton et al. 2015; =flexor fibularis sensu Argot 2002). The distal half of the tibiofibula is roughly quadrangular in section. On distal view, the lateral astragalotibial facet (Atil) is mediolaterally wide (Fig. 4k). The medial astragalotibial facet (Atim) is quite concave, extended anteroposteriorly following the trochleated astragalar Atim (Fig. 5a), and has a small posterior projection. In addition, the Atim is well extended distally, in such a way that the medial tibial malleolus strongly braces the astragalus medially (TMI: 2.3-2.6; see Table 2, Online Resource 3; Fig. 4j). In the fibular portion of the distal crus, the calcaneofibular facet (Cafi) is anteroposteriorly extended and concave (Fig. 4k) in order to accommodate the hinge-like calcaneus Cafi (Fig 5e-f). As the Atim, Cafi has a small posterior projection (Fig. 4k). The Afi is quite small and angled with respect to the Atil. In the posteromedial corner of the tibial malleolus, there is a well-developed groove for the flexors (Szalay 1994: fig. 7.26; Fig. 4j), the tendons of the flexor digitorum profundus and the tibialis posterior. On the surface of the distal and lateral fibular portion, there is a deep groove (ge: extensor groove; Szalay 1994: 96) for tendons of
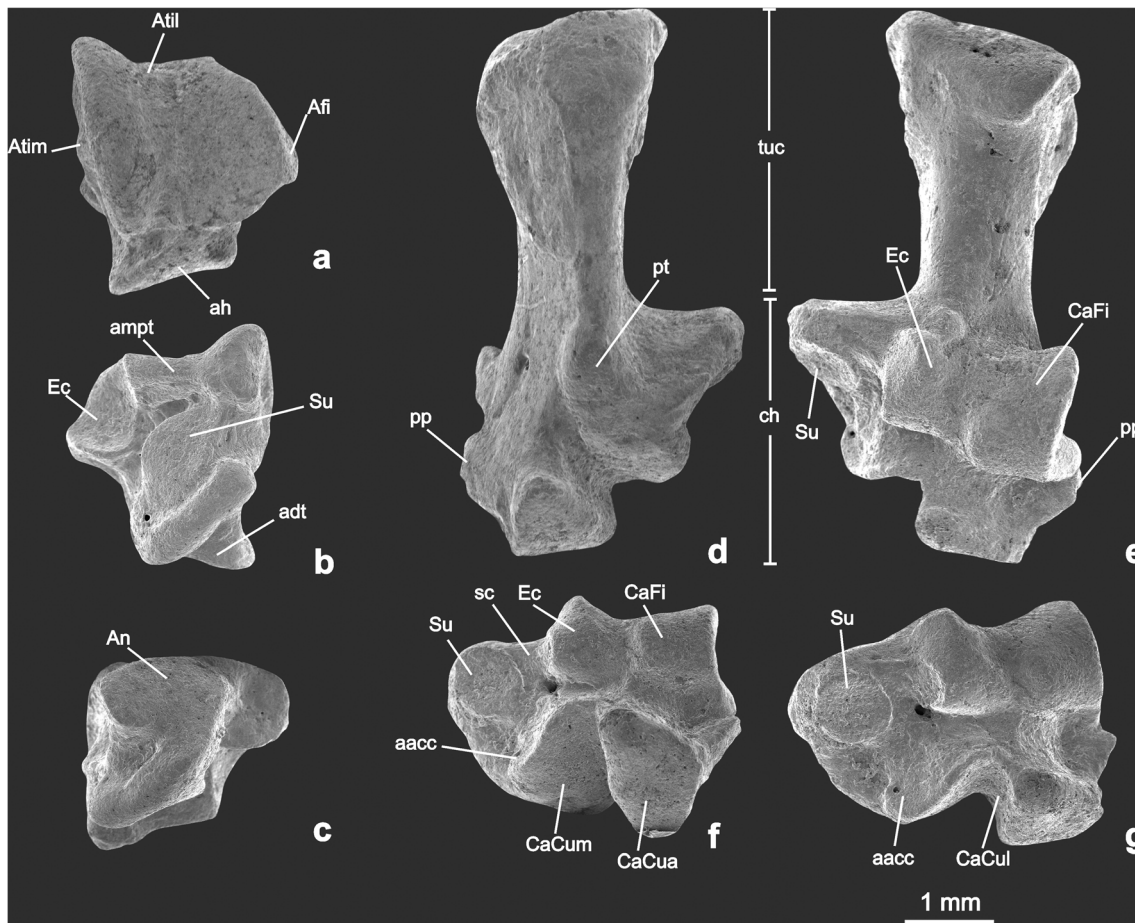
Fig. 5 Astragalus and calcaneus of *Argyrolagus*. Astragalus and calcaneus of *Argyrolagus scagliai* (MMP 785-S): **a-c**, right astragalus in dorsal (a), ventral (b), and distal (c) views; **d-g**, right calcaneus in ventral (d), dorsal (e), distal (f), and laterodistal (g) views. **Abbreviations: aacc**, accessory astragalocalcaneal contact; **adt**, astragalar distal tuber; **Afi**, astragalofibular facet; **ah**, astragalar head; **ampt**, astragalar medial plantar tuberosity; **An**, astragalonavicular facet; **Atil**, lateral astragalotibial facet; **Atim**, medial astragalotibial facet; **CaCua**, calacaneocuboid anterior facet; **CaCul**, calacaneocuboid lateral facet; **CaCum**, calacaneocuboid medial facet; **CaFi**, calcaneofibular facet; **ch**, calcaneal head; **Ec**, ectal facet; **pp**, peroneal process; **pt**, plantar tubercle; **sc**, sulcus calcanei; **Su**, sustentacular facet; **tuc**, tuber calcanei

the peroneus group and extensor digitorum brevis (Fig. 4j-k). Except for its larger size, the tibio-fíbula of *Argyrolagus* is mostly similar to the partially preserved tibio-fíbula of *Microtragulus reigi* (a left tibio-fibula lacking the distal end, see Simpson 1970: 25-26), and *M. bolivianus* (a distal fragment of right tibio-fíbula, Babot and García-López 2016: fig. 5).

Astragalus

The astragalus of *Argyrolagus* is only known by the specimen MMMP 785-S (Fig. 5a-c). The astragalar body is subquadrangular with a relatively large astragalar head, parasagitally set with respect to the anteroposterior axis of the astragalus, and has a neck wider than the head (Fig. 5a-b). The astragalus is characterized by a large and highly trochleated (sensu Szalay 1994) Atil facet, which is at a sharp (right) angle with the Atim (Fig. 5a). The angle made by the Atil and Atim facets is sharper than those of didelphids (including the terrestrial *Metachirus*) and arboreal australidelphians (e.g., *Trichosurus*) and resembles that occurring in paucituberculatans, sparassodonts, and highly terrestrial australidelphians (e.g., *Potorous* and macropodines). The astragalofibular facet (Afi) is quite small in relation to the Atil facet and slightly angled with respect to it (Fig. 5a). A less reduced Afi facet is common among both South American (e.g., *Caenolestes* and *Palaeothentes*) and australidelphian terrestrial marsupials (e.g., *Potorous* and *Macrotis*), and differs from South American (e.g., *Didelphis*) and australidelphian (e.g., *Trichosurus*) arboreal or scansorial species, where the Afi facet is well developed. Mirroring the calcaneus (see below), there is no continuity between the ectal (Ec) and sustentacular (Su) facets (Fig. 5b). The Ec facet is quite concave and is anteroposteriorly orientated (straight), while the Su facet is slightly convex and oblique, with its major axis proximomedially to distolaterally oriented (Fig. 5b). The ectal facet extends to the posterior edge of the astragalus. The Su facet is set above the astragalar medial plantar tuberosity (ampt), which occupies most of the proximoventral border of the astragalus and is not visible in dorsal view. As in caenolestids and sparassodonts, the Su facet does not reach the medial edge of the astragalar neck and has a ribbon-like extension running above the ampt (Szalay 1994: 211). The astragalonavicular facet (An) is wider transversally than dorsoventrally (Fig. 5c), and is vertically oriented. In addition, it extends to the ventromedial area of the head. The astragalar distal tuber is present and well developed (Fig. 5b). The astragalus and calcaneus of *Argyrolagus* (see below) are similar in all characters described to those homologous bones of *Microtragulus* (Ortiz et al. 2012: fig. 5; Babot and García-López 2016: fig. 6)

Calcaneus

The calcaneus of *Argyrolagus* was previously described by Szalay (1994; see also Lorente et al. 2016 and Beck 2017). Here, we extend the comparative description of some of the most important features and include those not previously contemplated. The calcaneus has a long and straight tuber calcanei and a wide calcaneal head (sensu Bassarova et al. 2009: fig. 3; Fig. 5d-e). As noted by Szalay (1994), one of the most significant features of the calcaneal head is the great size of the calcaneofibular facet (CaFi) (Fig. 5e). This facet is very large in all known argyrolagid calcanea. For example, a large CaFi is in the Miocene argyrolagid from Gaiman (Szalay 1994: fig 7.27 A-C), Pliocene *Argyrolagus* (Szalay 1994: fig. 7.27 D-F and 7.28 A-F), and *Microtragulus* (Ortiz et al. 2012: fig. 5C). In fact, the CaFi occupies almost half of the maximum width of the calcaneal head (Fig. 5e), thus differing from any other extant or extinct metatherian, where this facet is absent (e.g., didelphids) or relatively small. Such is the case in the paucituberculatans *Palaeothentes* and *Caenolestes* and some Itaboraian calcanea (e.g., Itaboraí Metatherian Group X, Szalay 1994:179; Paleocene, Brazil); the latter has a quite large CaFi in relation to the Ec facet, but none of them is as large as that of *Argyrolagus*. The CaFi is cylindrical, almost hinge-like in appearance, and anteroposteriorly longer than wider (Fig. 5e-g). There is no continuity between the Ec and Su facets, as occurs in *Dromiciops* and most of Australidelphia, which are characterized by a continuous lower ankle joint (CLAJP; Szalay 1982a, b). Instead there is a sulcus calcanei between both facets (Fig. 5f), as occurs in American metatherians (except *Dromiciops* and an indeterminate taxon of australidelphian affinities from the Eocene of Patagonia (Lorente et al. 2016) and in an isolated calcaneus (QM F30060) from the early Eocene (~54.6 Ma old), of Tingamarra Local Fauna of Australia (Beck 2012). The Ec is anteroposteriorly convex and dorsodistally orientated (Fig. 5e-f), with its major axis straight to slightly oblique (proximomedial to distolateral) relative to the long axis of the bone. The Su facet is flat, proximally restricted, and anteriorly oriented (Fig. 5e-g). As in *Dendrolagus,* it is raised in relation to the level of the sustentaculum. In addition to the proximally restricted Su facet, there is a secondary medial contact between the astragalus and the calcaneus, distal to the Su facet (Fig. 5f-g). This medial accessory contact is similar to that present in the australidelphian dasyurids (CaAd, sensu Szalay 1994: 225), and macropodids (CaAs, sensu Szalay 1994: 258). The surface of the calcaneocuboid joint (CaCu) is almost perpendicular to the anteroposterior axis of the calcaneus (Fig. 5e), as occurs in saltatorial marsupials (Bassarova et al. 2009). Three facets can be differentiated: calacaneocuboid medial (CaCum), lateral (CaCul), and anterior (CaCua), homologous to those of australidelphian

marsupials and paucituberculatans (Fig. 5f-g; see discussion). The CaCum and CaCua facets face distally and are "stepped," as was described by Szalay (1994), as the CaCum facet is proximally retreated from the more distal CaCua facet (Fig. 5f). The peroneal process is quite reduced, as in most terrestrial marsupials (e.g., dasyuromorphs and peramelemorphs), and distally placed (Fig. 5d). A moderately developed anterior plantar tubercle is present, ventral and posteriorly placed with respect to the CaCum facet (Fig. 5d). In the study of the calcaneus of *Argyrolagus scagliai*, MLP 87-XII-11-1 and MMMP 785-S, we observed some intraspecific variation, which is expressed in the larger size (30 percent longer and wider, see Table 3, Online Resource 3) of MLP 87-XII-11-1 with respect to MMMP 785-S. This difference may be due to MLP 87-XII-11-1 being an adult (male?) specimen as could be inferred from its craniodental morphology (deep mandible and stronger dental wear than MMP 785-S). On the other hand, the studied calcaneus of *Argyrolagus* sp. (MLP 91-IV-1-85) has the same morphology as that of MMMP 785-S.

Navicular, Cuneiform, Cuboid, and Metatarsals

The navicular, cuneiform, and cuboid of *Argyrolagus* were described and figured by Simpson (1970: 31-32, fig. 15) and Szalay (1994: 215, figs. 7.29 and 7.30). Of the three tarsal bones only the navicular is currently preserved. Current metatarsals are quite fragmentary with respect to the original left and right metatarsals III and IV. From the original and previous description, we know that the cuboid in *Argyrolagus* had CaCup and CaCua facets that mirrored those of the calcaneus. Notably cuboidal CaCud was much wider than the complementary facet on the calcaneus (Szalay 1994). The navicular was referred with doubts to the specimen MMMP 785-S by Simpson (1970) and subsequently described by Szalay (1994). We agree with Simpson's point of view as the navicular does not match in size with the much smaller astragalus. The metatarsals known in *Argyrolagus* are inferred to be III and IV. Our observations on these specimens at first hand are in agreement with the description given by Simpson (1970). Among the most notable characteristics are the metatarsals III and IV being closely in contact, the apparent lack of vestiges of metatarsals II and V and their contact facets on metatarsals III and IV, respectively. Metatarsals III and IV were elongated and had a relative length with respect to the femur and tibiofibula that is comparable to the one in bipedal rodents (see D/E, PES, and MRL indices in Table 3, Online Resource 3).

Caudal Vertebrae

We largely agree with the description of the caudal vertebrae of Simpson (1970: 26-27), and so we only highlight some functionally important traits. The preserved three anterior caudal vertebrae (Simpson 1970: fig. 7) have functional prezygapophyses (divergent laterally, and prominent anterodorsally) and well-developed mammillary processes. Differing from most extant marsupials studied here, the neural process of the anterior caudal vertebrae, is reduced. The foramen vertebrale is reduced, and flattened dorsoventrally. The transverse processes are flat and almost quadrangular, resembling those of anterior caudal vertebrae of *Metachirus* and *Potorous*. Posterior caudal vertebrae (Simpson 1970: fig 8) have reduced or absent postzygapophyses, non-functional prezygapophyses, and strong lateral paired processes on the anterior and posterior ends. Posterior caudal vertebrae exhibit a significant anteroposterior lengthening (they are roughly twice as long) and have more robust vertebral bodies, compared to the anterior ones.

Phylogenetic Analyses

Analysis of the combined morphological and molecular data set resulted in six most parsimonious trees (MPTs). The extinct australidelphian *Djartia* behaved as a wildcard taxon. Excluding *Djartia* from the analysis, a common topology was recovered in the resultant two MPTs with didelphimorphs as sister clade to Australidelphia, and Paucituberculata as the next closest relative to Australidelphia (Fig. 6a). Consistent with previous analysis (Sánchez-Villagra et al. 2000), the Argyrolagidae clade *Proargyrolagus* (*Argyrolagus* + *Microtragulus*) was obtained in each MPT. Argyrolagidae was placed within Australidelphia, sister to Peramelemorphia. The Argyrolagidae + Peramelemorphia clade had *Notoryctes* as its sister taxon. Morphology-based phylogenetic analysis resulted in six MPTs. In all MPTs, paucituberculatans were not monophyletic and included within Australidelphia, while Didelphimorphia was resolved as sister to Australidelphia (Fig. 6b). The topology of Argyrolagidae and its sister relationships with Peramelemorphia were recovered as in the combined analysis. In contrast to combined analysis, the Argyrolagidae + Peramelemorphia clade was grouped with paucituberculatans.

Discussion

Calcaneocuboid Joint Homologies and Their Phylogenetic Significance

In the original description of the *Argyrolagus* calcaneus, Szalay (1994) identified two CaCu facets, "CaCup" and "CaCud," which were noted in quotes because they were considered nonhomologous to those CaCu facets of didelphids (Szalay 1994: 215 and fig. 8.14). In addition, these facets were described as "stepped" (Szalay 1994), as the "CaCup" facet is

a

b

proximally retreated from the more distal "CaCud" facet. Recently, Lorente et al. (2016) and Beck (2017) noted that *Argyrolagus*, as well as the paucituberculatans *Palaeothentes* and *Caenolestes*, show a tripartite, australidelphian-like morphology of the CaCu. Based on their topological correspondences, the three facets in the CaCu of the mentioned taxa were proposed as homologous to those from the australidelphians, and the calcaneus QM F30060 (Eocene, Australia) as follows: the distal facet facing distally homologous to the CaCua, the lateral facet facing medially homologous to the CaCul, and the proximal facet facing distally homologous to the CaCum (Fig. 5f-g). For *Caenolestes* a 'lateral shelf' of the CaCu joint had been previously noted by Szalay (1982a), and identified as "cuboidcalcaneal facet outer shelf" by Horovitz and Sánchez–Villagra (2003). Here, we concur with Beck (2017: fig 9) that this facet is homologous to that the more distal CaCu facet of *Palaeothentes*, *Argyrolagus*, and australidelphians; so, according to its topological relationships, the "lateral shelf" in *Caenolestes* is identified as the CaCua facet.

In short, the CCJ in *Palaeothentes*, *Caenolestes*, and *Argyrolagus* is characterized by three facets, which are essentially identical in their topological relationships (including position, orientation, and connections) to those of australidelphians and QM F30060. In this way, this pattern exhibits a very different configuration to that of the Didelphimorphia (with two facets) and the extinct Sparassodonta (with only one facet). The identification of the topographic correspondences of these structures is crucial to identify the calcaneal- cuboid characters that can be confidently used in phylogenetic analysis of marsupials. From the comprehensive studies on metatherian crurotarsal morphology of Szalay (1982a, b, 1993, 1994), both CLAJP and the tripartite CaCu have been consistently considered the strongest morphological characters supporting Australidelphia monophyly. Our results are in part consistent with this proposal because in both analyses the tripartite CaCu resulted in a synapomorphy of Australidelphia. In the morphological analysis, CaCu evolved once, representing a synapomorphy of Australidelphia, while CLAJP diagnosed a less inclusive clade (*Djartia* + Dasyuromorphia +Diprotodontia, Fig. 6b). In the combined analysis, CLAJP occurred ambiguously at the Australidelphia node while tripartite CaCu originated twice, in Australidelphia and Paucituberculata. This latter result emerges by recovering Didelphimorphia as sister to Australidelphia, a hypothesis supported in some recent molecular analysis (Mitchell et al. 2014; May-Collado et al. 2015).

Argyrolagids and Peramelemorphs: Close Relatives or Convergent?

In both morphological and combined analyses, argyrolagid monophyly is supported only by craniodental characters: a well-developed alisphenoid, hypsodont molars, and a retrodental foramen (see discussion on retrodental foramen homology in Beck 2017). In both analyses, the sister-group relationships of argyrolagids and peramelemorphs are mostly based on postcranial characters, particularly those from the tarsal bones (see Online Resource 5). These characters include: straight astragalar Ec facet (9498^0) and the Atim and Atil facet equally extended posteriorly (9502^1), which grouped argyrolagids and peramelemorphs; in addition, depending on the analysis considered, some other tarsal characters emerged as synapomorphies of this clade: anterior edge of calcaneal Su facet equal or posterior to that of Ec facet (9516^1), and calcaneal Su facet not reaching anterior end of the calcaneus (9520^0), in the morphological analysis, and An facet not extended on medial side of the astragalar head (9488^0) and calcaneal Ec facet straight (9505^1), in the combined analysis.

Argyrolagid-peramelemorph monophyly is inconsistent with what we know about marsupial phylogeny (e.g., Sánchez-Villagra 2001; Beck 2017), and this conflict with previous proposals gives rise to doubt about our results as we are probably underestimating convergent evolution in the postcranium. Studies on postcranium in mammals have recognized that the foot, particularly the tarsus, is highly significant from a functional and phylogenetic point of view (Candela et al. 2017 and bibliography therein). Anatomy of the tarsus, accepted as the area of the skeleton that supports some of the most complex loads of the body (Szalay 1994; Szalay and Sargis 2001; Salton and Sargis 2009), can be greatly indicative of the type of movements of the foot, and it also expresses a marked influence on the phylogenetic history of each lineage. In marsupials, the tarsal anatomy, particularly that of the astragalus and calcaneus, has demonstrated to be strongly indicative of deep evolutionary-adaptative trends (Szalay 1994), being an important source of characters for cladistic analysis (e.g., Horovitz and Sánchez–Villagra 2003).

Taking into account that argyrolagids could be more closely related to other marsupials such as South American paucituberculatans (Sánchez-Villagra 2001; Beck 2017), convergences in tarsal morphology between argyrolagids and peramelids cannot be ruled out. The anteroposteriorly oriented Ec facet, the posteriorly positioned calcaneal Su facet combined with the separated Ec and Su facets (partially separated in peramelemorphs) all are characters that improve tarsal interlocking and restrict parasagittal movements of the foot. In addition, a mortise-tenon configuration of the UAJ (see UAJ discussion above) is shared by these groups and macropodoids, reinforcing the idea

of adaptive convergence to high impact locomotion. Thus, it is possible to assume homoplastic acquisition of tarsal characters in argyrolagids and peramelids, which express similar foot movements for stability and propulsion, in order to support complex and strong loads during locomotion, as runners or jumpers

Our phylogenetic results could be tested in futures studies, considering more complete evidence, both molecular and morphological, and broader taxon sampling. For example, many South American metatherians were not included in the present analysis, and most of the anatomy of *Proargyrolagus*, a plesiomorphic and early diverging argyrolagid (Sánchez-Villagra et al. 2000), is yet unknown. In any case, argyrolagid tarsal features reveal stimulating information to understand the evolution of these highly specialized marsupials.

Functional Analyses of Forelimbs

Glenohumeral Joint

Most of the scapula's significant functional features, such as the general shape (outline) (Argot 2001) and the size and orientation of the metacromion process (Seckel and Janis 2008) were not preserved. Among didelphids the shape of the glenoid fossa appears to not be related to a particular locomotor behavior (Szalay and Sargis 2001). However, among placental groups, such as primates, terrestrial forms have a narrower glenoid fossa than arboreal ones (Preuschoft et al. 2010). Among tupaiids, a narrow glenoid fossa may be related to a glenohumeral joint that is more restricted to parasagittal movements (Sargis 2002a). In *Argyrolagus*, matching the narrow glenoid fossa, the humeral head is laterally compressed indicating that anteroposterior movements were emphasized. However, the low height of the tuberosities with respect to the humeral head suggests that mobility at the glenohumeral joint was not so restricted as in most terrestrial marsupials (e.g., *Metachirus*, *Macrotis*; Argot 2001). The insertion areas of the infra- and supraspinatus on the robust greater tuberosity, and the subscapularis on the protruding lesser trochanter, indicate that these muscles largely stabilized the glenohumeral joint (Salton and Sargis 2008; Harvey and Warburton 2010), an important function especially for cursorial and leaping forms (Argot 2001), but also for those mammals with digging ability (Hildebrand 1985; Hildebrand and Goslow 2001). In sum, the set of glenohumeral joint features indicates that movements at this joint were not completely restricted to those in an anteroposterior direction. Low tuberosities and strong area of insertion for subscapularis, supraspinatus, and infraspinatus are in agreement with complex movements and stabilized articulation, an advantageous configuration for digging (Smith and Savage 1956) and agile locomotion.

Humerus

One of the most notable structures of the humerus of *Argyrolagus* is the large deltopectoral shelf and crest, which indicate that muscles related to arm retraction (deltoid pars spinalis; Argot 2001), abduction (deltoid pars acromialis and clavicularis; Harvey and Warburton 2010), and adduction-protraction (pectoralis muscles; Salton and Sargis 2008) were powerful. Strong development seems to be compensating for the relatively low Shoulder Moment Index (see SMI, Table 1, Online Resource 3). As was noted by Elissamburu and Vizcaíno (2004) and Salton and Sargis (2008), the interpretation of the deltopectoral region is complicated due to the interplay between the insertions of functionally different muscles, and its configuration probably reflects a compromise in response to different factors (e.g., recovery of steps and forces exerted during digging; see Elissamburu and Vizcaíno 2004; Elissamburu and de Santis 2011). The functional information derived by other muscles attached on the proximal humerus points to an enhanced flexion of the arm, which would be compatible with digging abilities. A strong retraction and adduction of the humerus are suggested by the inferred well-developed latissimus dorsi and teres major muscles. Despite the fact that insertion areas of these muscles are not distally placed, which would imply a reduced mechanical advantage, their remarked attachment on the humerus is strongly indicative of powerful flexion of the humerus on the scapula (Argot 2001). In addition, although the flexion of the arm is not the main function of the infraspinatus (Harvey and Warburton 2010), its contraction probably also contributed with the retraction of the arm.

On the distal half of the humerus, the broad insertion areas of triceps brachii caput laterale and anconeus indicate strong extension of the forearm, consistent with the functional inferences derived from the insertion areas of the remaining brachii muscles on the ulnar olecranon (see below). In addition to being an extensor of the forearm, the anconeus muscle acts in stabilizing the elbow joint (Argot 2001; Harvey and Warburton 2010). The relative size of the humeral entepicondyle, a site of attachment of carpal and digital flexors, reflects the degree of grasping and gripping function of the hands (Argot 2001; Warburton et al. 2011). *Argyrolagus* has a moderately sized entepicondyle and so, moderate development of hand flexors could be interpreted. However, the flexor digitorum profundus, the most informative muscle about adaptive differences originated in the entepicondyle (Szalay and Sargis 2001), is otherwise interpreted as well developed from its wide origin on the ulna and radius (see below). Therefore, an enhanced grasping function of the forepaws is suggested by the anatomy of the forelimb in *Argyrolagus*. Besides the flexor muscles, on the anterior face of the entepicondyle there is a well-marked origin area of the pronator teres. This muscle functions as pronator and flexor of the antebrachium and manus (Samuels and Van Valkenburgh 2008; Harvey and Warburton 2010).

Elbow Joint

In mammals the configuration of the trochlea and capitulum are indicative of supported loads and, along with the morphology of the olecranon fossa, ulnar notch, and radial head, these traits express the range and extent of movements at the elbow joint (Szalay and Sargis 2001). In *Argyrolagus* the equally high capitulum and trochlea, the extensive contact surfaces among the humerus and ulna (see UTNI, Table 1, Online Resource 3), and the strong humeral and ulnar trochlear crests, indicate close packing and great stability at this joint. Additional stability comes from the developed groove lateral to the capitulum; whether or not a radial sesamoid was present, this structure helps to stabilize the radius during its flexion on the humerus and rotation on the ulna (Szalay and Sargis 2001). The great stability at the elbow joint would represent an adaptive response to repetitive high impact loading during running and leaping locomotion (Szalay and Sargis 2001). In addition, it would be consistent with the suggested digging abilities of *Argyrolagus* (see above), as strong articulation is necessary to prevent dislocation and hyperextension because of the relative great forces developed against soil resistance when digging (Hildebrand 1985; Hildebrand and Goslow 2001). In *Argyrolagus*, the radial head is subcircular, indicating that at least some degree of supination was possible and, in view of the radioulnar joint and radial morphology, it could be speculated that the possible range of pronation–supination was not reduced.

Ulna

The ulna has strong muscle attachments for extensors of the forearm (i.e., triceps brachii and anconeus) and flexors of the digits (flexor digitorum profundus) indicating that these muscles played a major role in movements performed by the forelimb in *Argyrolagus*. Among mammals, these muscles are particularly modified in diggers in order to apply high forces against the soil during digging (Hildebrand 1985; Hildebrand and Goslow 2001). Likewise, the well-delimited scar for the pronator quadratus, a muscle that helps to maintain the integrity of the antebrachium (Argot 2001), points to a stabilized distal half of the forearm, as is necessary to counteract the forces applied on the forearm and to protect it against dislocation. In sum, the range of movements allowed by the ulnar morphology and inferred muscles attached to it are consistent with the enhanced capabilities for digging, as are expressed by the humerus and elbow joint configuration.

Radius

Several traits of the radius suggest enhanced (not reduced) capabilities of pronation-supination. Among them are the circular radial head (which mirrors the concave radial notch on the ulna, see above) and the anterior convexity of the proximal half of the shaft. The latter is related to an increase of the leverage of the pronator teres and supinator muscles (Argot 2001, 2003a). In addition, the well-developed origin areas of the flexor digitorum profundus and abductor pollicis longus are indicative of great prehensility of the manus (Argot 2003a). The general morphology of the radius points out that *Argyrolagus* would have had an important mobility of the forearm and manus.

Phalanges

The described general morphology of the ungual phalanges, particularly the lateral shape (the dorsoventral depth, length, and curvature), is comparable to that of living digging mammals (MacLeod and Rose 1993). The large size of the flexor tubercle is indicative of the degree of traction exerted by the tendons of M. flexor digitorum profundus (Argot 2001), inferred as a well-developed muscle based on its origin area on the forearm bones.

Functional Analyses of Hind Limbs

Pelvis

In order to increase the energy of the jump, the hip extensors (e.g., hamstrings and gluteal muscles), knee extensors (quadriceps femoris), and ankle extensors (e.g., gastrocnemius) of jumpers are large, more than in nonjumpers of the same body size, with the biceps femoris the most modified muscle in bipedal rodents (Emerson 1985). In *Argyrolagus*, given the observed large origin areas of gluteus medius + profundus, rectus femoris, biceps femoris, and semitendinosus, it can be inferred that these muscles were well developed and thus provided powerful extension to the hind limbs required for jumping. In addition to their inferred relative size, origin and insertion sites of certain extensors muscles, such as the gluteus medius close to the hip joint, are also indicative of jumping abilities (Emerson 1985). Saltatorial species have shortened ilia (Howell 1932; Emerson 1985; Chen and Wilson 2015), which implies a short lever arm for the hip extensor gluteal muscles. In this manner, gluteal muscles supply a large acceleration at the beginning of the propulsive stroke, which is mainly performed by the hamstrings muscles (Emerson 1985; Moore et al. 2017b). In *Argyrolagus*, the ilium is shorter than in the compared scansorial and arboreal marsupials (see IRI Table 1, Online Resource 3), thus indicating that gluteal muscles in *Argyrolagus* may have contributed to maximize the angular velocity of the hind limbs and acceleration during take-off. However, compared with terrestrial saltatorial *Potorous* and *Metachirus*, the ilium of *Argyrolagus* is longer. Eversion of the iliac wing, such as that shown by *Argyrolagus*, allows more medially space for the epaxial musculature

(Grand 1983; Argot 2002). An everted iliac wing is present in species with diverse substrate preferences and locomotion (Muizon 1998), but in view of the set of postcranial features in *Argyrolagus* it would have been more certainly related to jumping ability. For example, the everted iliac wing in saltatorial primates and marsupials allows well-developed epaxial muscles, which are related to the maintenance of semierect posture (Elftman 1929; Emerson 1985).

The size and depth of the iliac fossa are indicative of a moderately developed iliacus muscle, more than that of the typical saltatorial species but less than that of an arboreal one. The iliacus in *Argyrolagus* would have provided powerful flexion of the hip joint when the leg is fixed in position, which would be advantageous for digging activities. A relatively powerful flexion of the hip would provide an advantage to resist the forces generated during digging and to anchor firmly in the substrate.

Hip Joint

At the hip joint, the morphology of the acetabulum, deep and ventrolaterally oriented, is indicative of restricted and parasagittal movements, two attributes present in terrestrial and saltatorial species (Argot 2002). In addition, the salient borders that limit the acetabulum would have acted to buttress the hip articulation. In *Argyrolagus*, the greater trochanter of the femur would have been higher than the femoral head, indicating that the range of abduction was restricted. In sum, the shape of the hip joint would have provided a stabilized articulation, which is suitable for leaping. This morphology would also have been advantageous to avoid dislocation at this joint whereas relatively great forces are developed during digging, assuming that this ability was present in *Argyrolagus*.

Femur

In connection with the inferred well-developed gluteus medius (see above), the greater trochanter of the femur is robust. As noted above, from the morphology of the iliac fossa, the iliacus muscle (external rotator and protractor of the femur) is supposed to have been moderately sized, a condition correlated with the well-developed lesser trochanter of the femur. The lesser trochanter is usually large and medially oriented in arboreal and scansorial species, and small and posteriorly placed in terrestrial forms (Szalay and Sargis 2001; Argot 2002; Candela and Picasso 2008). These differences could be related to a more emphasized rotator function of the iliopsoas complex in the first, and a flexor function in the second (Szalay and Sargis 2001; Argot 2002; Candela and Picasso 2008). In *Argyrolagus*, the large lesser trochanter, which is posteromedially orientated, as occurs in certain saltatorial rodents (Carrizo et al. 2014), and its distal location relatively far from the hip joint indicate an increased effective lever arm of iliacus with respect to typically running marsupials (in which the lesser trochanter is less developed and proximally located). This feature would have provided an increased strength in flexing the hip joint when the leg is fixed in position, an action that would be advantageous for maintaining the hind limbs in a stabilized position during digging, as relatively great forces are developed to dig with anterior limbs.

Knee Joint

As occurs in terrestrial running and leaping marsupials, such as *Macrotis*, *Potorous*, and *Antechinomys*, the distal femoral epiphysis is anteroposteriorly deep and has a long and well-delimited femoral groove that acts as a pulley for the tendon of the quadriceps femoris (Szalay and Sargis 2001; Argot 2002). In correlation, the proximal tibia has a prominent tibial tuberosity for the quadriceps femoris insertion. Consequently, the whole morphology of the knee joint is indicative of an accentuated pull action of the quadriceps femoris, associated with agile movements of the hind limbs and leaping ability (Szalay and Sargis 2001; Argot 2002; Sargis 2002b). In addition, the condyles of the femur and proximal tibia are approximately symmetrical, as occurs in terrestrial marsupials (e.g., *Metachirus*, *Macrotis* and *Potorous*), as the femur is less abducted (there is a medial displacement of the load line) and the movements are more parasagittal (Szalay and Sargis 2001; Argot 2002) than in arboreal species. Moreover, the differences in the concavity between condylar articular surfaces of the tibia, which are separated by a well-developed eminence, indicate a stabilized knee joint, necessary for leaping (Argot 2002).

Tibio-Fibula

Tibia and fibula show several characters associated with jumping locomotion: elongation of both bones and partial fusion among them, anteriorly projected tibial tuberosity and proximally restricted tibial crest. Saltatorial species have elongated hind limbs, especially because of the lengthening of its medial and distal segments (i.e., tibio-fibula and metatarsals), which are also lightened by the fusion and/or reduction of bones (Emerson 1985; Hildebrand and Goslow 2001). Elongated hind limbs and the concentration of muscle mass (tibialis anterior, gracilis, and semitendinosus) close to the body (see below), allow fast movements of more distal segments of the hind limbs (Emerson 1985; Hildebrand and Goslow 2001). The lengthening of the distal bones of the leg, resulting in an increased out-lever arm of the foot, improves speed as well as the stride length during locomotion at the expense of force (Smith and Savage 1956; Carrano 1997). In addition, reacting as a single bone, tibio-fibula is strengthened against the impact occurring when landing (Argot 2002), increasing the stability and restricting the mobility at the ankle

joint (Salton and Sargis 2009). Compared to bipedal rodents, where the tibio-fibular juncture is relatively more proximal in more saltatorial species (Howell 1932), the proportion in *Argyrolagus* (50 % of fusion) is similar to that of the jumping *Pedetes* (Howell 1932). Projected tibial tuberosity and proximally restricted tibial crest are features present in jumping species but also in other agile terrestrial forms (Hopwood and Butterfield 1990; Argot 2002). The projection of the tibial tuberosity results in an improvement of the mechanical advantage of the quadriceps femoris for the rapid extension of the knee, a condition that is advantageous for saltatorial locomotion. In *Argyrolagus*, the deep and proximally located lateral fossa of the tibia indicates a very developed and proximally concentrated tibialis cranialis muscle (an important invertor of the ankle joint and dorsiflexor of the foot), such as occurs in some jumping marsupials (e.g., *Potorus* and *Macropus*). A short tibial crest also suggests a proximal insertion area of the gracilis and semitendinosus, which indicates a rapid rather than strong extension of the hip joint and flexion of the knee (Smith and Savage 1956). Additionally, the prominent anterior projection of this crest suggests a relatively strong development of these muscles, which would have provided strong propulsion for leaping. Thus, the proximal concentration of these muscles in *Argyrolagus* is compatible with jumping behavior. The insertion area of the popliteus indicates that this muscle was relatively large. This muscle is a flexor of the knee that also acts in stabilizing it against medial rotation of the tibia at the knee joint (Warburton et al. 2015), which would be an optimal condition for saltatorial habits. The very concave medial surface of the fibular shaft and the also concave proximolateral surface of the posterior tibia indicate a relatively well-developed flexor digitorum profundus, a plantarflexor of the digits, which seems to be related to the strong and rapid flexion of the digit during propulsion, but also during digging activities.

Upper Ankle Joint

At the UAJ there is a tricontact among calcaneus, astragalus, and fibula. The large CaFi and the quite small Afi indicate that the fibula bore the load directly through the calcaneus. In addition, as the fibula was not distally reduced in relation to the tibia, both fused bones contributed equally to the load-bearing role in relation to the proximal tarsals (Szalay 1994: 210). The general morphology of the calcaneus, especially the size proportions between calcaneal head and tuber calcanei, resembles that of terrestrial marsupials, especially that of jumping species (Bassarova et al. 2009). The cylindrical shape of the calcaneal CaFi and the trochleated astragalar Atil, indicate a restriction to anteroposterior movements. The tightly bracing tibia on the medial side complements the mortise-like function of the distal fibula on the lateral side. As noted by Szalay (1994: 237), the mortise-tenon configuration of the

UAJ in argyrolagids is only present, among metatherians, in peramelemorphs and macropodoids. In sum, the UAJ is well stabilized laterally and medially, and has a configuration that constrains the movements to those in an anteroposterior direction, which result optimal for saltatorial habits.

Lower Ankle Joint

The configuration of the calcaneal Ec and Su facets, the former convex and dorsally oriented and the latter flat and distally oriented (see description), suggests inability to invert-evert the foot, and a highly stable LAJ. Additionally, the secondary contact between the astragalus and the calcaneus indicates that movement among both bones was further restricted, as occurs in macropodoids (Szalay 1994: 258). Taking jointly the morphology of Su, Ec, and accessory lateral facets it can be inferred a reduced mobility at the LAJ of *Argyrolagus*, which resembles the locked LAJ of jumping macropodids.

Transverse Tarsal Joint and metatarsals

The configuration of the An facet (vertically oriented, wide, and deep) as well as that of CaCu facets (stepped and facing distally) indicates stability of the foot at the astragalonavicular (ANJ) and calcaneocuboid (CCJ) joints. Particularly, the orientation of the CaCu (perpendicular to the anteroposterior axis) points out restricted anteroposterior movements, as seen in jumpers (Bassarova et al. 2009). In sum, distal astragalus and calcaneus have a set of features that acts in stabilizing the joints, improving the interlocking of the tarsal bones, and restricting movements to the parasagittal plane, all of which improve the ability to jump. Metatarsals III and IV were closely appressed forming a single functional unit that would have improved the resistance of the metatarsals to bending loads and would have provided more strength against the impact forces during jumping locomotion (Hildebrand and Goslow 2001; Moore et al. 2015). In addition, as was suggested for digging caviomorph rodents (e.g., Candela et al. 2017), the closely-packed metatarsals constitute a compact unit, which seems to be an adaptation to resist the forces generated during digging, acting as a strong and secure support to anchor firmly in the substrate while digging. The lengthening of the metatarsals would have complemented that of the tibio-fibula, allowing increased stride length (Argot 2002; Moore et al. 2015). Almost certainly *Argyrolagus* stood on two digit feet (Simpson 1970). The probable loss of digits, or its reduction to some non-functional ones, is in line with the above mentioned functional requirements associated to jumping. The inferred characteristics make the feet of *Argyrolagus* similar to those of bipedal rodents such as the dipodoid *Salpingotus* (Berman 1985; Moore et al. 2015).

Functional Analysis of the Tail

On the anterior caudal vertebrae, the enlarged mammillary processes suggest a well-developed multifidus caudae muscle, which is involved in the vertical movements of the tail (Argot 2003b). The morphology of the transverse processes of these vertebrae, with strong attachment areas for the ischio-caudalis and abductor caudae dorsalis muscles, points to a well-developed basal musculature of the tail (Argot 2003a, b). These muscles flex the tail laterally and coupled with the multifidus caudae muscle, contribute to stabilize the animal when moving (Argot 2003b). In addition, the posterior caudal vertebrae are enlarged anteriorly and posteriorly by relatively well-developed processes, which suggest a strong attachment of the caudal musculature. The posterior caudal vertebrae are lengthened and robust. This and the inferred well-developed caudal musculature suggest that the tail in *Argyrolagus* was long and heavy, as originally proposed by Simpson (1970: 52), but also quite mobile. It is probable that, as occur in other bipedal jumpers, a tail with these characteristics played an important role as a balancing organ during jumping locomotion (Hatt 1932).

Jumping Locomotion

In terrestrial habitats, small agile mammals can perform, at relative high speeds, different asymmetrical gaits (i.e., when actions of the feet of a pair -fore or hind- are unevenly spaced in time or occur simultaneously) as bound and half-bound (Hildebrand 1977, 1985), and bipedal jumping (Emerson 1985). Half-bound and bound are quadruped gaits mostly used to move by means of a series of leaps on terrain that is uneven in relation to body size (Hildebrand 1977, 1985), while in jumping locomotion both hind legs are used simultaneously for providing the total propulsive thrust (Emerson 1985). These manners of moving impose certain morphological requirements for support, stability, and propulsion that in the *Argyrolagus* postcranium are expressed in several anatomical features. Anatomical features showed by the *Argyrolagus* postcranium that are common to runners and jumpers include those related to factors such as restriction of limb motion to sagittal planes and resistance to dislocation. Most of the articulations of the fore- and hind limbs in *Argyrolagus* express these latter requirements, particularly those of the hind limbs. However, the most notable postcranial characteristic related to locomotion in *Argyrolagus* is the relative length of the fore- and hind limbs (see intermembral indices (A+B)/(C+D) and A/C in Table 1, Online Resource 3). Jumpers do have longer hind limbs than nonjumpers, and this is particularly true when comparing species of similar body size (Berman 1985; Emerson 1985). When comparing *Argyrolagus* with a small marsupial such as the runner *Monodelphis,* it is shown that *Argyrolagus* had very long hind limbs (see intermembral

indices in Table 1, Online Resource 3). The elongated hind limbs produce the propulsive thrust, and in *Argyrolagus* the inferred development of the main muscles involved in the extension of the hip, knee, and ankle joints indicates that powerful forces were performed throughout the take-off. As in mammalian jumpers (e.g., Berman 1985), the forelimbs of *Argyrolagus* are shortened, having a relative length that approaches those of *Bettongia* among marsupials, and *Allactaga* among rodents (see intermembral indices in Table 1, Online Resource 3). The reduced forelimbs allow jumpers to shift the center of mass backward thus minimizing the torque and pitching produced during take-off (Emerson 1985). The reduction of torque could be complemented in *Argyrolagus* by having a long and heavy tail, as inferred by Simpson (1970: 52). Another trait noted by Simpson (1970: 52) as an indicator of bipedal gait was the quite ventral position of the foramen magnum, which would indicate that the head was held roughly at a right angle with respect to the neck. However, a recent comparative study shows that there is no relationship between foramen magnum position and locomotor pattern in mammals (Ruth et al. 2016).

Most medium to small mammals with saltatorial behavior, such as the macropodids *Potorous* and *Bettongia*, and *Dipodomys*, *Microdipodops*, and *Notomys* among rodents, show quadrupedal gaits at relative low speeds while during runs at higher speeds develop bipedal jumping (Marlow 1969; Nikolai and Bramble 1983; Baudinette et al. 1993; Webster and Dawson 2004). Therefore, it is probable that when moving in the terrestrial environment, *Argyrolagus*, as the mentioned mammals, used two different locomotion patterns, with quadrupedal and bipedal gaits operating over different ranges of speeds.

Digging Abilities and Food Manipulation

In the literature *Argyrolagus* has been recognized as a notable example of convergence with heteromyids and other small bipedal rodents (Simpson 1970; Emerson 1985; Mares 1993a, b), and maybe because of this, the few studies on the *Argyrolagus* postcranium and locomotion have focused on functional anatomy of the hind limbs and those characters directly involved in jumping (Simpson 1970; Straccia 1999). In contrast, the forelimb form and function have received little or no attention, despite the fact that these limbs in bipedal species are used for important ecological activities, such as burrowing, food manipulation, and grooming (Nikolai and Bramble 1983; Price 1993; Jouffroy et al. 2003; Harvey and Warburton 2010). In addition, as noted above, bipedal rodents and marsupials also use their forelimbs for body support and propulsion at relatively low speeds. Even in strongly bipedal species as kangaroos, forelimbs participate in supporting the body weight during slow "pentapedal" locomotion (Harvey and Warburton 2010).

Considering the functional information derived from the anatomy of the *Argyrolagus* forelimb (see above), it can be inferred that it had both abilities for digging and food handling. In *Argyrolagus*, digging abilities are expressed in several qualitative osteological traits and inferred muscle development but also in some functional indices that are indicators of digging behavior in mammals (Elissamburu and Vizcaíno 2004; Elissamburu and De Santis 2011; Warburton et al. 2013). Studies of locomotor behaviors in rodents have shown that values of, EI, IFA, and URI increase from cursorial to digging forms, and that EI and IFA, and URI are among the best predictors of digging abilities (Hildebrand 1985; Elissamburu and Vizcaíno 2004). HRI and URI values indicate the robustness of the humerus and ulna, respectively, and reflect their ability to resist the stress generated by forces of the main muscles involved in digging (Elissamburu and Vizcaíno 2004; Samuels and Van Valkenburgh 2008). These indices in *Argyrolagus* are higher than those of all marsupials (except *Macrotis*) and semifossorial rodent species compared, and are similar to those of quadrupedal fossorial rodents (Table 4, Online Resource 3). The EI, which indicates the development of pronator, supinator, and flexors of the forearm (Elissamburu and Vizcaíno 2004; Samuels and Van Valkenburgh 2008), has in *Argyrolagus* a higher value than those of marsupials and semifossorial rodents, and a similar or lower value than those of fossorial rodents, while the IFA, which expresses the mechanical advantage of the triceps (Elissamburu and Vizcaíno 2004; Samuels and Van Valkenburgh 2008), has a higher value than those of semifossorial rodent species and a lower value than those of semifossorial marsupials (Warburton et al. 2013) and fossorial rodents (Table 4, Online Resource 3).

Taken as a whole, this functional information suggests that *Argyrolagus* had forearms well equipped for digging, maybe as suited for this behaviour as those of extant bipedal rodents and semifossorial marsupials with a scratch-digging mode of burrowing (Nikolai and Bramble 1983; Warburton et al. 2013). Scratch diggers use their front limbs in an alternating pattern to break and loosen the soil on the surface as well as underground, and complement this activity by removing the loosened soil accumulated under the body kicking it backward with their hind limbs (Nikolai and Bramble 1983; Hildebrand 1985; Price 1993; Hildebrand and Goslow 2001). By analogy, hind limbs in *Argyrolagus* could have had an important role in digging behavior, and some morphological characters discussed above are consistent with this idea (e.g., great mechanical advantage of the gluteal muscles, well-developed iliac muscle, closely packed metatarsals).

On the other hand, the *Argyrolagus* forelimb exhibits a set of osteological characters that indicate neither restricted movements at the glenohumeral joint, nor reduced capabilities of pronation-supination, and well-developed pronator-supinator muscles and flexors-extensors of the digits, which as a whole are compatible with the capacity to reach for, grasp, and manipulate objects (Argot 2003a, 2003c). This inference is consistent with the proposed diet for *Argyrolagus* as it would have been based on food items such as leaves and seeds (Zimicz 2011), requiring the latter to be handled for eating.

Evolution of Jumping Locomotion in Argyrolagids

Jumping locomotion has received much attention as it is an unusual gait among mammals, which has evolved twice among marsupials (most macropodoids and argyrolagids; Simpson 1970, Kear et al. 2008), and four times among rodents (Dipodidae, Muridae, Heteromyidae, and Pedetidae; Berman 1985; Webster and Dawson 2004). The supposed benefits of bipedal jumping and the hypothesis of the adaptive origin of this particular mode of locomotion hinge on three main issues: (1) energetic efficiency, (2) freeing the forelimbs, and (3) enhancement of locomotor performance for predator avoidance (see Nikolai and Bramble 1983; Djawdan 1993; McGowan and Collins 2018, and bibliography herein cited).

In mammals of comparable body size, bipedal locomotion may be economical with respect to quadrupedal locomotion. This was proven for macropodoids (with body mass ≥3kg; Webster and Dawson 2004; Dawson and Webster 2010), while in most studies of small rodents (body mass ≤ 3kg) no differences were found between bipedal and quadrupedal species (e.g., Thompson et al. 1980; see McGowan and Collins 2018). In macropodoids, there is a relationship between speed and energy cost of locomotion in which as speed increases, metabolic cost becomes constant or decreases. In contrast, in quadrupedal runners of similar body size, the relationship between both variables is linear (Webster and Dawson 2004). These energetic benefits in macropodids have been explained by the storage and recovery of elastic strain energy in tendons of the hind limbs (e.g., Achilles tendons; Alexander and Vernon 1975) coupled with the lengthening of the strides, and a limited increase of stride frequency at high speeds (Webster and Dawson 2004; Dawson and Webster 2010). In quadrupedal runners, elastic energy storage occurs to a lesser extent (Alexander and Vernon 1975) and higher speeds are reached by a combination of increased stride length and stride frequency with a higher metabolic cost (Dawson and Webster 2010). Several studies have shown that the storage of strain energy in jumpers scales positively with body size, with small species having relatively robust tendons and therefore smaller storage capacity than larger species with long, thin tendons (Bennett and Taylor 1995; McGowan et al. 2008; McGowan and Collins 2018). This allometric relationship may account for the observed differences in energetic cost of locomotion of small vs large bipeds. Considering the above, *Argyrolagus* wouldn't have had an advantage in terms of energetic cost of locomotion over potentially coexisting small quadrupedal

mammals, nor energetic efficiency can be a plausible explanation for the origin of bipedalism in argyrolagids.

The releasing of the forelegs from the morphological constraints for agile quadrupedal locomotion, and their specialization for other activities as digging and food handling, has been considered another selective force shaping the evolution of bipedalism among rodents (Bartholomew and Cary 1954). This proposal has been rejected, among other arguments (see McGowan and Collins 2018), because studies on foraging behavior in heteromyids, which extensively use their forelimbs for seed handling and "pouching" (i.e., to store food items into external, fur-lined cheek pouches), have shown no differences in foraging performance between quadrupedal and bipedal species. The specialization for digging, on the other hand, appears an unlikely driving force for the evolution of bipedalism, even if more studies are still needed to evaluate the trade-offs between digging and locomotion in bipedal and quadrupedal rodents (McGowan and Collins 2018). Therefore, and similar to the evolution of bipedalism in rodents, it is probable that in argyrolagid history the development of handling abilities did not drive the evolution of bipedal locomotion, despite the fact that inferred herbivorous diet for *Argyrolagus*, *Microtragulus*, and other basal argyrolagids (e.g., *Proargyrolagus*, Sánchez-Villagra and Kay 1997) included food items such as seeds, dry fruits, and shoots (Sánchez-Villagra and Kay 1997; Zimicz 2011) that should have needed manipulation to some extent.

The third factor that has been considered favoring the evolution of bipedalism among small mammals is the performance of this type of locomotion in predator avoidance. Some studies have shown that small bipeds such as kangaroo rats and jerboas have enhanced predator evasion ability compared to sympatric quadrupedal species because of the complex locomotor behaviors that they can perform (Djawdan 1993; Moore et al. 2017a). Bipedal animals can shift from quadrupedal to bipedal locomotion, do rapid accelerations and turns as well as vertical leaps, which allow them increased maneuverability (Bartholomew and Caswell 1951; Djawdan 1993; Moore et al. 2017b). In addition, increasing the likelihood of locomotor behaviors they have an enhanced unpredictability of escape trajectories, a key capacity in the interaction with predators such as owls and snakes that have a ballistic interception strategy of hunting (Moore and Biewener 2015; Moore et al. 2017a).

These benefits of bipedal locomotion are clear in arid habitats where the risk for predation is high because vegetation for hiding places is sparse, and resources such as food and water are patchily distributed (Webster and Dawson 2004; Moore et al. 2017a). These are among the main arguments supporting the hypothesis of the origin of bipedalism in rodents as an adaptation to life in open, arid environments (e.g., Bartholomew and Caswell 1951; Thompson et al. 1980). However, more evidence supports the alternative hypothesis

that holds that in the evolutionary history of both marsupials and rodents, bipedal locomotion originated in humid and forested habitats (Voorhies 1975; Webster and Dawson 2004; Dawson and Webster2010; Wu et al. 2014; McGowan and Collins 2018). In this evolutionary scene, jumping could have been adaptive to exploit resources in structurally complex habitats (Webster and Dawson 2004; Wu et al. 2014) or open microhabitats (e.g., sand dunes on floodplains; Voorhies 1975), having enhanced strategies of predator avoidance (Wu et al. 2014; McGowan and Collins 2018). When changes in climatic and environmental conditions led to the drying out of continental areas and the spread of grasslands (e.g., late Miocene-Pliocene in Australia and Asia; Black et al. 2012; Wu et al. 2014), bipedal species were successfully "preadapted" (had an exaptation sensu Gould and Vrba 1982) for exploiting resources in the new conditions (Webster and Dawson 2004), with a subsequent specialization of this locomotion mode (Wu et al. 2014; McGowan and Collins 2018).

The evolutionary origin of bipedalism in argyrolagids is yet an enigma due to the absence of a postcranial fossil record for the earliest members of the clade, but also because of the uncertainties about the environments where they lived early in their history. The first and most plesiomorphic argyrolagid *Proargyrolagus boliviensis* is recorded in the late Oligocene (Deseadan) of Bolivia (Salla Beds; Wolff 1984; Sánchez-Villagra and Kay 1997). Based on several skull characteristics indicating granivorous diet, and nasal region with capabilities for water conservation and detection of seeds on the ground, *P. boliviensis* was interpreted as a seed eater, ground-dweller mammal that inhabited semiarid environments (Sánchez-Villagra and Kay 1997). However, there is still no consensus on environmental conditions for the Salla beds and its different stratigraphic levels, as they were inferred to be open and semiarid or humid and vegetated (Croft 2001; Pérez et al. 2018). Another *Proargyrolagus* species, *P. argentinus*, which is known only by teeth (Goin and Abello 2013), is subsequently registered in early Miocene sediments (Colhuehuapian) from Patagonia (Argentina). In contrast to the uncertain environmental context for *P. boliviensis,* environments for stratigraphic levels of occurrence of *P. argentinus* have been reconstructed as wooded-grasslands and riparian forest developed under sub-humid conditions (Bellosi and Gonzalez 2010; Goin and Abello 2013). Therefore, if bipedalism was proven for late Oligocene-early Miocene argyrolagids, the possibility exists that their origin in humid and vegetated habitats could have been coincident with the evolutionary origin of the bipedalism in other mammals, such as macropodids and jerboas. Postcranial elements that allow inferring more confidently substrate preferences and locomotor behavior among argyrolagids appear just from the Pliocene (Simpson 1970; Ortiz et al. 2012; Babot and García-López 2016). Diverse evidence (sedimentological, paleobotanical, ichnological,

and faunal) indicates open, subhumid to semiarid environments (e.g., grasslands and palm groves with other subdominant arboreal species, Erra et al. 2010; Erra pers. com.), for stratigraphic levels where *Argyrolagus* spp. (Irene "Formation" and Chapadmalal Formation, Pliocene; Cione et al. 2015; Table 1), *Microtragulus reigi* (Chapadmalal Formation and Punta Martínez de Hoz alloformation, Pliocene; Gasparini and Tonni 2016), and *M. bolivianus* (Uquía Formation, Pliocene; Reguero et al. 2007) were recorded. Only by the early Pleistocene, when the latest records of *M. reigi* occur (Punta San Andrés alloformation; Cione et al. 2015), more cold and arid conditions were established, marking an important climatic change with respect to previous times (Cione et al. 2015). In the noted habitats, argyrolagids should have been successful because of their locomotor behaviors that allowed them enhanced predator evasion and escape, and to exploit resources in exposed microhabitats. In this regard, finds of *M. bolivianus* in the northwest of Argentina provided valuable information about interactions with putative argyrolagid predators, as several remains referable to this species appeared in concentrations of microvertebrate remains interpreted as owl-pellet accumulations (Ortiz et al. 2012).

Finally, we consider that in contrast to the idea of argyrolagids as inhabitants of arid regions (e.g., Mares 1985, 1993a, b; Abello et al. 2002; Ortiz et al. 2012; Babot and García-López 2016), the occurrence of argyrolagids in the late Cenozoic record must be interpreted with caution from a paleoenvironmental standpoint. For example, the records of *M. bolivianus* in the Uquía Formation (Pliocene; Table 1) were considered as indicators of an arid pulse during this temporal lapse (Ortiz et al. 2012). However, porcupines, hydrocherids, and crocodylids, which seem to be sensible indicators of relatively humid and forested habits, were also recovered in this stratigraphic unit (Reguero et al. 2007) suggesting warmer, humid, and heterogeneous environments. Therefore, based on their locomotor strategies and the independent paleoenvironmental evidence available to date (see above), we suggest that Pliocene argyrolagids should be interpreted as inhabiting subhumid to semiarid environments, at least heterogeneous with respect to vegetation cover, being able to exploit open microhabitats. In addition, we think that more data about the environmental conditions occupied by argyrolagids are required. So for example, the precise environmental reconstruction based on sedimentological, paleobiological, paleobotanic, and isotopic evidence is not yet available for the Andalhuala Formation (Catamarca Province; see Table 1) and other Neogene units of southern South America. To sum up, more comprehensive research will allow testing the paleoecological hypothesis proposed above and disclosing the paleoenvironmental significance of the argyrolagids in the fossil record of the Cenozoic of South America.

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